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A new species of the rodent genus *Hylomyscus* from Angola, with a distributional summary of the *H. anselli* species group (Muridae: Murinae: Praomyini)

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Abstract

A new species of *Hylomyscus*, *H. heinrichorum*, is described from mountains in western Angola. Based on morphological traits and cranial morphometry, the new species is assigned to the *H. anselli* species group and is hypothesized to be most closely related to *H. anselli* Bishop proper, a species named from Zambia. Members of both the *H. anselli* and *H. denniae* species groups occupy the Afromontane Biotic Zone, found in various mountain systems to the south and east of the Congo Basin. Evidence is reviewed that supports the independent radiation of these two species groups within montane forest from different Guineo-Congolian ancestral stocks.

Key words: Afromontane, biogeography, taxonomy, traditional morphometrics

Introduction

This paper addresses the taxonomic status of populations of the rodent genus *Hylomyscus* Thomas (Muridae, Murinae) that occur in the highlands of westcentral Angola. In early faunal reports, only a single species of *Hylomyscus*, *H. carillus* Thomas (1904), was identified in Angola (Hill & Carter, 1941; Crawford-Cabral, 1986, 1998). Musser & Carleton (1993, 2005), however, drew attention to the presence of at least three *Hylomyscus* species in Angola, *H. carillus* and *H. stella* Thomas distributed within the northern lowlands and an unnamed form from the high-mountain region, along the western rim of the Angolan Plateau. The existence of the highland form was first discerned based on material preserved in the Field Museum of Natural History (FMNH), Chicago, that was independently examined by Carleton (Sep 1984) and Guy G. Musser (May 1992). They provisionally identified the FMNH specimens as *H. denniae* Thomas (Musser & Carleton, 1993, 2005), a species whose distribution was then understood to be restricted to the East African highlands (ca. 1800–3800 m in mountains of westcentral Kenya and those bordering the Albertine Rift). The FMNH Angolan specimens were collected in 1954 by the naturalist Gerd H. Heinrich at Mount Moco and Mount Soque during an expedition conducted for both the FMNH and the Zoologisches Institut und Zoologisches Museum, Hamburg (Heinrich, 1958a–c). Carleton & Stanley (2005:637) later associated these two FMNH series with the *H. anselli* complex, not the *H. denniae* complex, a species-group distinction elaborated by Carleton *et al.* (2006) in their revision of *H. denniae* and its allies (*H. endorobae* Heller, *H. vulcanorum* Lönnberg & Gyldenstolpe).

We herein present morphological and morphometric evidence that sustains the recognition of the Angolan form as a species distinct from other members of the *H. anselli* species group (*H. anselli* Bishop, *H. arcimontensis* Carleton & Stanley, *H. kerbispeterhansi* Demos, Agwanda, & Hickerson) and summarize the distributions of the two *Hylomyscus* species groups characteristic of the Afromontane biotic region (sensu White, 1978, 1981).

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Material and methods

Specimens examined as the basis of this report 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); 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 Carleton to 0.01 mm, using hand-held digital calipers (accuracy rated as ± 0.02 mm) while viewing crania under a stereomicroscope. These measurements, their anatomical landmarks, and their abbreviations as used in text and tables, are: occipitonasal length (ONL), from the supraoccipital, just above the foramen magnum, to the nasal tips; greatest zygomatic breadth (ZB), as measured across the squamosal portion of the zygomatic arches or at the squamosal-jugal suture; breadth of braincase (BBC), measured across the parietal flanges just behind the zygomatic arches; breadth across occipital condyles (BOC), at the upper lateral edges of the articular processes of the exoccipital bones; interorbital breadth (IOB), a least breadth measured at the lateral edges of the frontals; length of rostrum (LR), from the innermost bevel of the right zygomatic notch to the end of the nasals at their mid-sagittal junction (i.e., measurement is slightly oblique to the longitudinal cranial axis); breadth of rostrum (BR), as measured across the capsular projections in front of the zygomatic plates; postpalatal length (PPL), from the anterior rim of the mesopterygoid fossa to the mid-notch of the basioccipital; length of bony palate (LBP), from the anterior margin of the mesopterygoid fossa to the posterior end of the left incisive foramen; breadth of bony palate (BBP), as measured across the maxillary bones above the second molars; length of incisive foramen (LIF), the maximum anterior-posterior expanse of the left foramen; length of diastema (LD), from the posterior curvature of the left incisor, just below the premaxillary, to the enamel-dentine junction (gum line) on anterior margin of the left M1; breadth of zygomatic plate (BZP), from the rear edge of the right zygomatic plate to its anterodorsal margin where it is vertical; length of auditory bulla (LAB), from the posteriormost bevel of left auditory bulla to the anteromedial notch of eustachian tube (i.e., where opaque bone of the eustachian tube meets translucent bone of the tympanic capsule); coronal length of maxillary toothrow (CLM), as measured on the right molar row, from the posterior margin of M3 to the enamel-dentine junction on anterior face of M1 (not on the forward sloping anterior root); width of the upper first molar (WM1), a greatest width measured across the middle lamina (t4–t6) of the upper right M1. 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). External data for most samples from Tanzania were recorded in the field by Stanley, reducing among-collector variability for these big, extremely age-sensitive, dimensions. Head-and-body length of specimens that lacked this 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 described by Carleton & Martinez (1991).

Morphometric differentiation of the Angolan specimens is assessed within the context of 11 analytical samples or operational taxonomic units (OTUs), one each representing the Angolan form, *H. anselli*, and *H. kerbispeterhansi* and 8 representing *H. arcimontensis*, as listed below; see Appendix for museum catalog numbers of specimens measured. To anchor recognition of *H. anselli*, we have included three specimens of Bishop's (1979) type series from Zambia (see Appendix). Catalog numbers and full locality data for the geographic samples of *H. anselli* and *H. arcimontensis* were provided by Carleton & Stanley (2005). Here, and throughout the text, formally named mountains are abbreviated as "Mts" or "Mt" and Forest Reserve as "FR."

Hylomyscus anselli: Tanzania, Mbizi Mts, Mbizi FR (*N* = 12).

Hylomyscus arcimontensis, all samples from Tanzania: OTU 1—South Pare Mts, Chome FR (*N* = 6); OTU 2—West Usambara Mts (*N* = 54); OTU 3—East Usambara Mts (*N* = 24); OTU 4—Nguu Mts, Nguru North FR and Nguru Mts, Nguru South FR (*N* = 5); OTU 5—Ukaguru Mts, Mamiwa-Kisara FR (*N* = 10); OTU 6—Uluguru Mts, Uluguru North FR (*N* = 16); OTU 7—Udzungwa Mts, Udzungwa Scarp FR (*N* =18); OTU 8—Mt Rungwe, Rungwe FR (*N* = 16).

Hylomyscus kerbispeterhansi: Kenya, Kenyan Mts (*N* = 8).

Hylomyscus species indeterminate: Angola, Mt Moco (*N* = 14).

Standard descriptive statistics (mean, range, and standard deviation) were derived for adult specimens (young, full, and old age classes combined) of the 11 OTUs. In view of the lack of appreciable sexual dimorphism so far demonstrated in species of *Hylomyscus* (e.g., *H. arcimontensis* and *H. denniae*—Carleton & Stanley, 2005; *H. alleni* Waterhouse—Nicolas *et al.*, 2008) or other species of Praomyini (e.g., *Praomys melanotus* Allen & Loveridge—Carleton & Stanley, 2012), we combined mensural data of males and females in our analyses and tabular summaries. Means and ranges of external variables are tabulated as guidance to identification but were not input to morphometric analyses. 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 principal components or canonical variates with the log-transformed original cranial measurements. Hierarchical clustering of analytical samples was based on Mahalanobis distances between OTU centroids and generated by the unweighted pair-group method using arithmetic averages (UPGMA). Analytical procedures were implemented using statistical packages contained in SYSTAT (Version 11.0, 2004) or PAST (Hammer *et al.*, 2001; Version 2.07, 1999–2011).

Results

The FMNH specimens from Mts Moco and Soque, Angola, possess the few qualitative traits identified for the *Hylomyscus anselli* species group, as here contrasted to the condition typical of the *H. denniae* species group (Carleton & Stanley, 2005; Carleton *et al.*, 2006). Adult females lack a pectoral pair of mammary glands, the mammae count totaling six, arranged as one post-axial pair and two inguinal pairs; females in the *H. denniae* species group possess the pectoral pair, their mammae count totaling eight. The rostrum and incisive foramina are medium in length, the latter extending to the anterior rim or middle of the anterior root of M1 (LIF/LD ratio usually < 0.8); specimens of the *H. denniae* species group are characterized by longer rostra and incisive foramina, the latter extending to the level of the anterior lamina (anterocone) of M1 (LIF/LD ratio usually > 0.8). The subsquamosal foramen is consistently developed, medium in size compared with the larger postglenoid foramen, and the hamular process is relatively long and slender (see Carleton & Stanley, 2005: Fig. 6); in examples of the *H. denniae* species group, the subsquamosal foramen is tiny, wholly occluded or absent in some specimens, and the hamular process is relatively short and wide. Other qualitative craniodental features exhibited by the series from Mts Moco and Soque—upper incisors weakly opisthodont, t3 on M1 medium-sized, t9 indistinct, interorbital region marked by a weak shelf—resemble those observed in examples of the *H. denniae* species group.

As is generally the case for closely related (congeneric) species of Muroidea, additional morphological evidence for specific differentiation rests upon subtle contrasts in cranial size and shape, differences which can be usefully distilled from morphometric evaluation of mensural data. In the following ordinations, using the 16 log-transformed craniodental variables, we first compared the Angolan form to the geographically nearest species, *H. anselli* (Zambia and westcentral Tanzania) and *H. arcimontensis* (central Tanzania), and next compared it with the geographically distant form *H. kerbispeterhansi* (westcentral Kenya). For both sets of morphometric comparisons, we present patterns of among-group differentiation, as visualized by canonical variates extracted from discriminant function analysis of pre-defined geographic samples, and also examine patterns of dispersion among individual specimens, as revealed in principal components extracted from the original log-transformed variables.

Angolan form compared with *H. anselli* and *H. arcimontensis*. Projection of individual scores onto the first two canonical variates extracted discloses well defined morphometric structure (Wilks' lambda = 0.004, F = 8.5, P ≤ 0.0001), and those two CVs summarize approximately 70% of the among-group craniodental variation (Fig. 1A; Table 1). The OTUs representing *H. anselli* and the Angolan population are entirely isolated, but those representing *H. arcimontensis* (OTUs 1–8) extensively overlap one another, although the bounding polygons of all eight are more or less incongruent, staggered unevenly along CV1. Consistent with the wide separation of their group centroids, all specimens of the *H. anselli* and Angolan samples were accurately assigned in a jackknifed classification matrix generated from a posteriori probabilities for group membership. Among the 8 OTUs representing *H. arcimontensis*, however, misclassifications ranged from 0 to 67%, although no specimen was statistically associated with either the sample of *H. anselli* or that from Angola; only the 6 individuals from the S Pare Mts (OTU 1) were all correctly classified. The positive signs and moderate to large correlations of nearly all input variables with CV1 implicate size as a general influence of dispersion along that factor; accordingly, univariate means derived for the craniodental variables generally reinforce the smaller size of *H. arcimontensis* compared with the more robust dimensions of *H. anselli* and the Angolan sample (Table 6). Fewer variables load significantly on CV2, but these accentuate the separation of the *H. anselli* sample from both *H. arcimontensis* and the Angolan series. Noteworthy are the more substantial size of the neurocranium (BBC, IOB), rostrum (BR, LR, LD), and bony palate (HPL) attained by specimens of *H. anselli* (Tables 1, 6). The three Zambian specimens from Bishop's (1979) type series of *anselli*, entered as unknowns in the discriminant function analysis, cluster tightly with those from the Mbizi Mts, in westcentral Tanzania, and reinforce the identification of the latter sample as *H. anselli* (Fig. 1A; also see Carleton & Stanley, 2005). No differentiation among the three major groups is evidenced by the variables that load on CV3 (not illustrated); instead, the variation associated with that canonical axis emphasizes differences among the OTUs of *H. arcimontensis*, in particular the narrow rostrum (BR) and zygomatic plate (BZP) and smaller auditory bulla (LAB) of those samples from the S Pare and W Usambara Mts (Table 1; for other sample statistics, see Carleton & Stanley, 2005: Appendix 1).

TABLE 1. Results of 10-group discriminant function analysis performed on 16 log-transformed craniodental measurements of *Hylomyscus anselli* ($N = 12$), *H. arcimontensis* ($N = 147$), and the Angolan sample ($N = 13$). See Fig. 1 for a scatterplot of the first two canonical variates extracted and Materials and Methods for variable abbreviations.

	Correlations		
Variable	CV 1	CV 2	CV 3
ONL	0.66***	0.36***	0.05
ZB	0.58***	0.25	-0.14
BBC	0.69***	0.35***	0.02
IOB	0.52***	0.66***	0.05
BOC	0.46***	0.28*	0.44***
LR	0.57***	0.46***	-0.15
BR	0.19	0.43***	0.35***
PPL	0.52***	0.25	0.06
HPL	0.25*	0.66***	0.01
LIF	0.75***	-0.14	0.10
LD	0.46***	0.30**	0.11
BBP	0.78***	0.24	0.25*
BZP	0.49***	-0.01	0.34***
LAB	0.49***	0.53***	0.37***
CLM	0.94***	0.17	0.15
WM1	0.91***	0.12	0.17
Canonical Correlations	0.93	0.81	0.75
Eigenvalues	6.34	1.98	1.32
% Variance	53.8	16.8	11.1

$^{*} = P \leq 0.05$; $^{**} = P \leq 0.01$; $^{***} = P \leq 0.001$

Mahalanobis distances between group centroids yielded a phenetic diagram that links the Angolan sample with *H. anselli*, a pair-group distinctly set apart from the 8 OTUs representing *H. arcimontensis* in nearly all bootstrapping iterations (Fig. 1B). Nevertheless, the *H. anselli* and Angolan samples are each strongly divergent, not joining until the penultimate clustering cycle. Structure within the *H. arcimontensis* cluster was less consistently recovered; as reported by Carleton & Stanley (2005), similarity and linkage between the mountain samples weakly correspond to geographic contiguity among those mountain systems. Noteworthy is the strong separation and usual association of the S Pare-W Usambara pair-group, representing mountains located at the northernmost reaches of the Eastern Arc Mts; however, in the next common phenetic topology recovered (not illustrated), the W Usambara and S Pare samples link individually to the stem subtending the larger cluster containing the E Usambara through Mt Rungwe OTUs.

Discrimination among the three principal geographic groupings is apparent but less well defined in principal component analysis, an ordination method that distills covariation patterns based on the log-transformed specimen data rather than a priori definition of groups. Size is reflected on PC I, as indicated by the large, positive correlation coefficients ($r = 0.60$-0.95, Table 2), grading from the lower scores derived for specimens of *H. arcimontensis* to the large values obtained for those of *H. anselli* and the Angolan sample (Fig. 2). Variables that correlate significantly with PC II emphasize the maximal separation of *H. arcimontensis* from *H. anselli*, with representatives of the Angolan sample falling intermediate (Fig. 2A); whereas, those that load strongly on PC III account for maximal separation of *H. arcimontensis* from the Angolan sample, with representatives of *H. anselli* dispersed intermediately (Fig. 2B). The oblique orientation of specimen scores relative to the component axes reflects both age-related size increases and taxon-specific size differences. Accordingly, one-way ANOVAs disclose significant categorical influences of OTU and age class on specimen scores for both PC I and PC II (Table 3). Sex as categorical effect is inconsequential with regard to all three components (Table 3), a post hoc finding that sustains pooling of the sexes in our multivariate analyses. Nevertheless, the substantial contribution of post-weaning size increases in the unrotated PC results obscures interpretation of actual size differences between taxa and informative variables, especially between the two large-bodied samples, those representing Angola and *H. anselli*, whose disposition in multivariate space is compressed relative to the much smaller *H. arcimontensis* (e.g., see Table 6).

TABLE 2. Results of principal component analysis performed on 16 log-transformed craniodental measurements of intact specimens representing *Hylomyscus anselli* ($N = 12$), *H. arcimontensis* ($N = 147$), and the Angolan sample ($N = 13$). See Fig. 2A, B for scatterplots of principal component scores and Materials and Methods for variable abbreviations.

	Correlations		
Variable	PC I	PC II	PC III
ONL	0.95^{***}	-0.17^{*}	-0.01
ZB	0.85^{***}	-0.18^{*}	-0.05
BBC	0.78^{***}	0.12	0.16^{*}
IOB	0.69^{***}	0.07	0.24^{**}
BOC	0.75^{***}	-0.01	-0.03
LR	0.85^{***}	-0.24^{**}	0.11
BR	0.70^{***}	-0.45^{***}	-0.09
PPL	0.85^{***}	-0.21^{**}	-0.22^{**}
HPL	0.60^{***}	-0.40^{***}	0.57^{***}
LIF	0.78^{***}	0.18^{*}	-0.38^{***}
LD	0.83^{***}	-0.41^{***}	-0.12
BBP	0.83^{***}	0.29^{***}	0.03
BZP	0.69^{***}	0.10	-0.40^{***}
LAB	0.66^{***}	0.08	0.19^{*}
CLM	0.78^{***}	0.55^{***}	0.17^{*}
WM1	0.72^{***}	0.60^{***}	0.21^{**}
Eigenvalues	0.021	0.004	0.003
% Variance	58.2	11.9	7.3

$^{*} = P \leq 0.05$; $^{**} = P \leq 0.01$; $^{***} = P \leq 0.001$

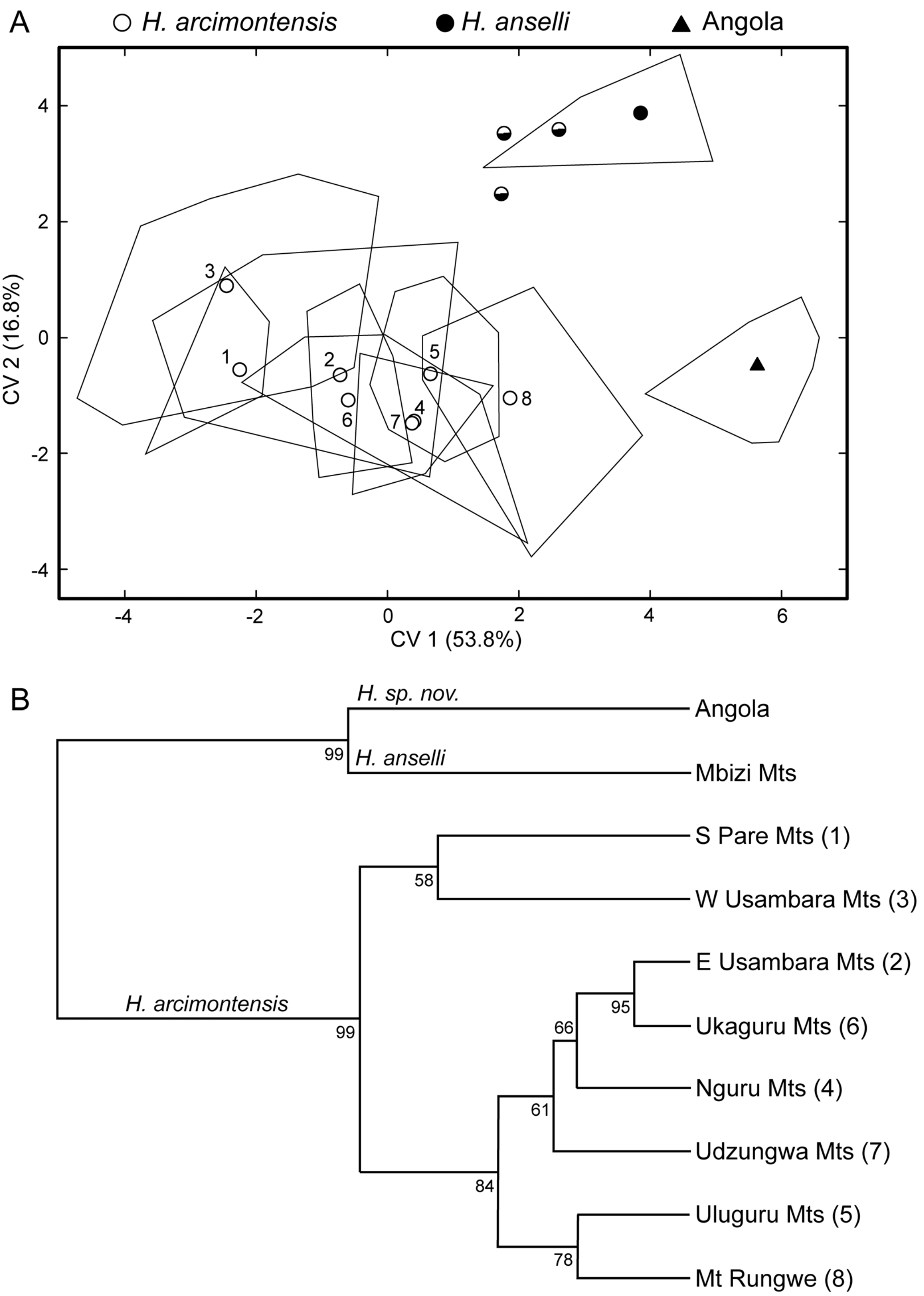

FIGURE 1. Results of discriminant function analysis performed on 16 log-transformed craniodental variables, as measured on 175 intact adult specimens representing 10 OTUs of the *Hylomyscus anselli* species group. A) Projection of OTU centroids onto first two canonical variates (CV) extracted (see Table 1 for variable loadings). Polygons enclose maximal dispersion of individual specimen scores around each group centroid; half-filled circles indicate the scores of the three Zambian specimens from the type series of *anselli* Bishop (1979), which were entered as unknowns. B) Cluster diagram (UPGMA) based on average Mahalanobis distances between the 10 OTU centroids as derived from discriminant function analysis (coefficient of cophenetic correlation = 0.934). Bootstrapping values are indicated for all nodes (1000 iterations); mountain system and OTU identifier are indicated for each terminal OTU, along with species recognized herein at those stems that subtend major geographic associations.

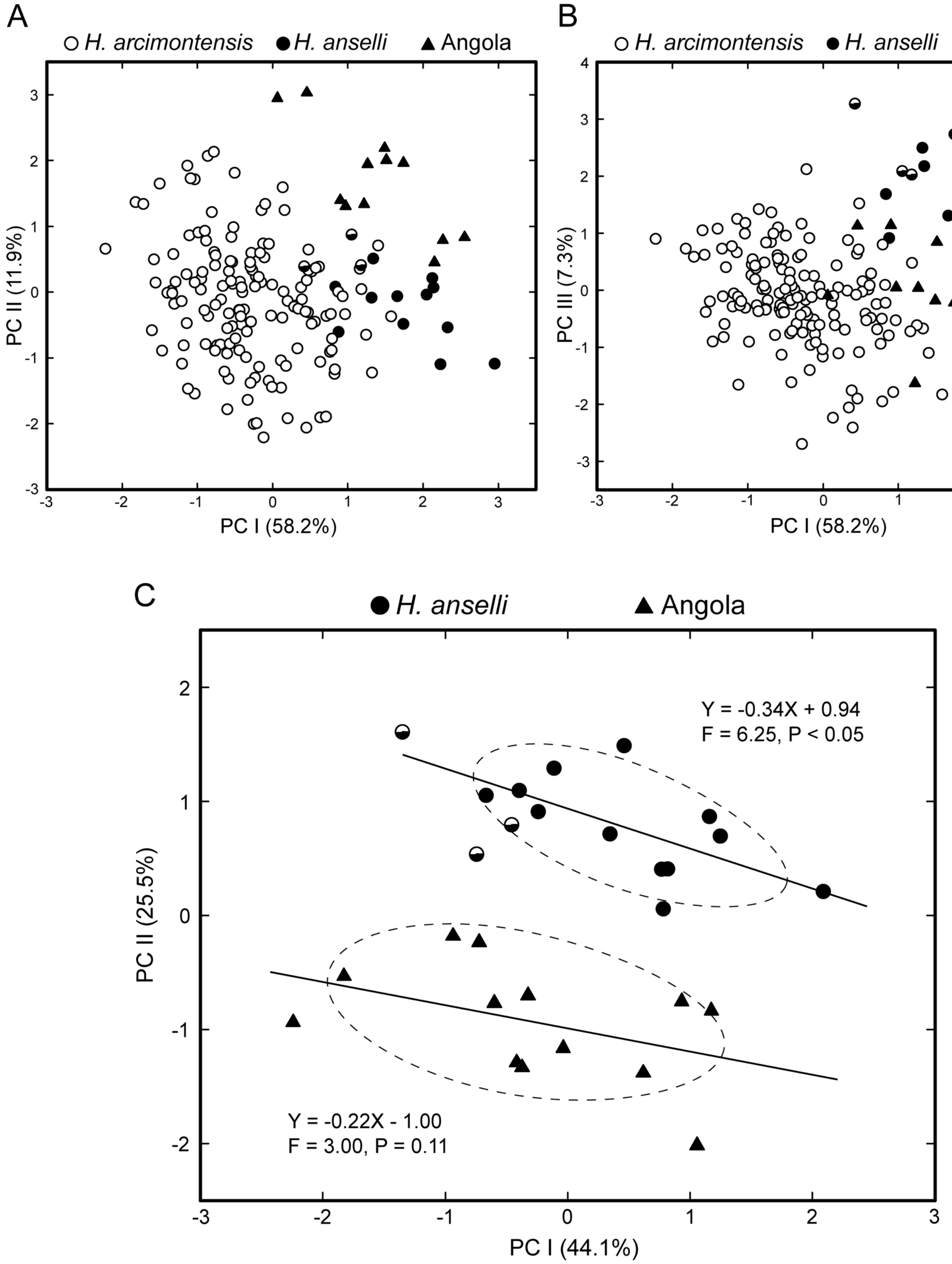

FIGURE 2. Three scatterplots depicting results of principal component (PC) analyses of 16 log-transformed craniodental variables as measured on 175 intact crania representing the *Hylomyscus anselli* species group. A) Projection of individual scores onto components I and II extracted from ordination of specimens representing *H. anselli* (N = 15), *H. arcimontensis* (N = 147), and the Angolan sample (N = 13). B) Projection of specimen scores onto components I and III extracted from the same ordination as performed in plot A. C) Projection of individual scores onto the first two components extracted from ordination of specimens representing *H. anselli* (N = 15) and the Angolan sample (N = 13); major axes of the species constellations and regression statistics are indicated; the Y intercepts differ significantly (F = 8.23, P = 0.009), but not their slopes (F = 0.38, P = 0.546) (see text for discussion). For scatterplots A and B, see Table 2 for variable correlations and variance explained; for scatterplot C, see Table 4; variable abbreviations are given in the Materials and Methods. The half-filled circles in all three plots indicate the scores of the three Zambian specimens from the type series of *anselli* Bishop (1979).

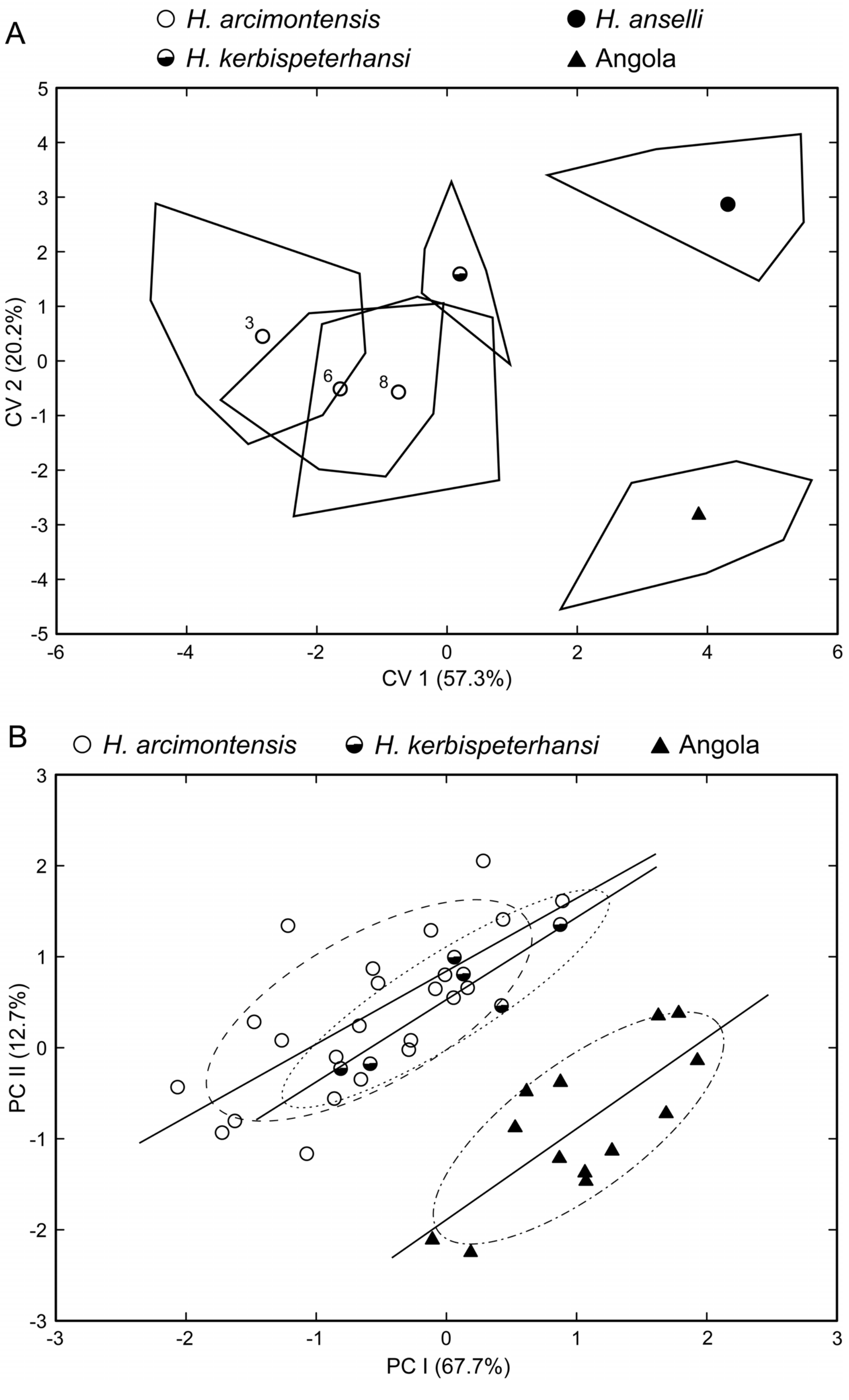

FIGURE 3. Morphometric comparisons of the Angolan sample with *Hylomyscus kerbispeterhansi* based on analyses of 16 log-transformed craniodental variables; selected representatives of related species were included to provide multivariate context (see Material and Methods for variable abbreviations and Table 5 for variable loadings). A) Scatterplot of OTU centroids for the first two canonical variates (CV) extracted from six-group discriminant function analysis (*H. anselli*, *N* = 12; *H. arcimontensis*, *N* = 55—OTUs 3, 6, and 8; *H. kerbispeterhansi*, *N* = 6; Angolan sample, *N* = 13). Irregular polygons circumscribe maximal dispersion of specimen scores around an OTU centroid. B) Scatterplot of individual scores for the first two principal components (PC) extracted from ordination of specimens representing *H. arcimontensis* (OTU 3, *N* = 23), *H. kerbispeterhansi* (*N* = 6), and the Angolan sample (*N* = 13). Major axes of the species constellations and 1 SD confidence ellipses around the sample centroid are indicated (see text for discussion).

TABLE 3. Results of one-way ANOVAs for various post hoc categorical effects on the dispersion of specimen scores for the first three principal components (PC) extracted for the complete dataset (See Figs. 2A and 2B for scatterplots). Statistics tabulated are F values, attained probability levels (P), and degrees of freedom (df).

PC	F (OTU)	F (Age)	F (Sex)
PC I	29.2, $P \leq 0.0001$, df = 9/162	10.3, $P \leq 0.0001$, df = 3/171	3.4, $P = 0.063$, df = 1/173
PC II	15.8, $P \leq 0.0001$, df = 9/162	17.5, $P \leq 0.0001$, df = 3/171	2.4, $P = 0.119$, df = 1/173
PC III	8.6, $P \leq 0.0001$, df = 9/162	1.6, $P = 0.185$, df = 3/171	0.3, $P = 0.612$, df = 1/173

Principal component analysis of specimens representing only *H. anselli* and the Angolan sample yielded distinctly isolated constellations in a scatterplot of the first two components extracted (Fig. 2C). This morphometric comparison separates the influences of age class and OTU. Thus, one-way ANOVAs of age class as categorical effect are highly significant for PC I (F = 8.49, P = 0.0015, df = 2/25), but not for PC II (F = 3.20, P = 0.058, df = 2/25); conversely, influence of OTU-related differences is confined to dispersion of scores along PC II (F = 93.28, $P \leq 0.0001$, df = 1/26) and contributes trivially to PC I (F = 2.04, P = 0.165, df = 1/26). Differentiation of the Angolan sample from that of *H. anselli* is most clearly expressed by those six variables that load strongly on the second component, which is aligned more perpendicular to the major axes of the sample ellipses. The sign and magnitude of those loading coefficients describe a skull (Angolan sample, lower constellation) with a shorter and wider hard palate (HPL, BBP), longer incisive foramina (LIF), slightly more robust molars (CLM, WM1), and broader zygomatic plate (BZP); in contrast to one (*H. anselli*, upper constellation) with a longer and narrow palate, shorter incisive foramina, smaller molars, and narrower zygomatic plate (Table 4). The means of all six variables correspondingly differ significantly in one-way ANOVAs for testing homogeneity of group means (Table 4).

TABLE 4. Results of principal component analysis performed on 16 log-transformed measurements of *Hylomyscus anselli* (*N* = 12) and the Angolan sample (*N* = 13), complemented with one-way ANOVAs of input variables with OTU as categorical effect (df = 1/26). See Fig. 2C for a scatterplot of principal component scores and Materials and Methods for variable abbreviations.

	Correlations		
Variable	PC I	PC II	F (OTU)
ONL	0.94^{***}	0.02	1.57
ZB	0.88^{***}	0.20	5.84^{*}
BBC	0.46^{*}	0.24	2.99
IOB	0.55^{**}	0.36	10.58^{**}
BOC	0.65^{***}	-0.25	0.04
LR	0.82^{***}	0.30	5.78^{*}
BR	0.77^{***}	0.30	15.02^{***}
PPL	0.92^{***}	-0.19	0.42
HPL	0.49^{**}	0.69^{***}	36.70^{***}
LIF	0.49^{**}	-0.70^{***}	14.02^{***}
LD	0.87^{***}	0.06	1.93
BBP	0.41^{*}	-0.68^{***}	10.26^{**}
BZP	0.43^{*}	-0.77^{***}	9.28^{**}
LAB	0.57^{**}	0.34	15.94^{***}
CLM	0.41^{*}	-0.43^{*}	2.31
WM1	-0.20	-0.42^{*}	9.62^{**}
Eigenvalues	0.013	0.08	
% Variance	44.1	25.5	

$^{*} = P \leq 0.05$; $^{**} = P \leq 0.01$; $^{***} = P \leq 0.001$

Angolan Form compared with *H. kerbispeterhansi*. The Angolan sample retained its unambiguous isolation in discriminant function analysis that included *H. kerbispeterhansi*, along with *H. anselli* and select OTUs of *H. arcimontensis* (Fig. 3A; Wilks' lambda = 0.004, F = 8.7, $P \leq 0.0001$). The among-group variation explained by the first two canonical variates disclosed representatives of *H. kerbispeterhansi* to be phenetically most similar to examples of *H. arcimontensis*, the smaller cranial size of these two species reflected by the uniformly large and positive variable loadings on CV 1 (Table 5). Dispersion of specimen scores along CV 2 again accentuated differentiation of the Angolan sample from that of *H. anselli*. Samples of *H. arcimontensis* from the Eastern Arc Mts were purposely chosen to broadly represent size variation apparent within the species (see Carleton & Stanley, 2005: 634), including one each from the northeastern portion of its geographic distribution (OTU 3, East Usambara Mts), from the middle section (OTU 6, Ululguru Mts), and from its southwestern range (OTU 8, Mt Rungwe). Based on Mahalanobis distances (MD^2) between group centroids, the sample of *H. kerbispeterhansi* most closely resembled the latter two OTUs of *H. arcimontensis* ($MD^2 = 28.6, 30.5$), not that (OTU 3) from the northeastern part of the specific range ($MD^2 = 41.5$).

TABLE 5. Results of ordinations performed on 16 log-transformed craniodental measurements of *Hylomyscus anselli* (*N* = 12), *H. arcimontensis* (*N* = 55), *H. kerbispeterhansi* (*N* = 6), and the Angolan sample (*N* = 13). See Fig. 3A for a scatterplot of the first two canonical variates (CV) extracted and Fig. 3B for a scatterplot of the first two principal components (PC) extracted; variable abbreviations are given in the Materials and Methods.

	CV Correlations		PC Correlations	
Variable	CV 1	CV 2	PC I	PC II
ONL	0.66***	0.06	0.96***	0.15
ZB	0.52***	0.17	0.85***	0.29
BBC	0.67***	0.10	0.82***	-0.15
IOB	0.74***	0.28**	0.76***	-0.09
BOC	0.38***	-0.09	0.80***	0.07
LR	0.67***	0.25*	0.87***	0.25
BR	0.31**	0.22*	0.75***	0.49**
PPL	0.52***	0.01	0.88***	0.24
HPL	0.51***	0.45***	0.58***	0.30
LIF	0.46***	-0.43***	0.89***	0.00
LD	0.47***	0.14	0.82***	0.44**
BBP	0.78***	-0.26*	0.87***	-0.31*
BZP	0.49***	-0.38***	0.85***	-0.07
LAB	0.49***	0.23*	0.79***	-0.24
CLM	0.87***	-0.19	0.82***	-0.53***
WM1	0.83***	-0.28**	0.71***	-0.65***
Canonical Correlations	0.94	0.86	--	--
Eigenvalues	8.19	2.89	0.030	0.006
% Variance	57.3	20.2	67.7	12.7

$^{*} = P \leq 0.05$; $^{**} = P \leq 0.01$; $^{***} = P \leq 0.001$

Principal component analysis was designed to highlight cranial size and shape variation among specimens of the Angolan form, *H. kebispeterhansi*, and the series of *H. arcimontensis* from the East Usambara Mts (OTU 3), which includes the type locality of the species. A scatterplot of the first two principal components reinforced the singular definition of the Angolan series, whereas those of *H. arcimontensis* and *H. kerbispeterhansi* overlapped substantially in morphometric space (Fig. 3B). The exceptionally large size of the Angolan form relative to series of *H. arcimontensis* and *H. kerbispeterhansi* comports with the large, positive correlation coefficients derived for PC I (Table 5); loadings on PC II emphasize the robust molars (CLM, WM1) of the Angolan series and relatively longer diastema (LD) and broader rostrum (BR) that characterize the samples of *H. arcimontensis* and *H.*

kerbispeterhansi (Tables 5, 6). Accordingly, the major axis of the Angolan constellation differs significantly in its Y intercept in contrast to those of *H. arcimontensis* (F = 56.1, P ≤ 0.0001, df = 1/32) and *H. kerbispeterhansi* (F = 48.0, P ≤ 0.0001, df = 1/15), but not the slopes of all three samples (F = 0.2, P = 0.809; df = 2/36). On the other hand, the major axes of the ellipses of *H. arcimontensis* and *H. kerbispeterhansi* are not significantly different in their Y intercepts (F = 1.2, P = 0.286, df = 1/25). Statistically, the examples of *H. arcimontensis* and *H. kerbispeterhansi* emerged as indistinguishable *based on our measurement set and in this particular comparison of population samples*.

In their description of *H. kerbispeterhansi*, Demos *et al.* (2014b) included as their comparative standard of *H. arcimontensis* samples from the northeastern portion of its range (namely, South Pare, West Usambara, and East Usambara Mts). Carleton & Stanley (2005) documented that populations of *H. arcimontensis* are smaller in the northeastern sector and irregularly trend toward larger animals in the southwestern portion of the range, e.g., those from the Uluguru Mts and Mt Rungwe. They attributed this size trend to geographic variation, but invited the application of other data to evaluate the morphometric patterns discernable within *H. arcimontensis* as they recognized the species. Such a follow-up evaluation remains a worthwhile project. For our purposes here, however, the morphological distinction of *Hylomyscus* populations in Angolan mountains from those in the Kenyan Highlands (*H. kerbispeterhansi*) is unequivocal.

Summary. Morphometric comparisons have delineated several diagnosable themes of craniodental differentiation among these samples of the *Hylomyscus anselli* species group, observable in principal component, discriminant function, and clustering analyses, each of which disclose cohesive patterns of morphological similarity congruent with major geographic regions. Three of these craniodental themes have previously received names: *H. anselli* (Bishop, 1979), distributed across mountains in northern Zambia to contiguous westcentral Tanzania; *H. arcimontensis* Carleton & Stanley, 2005, occurring patchily throughout the Eastern Arc Mts of central Tanzania to Mt Rungwe and northern Malawi; and *H. kerbispeterhansi* Demos, Agwanda, & Hickerson, 2014b, documented from the highlands of western Kenya. A fourth diagnosable theme as revealed herein—the sample from the highlands of westcentral Angola—lacks a name and is described below as a new species. Our description emphasizes differentiation of the new form with respect to the geographically closer species, *H. anselli* and *H. arcimontensis*, not the newly named form from the highlands of Kenya, *H. kerbispeterhansi*.

***Hylomyscus heinrichorum*, new species**
(Figs. 5–7; Table 6)

Hylomyscus carillus, Hill & Carter, 1941: 97 (part, faunal report); Crawford-Cabral, 1998: 79 (part, faunal report).

Praomys carillus, Crawford-Cabral, 1986: 163 (part, name combination, zoogeography).

Hylomyscus denniae, Musser & Carleton, 1993: 599, 2005: 1336 (part, systematic checklists, referenced as isolated population of indeterminate status).—Dieterlen, 2013: 435 (part, faunal report, distribution).

H[*lomyscus*]. cf. *anselli* group, Carleton & Stanley, 2005: 629 (taxonomic revision, definition of the *H. anselli* species group and its contents).

Holotype. FMNH 83796, an adult male prepared as skin and skull, captured 7 October 1954 (skin tag reads "7 X 1954") by Gerd H. Heinrich; the field number is recorded on the skin tag as 8778 and as GH 8778 on the now loose skull tag. Machine-printed on back of the tag is "Angolan Zoological Expedition, 1954." Written in black pen in the collector's script are the external measurements ("T.L.: 245, Tail: 145, H.F.: 22, Ear: 19") and habitat ("Evergreen wood. – High mountain region"); the testes were noted as scrotal in position. See Table 6 for cranial measurements of the holotype. The skin is well prepared, in fine condition, and the skull is intact, in good condition with minor damage confined to the left orbital wall.

Type locality. Angola, Provincia Huambo, Mount Moco, ca. 12°27.712′S, 15°10.600′E (per the U.S. National Geospatial-Intelligence Agency).

The locality as recorded on the skin tag reads only "Angola, Mount Moco." Heinrich collected at two localities on Mt Moco, as evidenced by locality modifiers recorded in the field catalog and by an annotated, X-marked field map accessioned with that catalog (both documents maintained in the FMNH Mammal Division). One X-marked site is centered near the peak of Mt Moco, and a second X is located nearby to the southeast. Specimens obtained at the latter place were labeled "foot" and collected 14–20 Sep 1954. Heinrch then relocated to a higher elevation and settled in a "high mountain region," presumably corresponding to the former X, where he remained for over three weeks, 22 Sep–16 Oct 1954. The type specimen and referred specimens from Mt Moco all originated from the high mountain locality.

Paratypes. All material here assigned to *H. heinrichorum* originates from two localities in Angola, Provincia Huambo. These include 14 additional specimens from Mt Moco (FMNH 83793–83795, 83797–83799, 83801–83807, 83895), collected from 5–10 Oct 1954 by G. Heinrich; and 10 specimens from Mount Soque, 42 km WSW Luimbale (FMNH 83783–83792), collected 24–28 Aug 1954 by G. Heinrich.

Heinrich's Mount Soque (also as Serra Ussoque) is a ridge-shaped inselberg (12°17.450′S, 15°08. 633′E), located approximately 20 km NNW Mt Moco and 20 km WSW Luimbale, its peak elevation ca. 2165 m. We presume that Heinrich's locality modifier, "42 km WSW Luimbale," was a by-road calculation.

Diagnosis. A species of the *Hylomyscus anselli* group characterized by larger size (ONL ≈ 26.0–27.5 mm; CLM ≈ 4.1–4.3 mm) compared with examples of *H. arcimontensis* and *H. kerbispeterhansi* (ONL ≈ 24.5–26.5 mm; CLM ≈ 3.5–4.0 mm), as reflected in most craniodental dimensions recorded (Table 6). Compared with examples of *H. anselli*, size comparable, but bony palate notably shorter with absolutely and proportionally longer incisive foramina (LIF ≈ 75–80% of LD) that penetrate between the anterior roots of the first molars; molars slightly more robust and zygomatic plate broader; head-and-body and tail average shorter in length, and rostral dimensions (LR, LD) average smaller.

Distribution. Restricted to high mountainous region of westcentral Angola as so far known (Fig. 4).

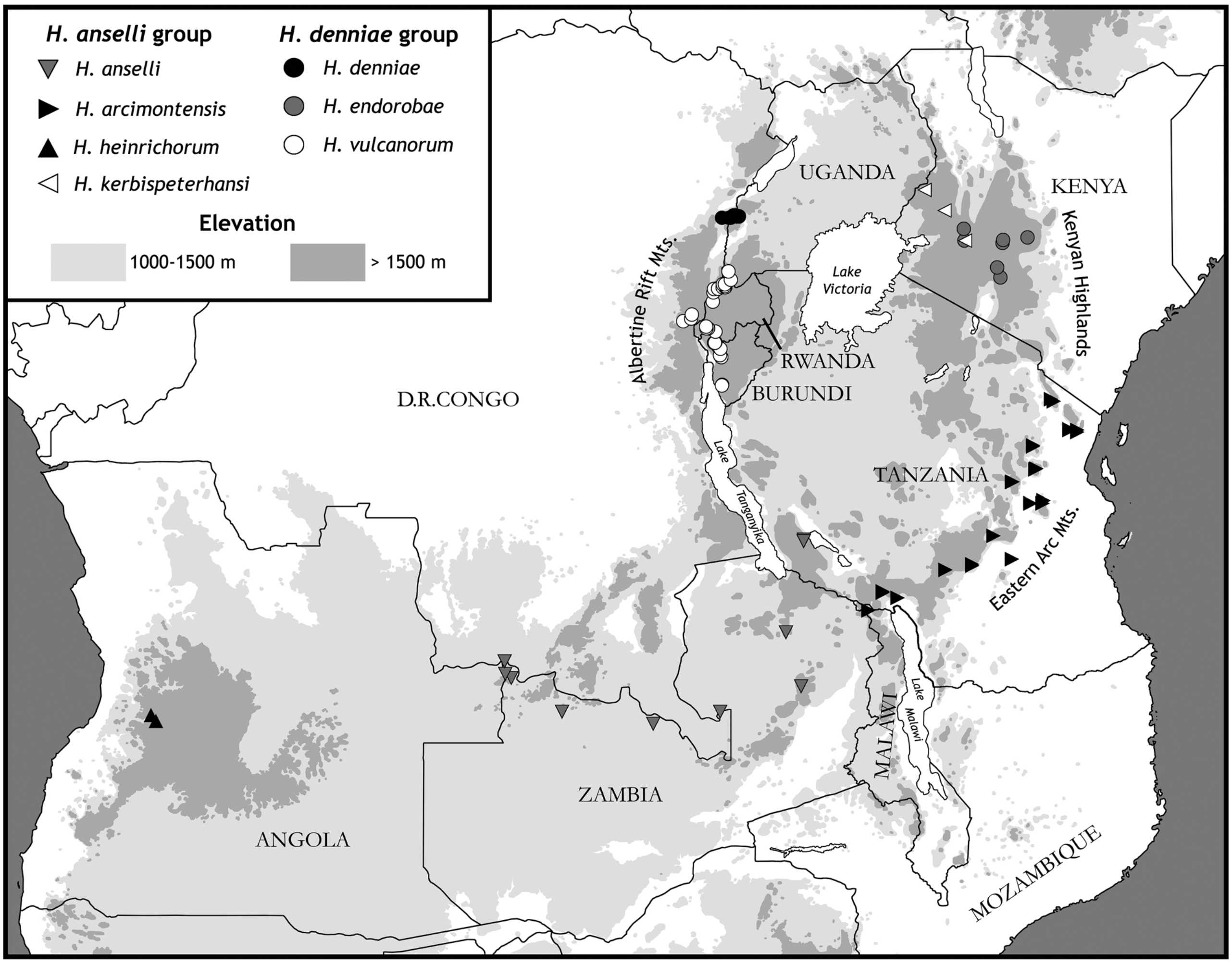

FIGURE 4. Distributions of species representing the *Hylomyscus anselli* and *H. denniae* groups and their relation to principal mountainous systems of central Africa. Localities of the *H. anselli* group are based on specimens documented herein and by Ansell (1957, 1978), Carleton & Stanley (2005), and Carleton *et al.* (2006); see Demos *et al.* (2014) for additional localities of *H. kerbispeterhansi*. Localities of the *H. denniae* group are based on specimens previously reported by Carleton *et al.* (2006).

FIGURE 5. Dorsal (left set) and ventral (right set) views of adult round skins (about 0.5 ×), illustrating typical pelage patterns of the three species of the *Hylomyscus anselli* group discussed herein: AA′, *H. arcimontensis* (FMNH 151244), a male from 12.5 km NW Korogwe, Tanga Region, West Usambara Mts, 1300 m, Tanzania; BB′, *H. heinrichorum* (FMNH 83796, holotype), new species, a male from "High mountain region" of Mt. Moco, Provincia Huambo, Angola; CC′, *H. anselli* (FMNH 171353), a male from 0.5 km S and 3 km E Wipanga, Mbizi FR, Mbizi Mts, Rukwa Region, 2300 m, Tanzania. Total length of each skin, as measured in the field, = 245 mm, but lengths of the prepared skin as photographed appear different due to the circumstances of individual preparation and drying conditions.

Description and comparisons. *Hylomyscus heinrichorum* can be associated with the other species so far recognized in the *H. anselli* group (*H. anselli*, *H. arcimontensis*, *H. kerbispeterhansi*) based on certain qualitative traits. Foremost among these are the lack of pectoral mammae; the large expanse of the subsquamosal fenestrum, which together with the postglenoid foramen defines a slender and long hamular process (see Carleton & Stanley, 2005: Fig. 6); and its relatively shorter incisive foramina (namely, shorter in comparison with members of the *H. denniae* group). The number of mammary glands in *H. heinrichorum*—six, distributed as one post-axial pair and two inguinal pairs—was verified on several prepared round skins (FMNH 83793, 83795, 83802–83804), all females that were apparently in late-term pregnancy or lactating.

Although we excluded external variables in our multivariate analyses, mean differences were highly significant for TOTL, TL, and HBL in one-way ANOVAs that compared our tabulated samples of *H. heinrichorum* and *H. anselli* (F values = 13.8–14.4, $P < 0.001$, df 1, 35), but not for HFL ($F = 0.02$, $P = 0.884$, df 1, 35). The sample of *H. heinrichorum* averaged smaller than that of *H. anselli* for all three significantly different skin variables (Table 6). Our samples of the two species were obtained by different collectors, and such external variables are notoriously variable depending upon investigator habit and field experience. Even so, the disparity in means seems suitably large to convey real taxonomic differences.

TABLE 6. Measurements of the holotype (FMNH 83796) of *Hylomyscus heinrichorum*, new species, and descriptive statistics for samples of the *H. anselli* group (Statistics include the sample mean, standard deviation, observed range, and sample size in parentheses; see Materials and Methods for variable abbreviations).

	H. heinrichorum		*H. anselli*	*H. arcimontensis*	*H. kerbispeterhansi*
Variable	Holotype	Angolan Highlands	Mbizi Mts	E Usambara Mts	Kenyan Mts
TOTL	245.0	231.4 ± 12.5 207–255 (25)	246.1 ± 7.4 238–264 (12)	224.4 ± 17.1 186–247 (24)	219.3 ± 13.3 195–231 (7)
HBL	100.0	94.0 ± 6.6 82–106 (25)	101.6 ± 3.8 95–109 (12)	88.1 ± 8.3 72–110 (24)	90.3 ± 7.8 76–100 (7)
TL	145.0	137.3 ± 7.4 121–150 (25)	146.3 ± 5.0 141–159 (12)	136.5 ± 10.1 116–150 (24)	129.0 ± 6.8 119–138 (7)
HFL	22.0	21.1 ± 1.0 18.5–22 (25)	21.2 ± 0.7 20–22 (12)	19.5 ± 1.3 17–22 (24)	19.1 ± 1.2 17–21 (8)
EAR	19.0	18.5 ± 0.9 17–20 (24)	20.1 ± 0.5 19–21 (12)	17.8 ± 1.0 15–19 (24)	18.6 ± 0.8 17–19.5 (8)
WT	--	--	28.5 ± 3.1 22.0–34.5 (12)	20.2 ± 4.4 12.0–29.0 (24)	21.5 ± 3.3 18.0–26.0 (6)
ONL	27.4	26.7 ± 0.8 25.0–28.1 (14)	27.4 ± 0.7 26.3–28.6 (12)	25.2 ± 1.0 23.0–27.0 (24)	25.5 ± 0.8 24.6–26.9 (6)
ZB	13.5	13.0 ± 0.4 12.4–13.8 (14)	13.5 ± 0.2 12.9–13.7 (12)	12.5 ± 0.5 11.6–13.7 (24)	12.7 ± 0.6 12.0–13.5 (6)
BBC	11.8	11.7 ± 0.2 11.3–12.1 (14)	11.9 ± 0.2 11.5–12.3 (12)	11.2 ± 0.2 10.7–11.8 (24)	11.3 ± 0.2 10.8–11.5 (6)
IOB	4.4	4.5 ± 0.1 4.4–4.7 (14)	4.6 ± 0.1 4.5–4.8 (12)	4.3 ± 0.1 4.0–4.7 (24)	4.3 ± 0.1 4.2–4.6 (6)
BOC	6.5	6.2 ± 0.2 6.0–6.5 (13)	6.2 ± 0.1 5.9–6.5 (12)	6.0 ± 0.2 5.5–6.5 (24)	6.0 ± 0.1 5.8–6.2 (6)
LR	8.2	8.2 ± 0.5 7.2–8.9 (14)	8.7 ± 0.3 8.3–9.1 (12)	7.7 ± 0.4 7.1–8.4 (24)	7.9 ± 0.2 7.6–8.1 (6)
BR	4.7	4.4 ± 0.2 4.1–4.8 (14)	4.7 ± 0.2 4.5–5.0 (12)	4.3 ± 0.2 3.9–4.7 (24)	4.5 ± 0.2 4.3–4.8 (6)
PPL	9.4	9.3 ± 0.5 8.6–10.1 (14)	9.5 ± 0.4 8.9–10.1 (12)	8.7 ± 0.4 7.6–9.4 (24)	8.7 ± 0.6 8.0–9.6 (6)
HPL	4.7	4.4 ± 0.2 4.0–4.7 (14)	4.8 ± 0.2 4.5–5.0 (12)	4.3 ± 0.2 4.0–4.7 (24)	4.4 ± 0.2 4.2–4.8 (6)
LIF	5.9	5.7 ± 0.3 5.2–6.4 (14)	5.5 ± 0.1 5.3–5.8 (12)	5.2 ± 0.2 4.6–5.6 (24)	5.3 ± 0.1 5.1–5.5 (6)
LD	7.4	7.4 ± 0.4 6.7–8.1 (14)	7.7 ± 0.3 7.4–8.4 (12)	7.0 ± 0.3 6.4–7.7 (24)	7.5 ± 0.3 7.1–7.9 (6)
BBP	5.5	5.3 ± 0.1 5.1–5.5 (14)	5.2 ± 0.1 5.1–5.4 (12)	4.9 ± 0.1 4.6–5.1 (24)	5.0 ± 0.1 4.8–5.2 (6)
BZP	2.8	2.5 ± 0.1 2.2–2.8 (14)	2.4 ± 0.1 2.2–2.6 (12)	2.3 ± 0.1 2.1–2.6 (24)	2.3 ± 0.1 2.1–2.5 (6)
LAB	4.4	4.4 ± 0.1 4.3–4.6 (14)	4.5 ± 0.1 4.5–4.7 (12)	4.1 ± 0.1 3.9–4.3 (24)	4.4 ± 0.1 4.2–4.6 (6)
CLM	4.30	4.21 ± 0.12 4.02–4.39 (14)	4.16 ± 0.11 3.87–4.28 (12)	3.70 ± 0.12 3.37–3.89 (24)	3.80 ± 0.04 3.76–3.89 (6)
WM1	1.32	1.29 ± 0.04 1.20–1.34 (14)	1.24 ± 0.04 1.17–1.29 (12)	1.13 ± 0.03 1.06–1.18 (24)	1.17 ± 0.01 1.16–1.19 (6)

FIGURE 6. Dorsal (top row) and ventral (bottom row) views of adult crania (ca. 2.75 ×) representing members of the *Hylomyscus anselli* species group: A, *H. arcimontensis* (FMNH 147260; ONL = 24.9 mm), a male from Tanzania, Tanga Region, West Usambara Mts; B, *H. heinrichorum*, new species (FMNH 83796, holotype; ONL = 27.3 mm), a male from Angola, Provincia Huambo, Mt Moco; C, *H. anselli* (FMNH 171367; ONL = 28.1 mm), a male from Tanzania, Rukwa Region, Mbizi FR.

The pelage of *H. heinrichorum* resembles that observed in other members of the *H. anselli* group, being soft and fine in texture, short and closely adpressed to the body. The most notable pelage contrast of the Angolan form involves dorsal pelage color. Individual dorsal hairs can be characterized as medium plumbeous gray tipped with bright buff; the overall effect, however, is not so dark and somber a brown as in examples of *H. anselli* and *H. arcimontensis* (Fig. 5), but rather an even toned, dull yellowish brown (buckthorn brown), light to moderate in saturation. Guard hairs are brown with hyaline tips, only a little longer than the dorsal fur except over the rump. There is little tendency toward darker over the middle dorsum or conspicuously brighter flanks as is common in the other two species; color is generally evenly graded in expression over the entire dorsum, from the middle back to the flanks. A few individuals of *H. heinrichorum* exhibit brighter ochraceous-tipped hairs along the upper leg and shoulder and side of the head; nevertheless, the dorsal pelage color is predominantly even toned in appearance. Dorsal-ventral pelage contrast is well marked but not accentuated by a brighter lateral line. In all three species, the ventral hairs are basally gray and tipped with white, imparting a grayish-white effect. The three can be crudely sorted as bright gray (*H. arcimontensis*), medium gray (*H. heinrichorum*), and dark gray (*H. anselli*), with much variation and overlap among them. The tail of *H. heinrichorum*, as in other members of the *H. anselli* group, is notably longer than the head and body (TL ≈ 142–146% of HBL), its color dusky-brown and wholly dark around the circumference; caudal scales are finely textured and hairs short, imparting a naked appearance over most of its length, the fine caudal hairs becoming macroscopically visible toward the tip. The hind foot is short and narrow, as per the genus, with digit 5 nearly as long as digits 2–4; the naked plantar surface bears six well-formed, cushiony pads. Pale brown hairs of the limb usually continue onto the ankle and proximal metatarsum, forming a dusky medial metatarsal streak in some individuals, replaced by white hairs over the distal metatarsum and phalanges; glistening white ungual tufts are present. Pinnae are pale brown to dark tan in the Angolan species, compared with darker, more blackish brown ears in the other two.

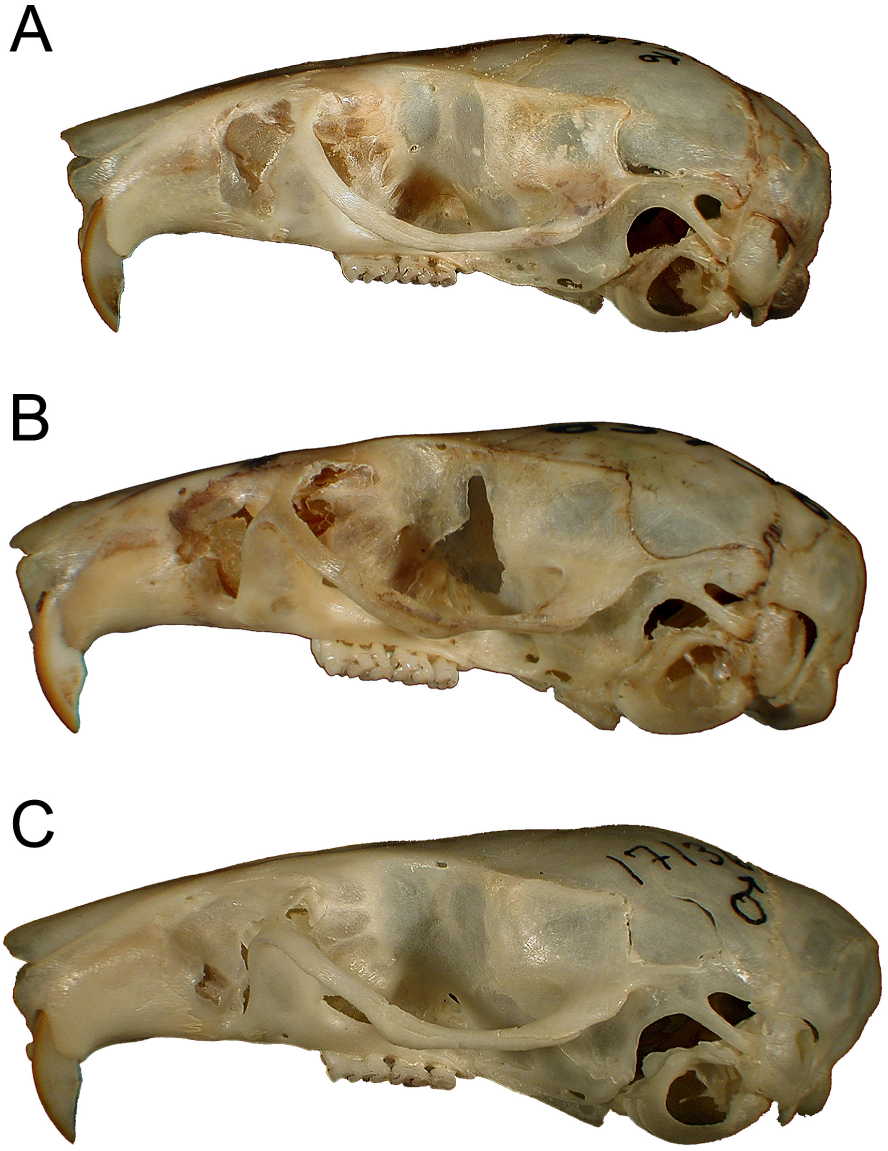

FIGURE 7. Lateral views (ca. 4.25 ×) of adult crania of the same specimens portrayed in Fig. 6: A, *H. arcimontensis*; B, *H. heinrichorum*, new species; C, *H. anselli*.

As a gestalt observation, the skull of *H. heinrichorum* is approximately equal to or only slightly smaller than *H. anselli*, albeit heavier in build, but both are substantially larger than *H. arcimontensis* (Figs. 6, 7). Thus, standard external measurements and those we recorded for the skull and molar rows easily serve to distinguish examples of *H. heinrichorum* from those of the smaller *H. arcimontensis* and *H. kerbispeterhansi* (Table 6); size routinely emerged as the preeminent factor accounting for their separation in multivariate space (Figs. 1, 3). Mensural differences between *H. heinrichorum* and *H. anselli*, on the other hand, are not readily grasped when eyeballing series of skulls, yet specimens of each did conform to distinct morphometric footprints based on the cranial measurements we obtained (see Figs. 1, 2C). However, fewer variables contributed to their discrimination, rendering their cranial separation correspondingly more difficult, based on subtle distinctions. Configuration of the hard palate relative to the length of the incisive foramina offers particularly important contrasts, those variables (BBP, HPL, LIF) loading strongly on that principal component which captured their separation in multivariate space (Fig. 2C, Table 4). As practical anatomical landmarks when viewing skulls, these loadings translate as absolutely shorter incisive foramina (LIF ca. 69–73% of LD) whose posterior end falls just short of or about level with the anterior border of the M1 anterior root in *H. anselli*, versus longer incisive foramina (LIF ca. 75–80% of LD) that extend beyond the anterior roots about to the rim of the first lamina of M1 in *H. heinrichorum*. Therefore, the incisive foramina in *H. heinrichorum* are proportionately the longest within the *H. anselli* group, albeit not so "long" as members of the *H. denniae* group. The absolutely longer bony palate documented in *H. anselli*, compared with a shorter palate in *H. heinrichorum*, is a reciprocal geometric corollary of the different foraminal lengths (Table 6). The shape of the incisive foramina, however, is similar in both: broader over the anterior portion, narrowing slightly over the posterior half. The dorsal notch formed between the upper zygomatic plate and rostrum appears slightly deeper and wider in specimens of *H. heinrichorum* compared with crania of *H. anselli* and *H. arcimontensis* (Fig. 6), a visual impression consistent with the actually broader zygomatic plate recorded in the former (Table 6) and the important contribution of this variable (BZP) to between-group discrimination (Table 4). The interorbital region of *H. heinrichorum* conforms to that described for the *H. anselli* group: relatively narrow and amphoral in shape over its anterior portion, with post-orbital shelving weakly expressed in full and old adults, its edges lacking supraorbital ridging or beading. When examining series of skulls arrayed side-by-side (Figs. 6, 7), examples of *H. anselli* exhibit the longest, more attenuate rostrum, those of *H. arcimontensis* the shortest and most truncate, and those of *H. heinrichorum* appear intermediate in rostral length and shape. These macroscopic impressions find some statistical precision in the sample statistics (Table 6), variable loadings of the ordinations performed (Tables 1, 2, 5), and/or one-way ANOVAs (Table 4).

Specimens of *H. heinrichorum* dentally resemble those of *H. anselli* and *H. arcimontensis* in the slight curvature of the upper incisors (nearly orthodont or weakly opisthodont), molar proportions, and cusp development. Pigmentation of the enamel face of the upper incisors in *H. heinrichorum* is a more saturated, medium orange compared with pale yellow-orange in *H. anselli* and *H. arcimontensis*; the tone is drab in all three.

Ecological notes. Other species of the *Hylomyscus anselli* group are known to be closely associated with Afromontane forest, typically found within an elevational belt of 1000–2500 m (Carleton & Stanley, 2005; Carleton *et al.*, 2006; Demos *et al*., 2014b). The habitat information recorded on the skin tag of all *Hylomyscus* specimens collected at Mt Moco—"Evergreen wood. – High mountain region"—fits this ecological and topographical setting. Also, a photograph, taken by some member of Heinrich's field team and labeled only Mt Moco, captures a substantial stand of closed-canopy, high forest in the vicinity of a campsite that we believe to represent Heinrich's "High mountain" collecting locality (Fig. 8).

Mills *et al.* (2011) documented the condition of Afromontane forest on Mt Moco as part of their ongoing studies of the endangered Swierstra's Francolin (*Francolinus swierstrai* Roberts), a partridge-like bird endemic to Angola. High forest persists as small patches, the largest about 25 hectares, restricted to narrow ravines and steep valleys in the remotest parts of the mountain; these isolated fragments are distributed over an elevation of 2000 to 2400 m, a range that falls within the 1400 mm annual rainfall isohyet. Characteristic genera include the Gondwanan conifer *Podocarpus* along with other evergreen, flowering trees and shrubs (species of *Apodytes*, *Ficus*, *Halleria*, *Ilex*, *Olea*, *Pittosporum*, *Polyscias*, and *Syzygium*—Huntley & Matos, 1994; Mills *et al.*, 2011). Canopy height tends to be irregular, conforming to the steep slopes and rugged valleys that retain forest coverage. Montane grasslands, both natural and anthropogenic, and Miombo woodlands, dominated by *Brachystegia*, *Isoberlinia*, and *Julbernardia*, sprawl in between the high-forest patches; the latter woodlands, a relatively mesic savanna association (Zambezian Woodland Biotic Zone), cover most of the mountain. Presumably, tracts of Afromontane forest were more extensive when Heinrich visited Mt Moco in 1954.

FIGURE 8. Camp site labeled as Mount Moco, which we believe represents the "High mountain region" visited by Gerd and Hildegarde Heinrich in Sep–Oct 1954. Their camp is located amidst a variety of habitats, including an appreciable stand of tall, multi-strata forest pictured in the background. This forest may correspond to the "Evergreen wood" where the Heinrichs obtained the sample of small, long-tailed murine that we here describe as *Hylomyscus heinrichorum*, new species. Photograph by Hildegarde Heinrich; reproduced with permission of Bernd Heinrich.

Most skin tags of *H. heinrichorum* from Mt Soque indicate their capture "Along mountain brook through tall grass. – Below mt. top." Whether remnant Afromontane forest existed in proximity to Heinrich's trap line is indeterminate from this scant description. When Mills canvassed Mt Soque for Swierstra's Francolin in 2005, he (Mills *et al.*, 2011: 6) recorded that Afromontane forest no longer existed, but a few pairs of the endangered francolin were discovered in "dense herbaceous and shrubby growth in gullies and around the mountain summit [peak at 2165 m]."

Other rodents collected with *Hylomyscus heinrichorum* over the same range of dates at both Mt Soque (24–28 Aug 1954) and Mt Moco (5–10 Oct 1954) include *Funisciurus congicus* Kuhl, *Graphiurus murinus* Desmarest, *Dendromus nyikae* Wroughton, *Grammomys dolichurus* Smuts, *Lophuromys angolensis* Verheyen, Dierckx, & Huselmans, *Myomyscus angolensis* Bocage, *Oenomys hypoxanthus* Pucheran, and *Pelomys campanae* Huet. Examples of *Aethomys namaquensis* A. Smith, *Graphiurus rupicola* Thomas & Hinton, *Mus triton* Thomas, *Otomys cuanzensis* Hill & Carter, and *Cryptomys mechowi* Peters were captured in sympatry with *H. heinrichorum* only at Mt Soque, but not Mt Moco; specimens of *Mus minutoides* Smith, *Cryptomys hottentotus* Lesson, and *Thryonomys gregorianus* Thomas were also obtained at Mt Moco, but not at Mt Soque. Certain species in some of these genera have been documented in moist forest at high elevations (e.g., *Graphiurus*, *Dendromus*, *Grammomys*, *Lophuromys*—Stanley *et al.*, 1998); still more of them are commonly associated with non-forest habitats—grasslands, open woodlands, marshes and riverine vegetation, thickets and forest edges—environments that are also represented on Mt Moco and were around Heinrich's campsite at the time of their survey (Fig. 8).

At this stage of understanding, *Hylomyscus heinrichorum* may be reasonably characterized as endemic to Afromontane forest based on the habitat recorded for the Mt Moco series and on the known affinity of its species-group relatives for highland forest. However, without knowing the exact placement of Heinrich's trap line and traps, its strict ecological reliance upon this biome must remain inferential pending renewed field surveys. Fresh autecological study is obviously in order.

Remarks. To our knowledge, specimens of *Hylomyscus heinrichorum* have not been collected since the 1954 Heinrich expedition. Until new field assessments are conducted, the conservation status of *H. heinrichorum* is plausibly considered Near Threatened, if not Vulnerable, in view of the continuing decline in extent and quality of Afromontane forest in Angola (Huntley & Matos, 1994; Mills *et al*., 2011). Unlike the Endangered classification of Swiestra's Francolin (IUCN Red List, accessed Jul 2014), a comestible, partridge-sized bird subjected to hunting pressure compounded by disappearance of its preferred habitat, populations of a small murid rodent like *H. heinrichorum* should remain resilient to habitat loss so long as even minimal forest cover, primary or secondary, persists. The recent documentation of substantial tracts of Afromontane forest in the Namba Mts (Mills *et al*., 2013), situated in southern Cuanza Sul Province about 80 km northwest of Mt Moco, augurs that ample populations of *H. heinrichorum* still exist.

Etymology. Our specific epithet honors both Gerd Hermann Heinrich (1896–1984) and Hildegarde Maria Buruvna (1917–2012), husband and wife (Fig. 9), to belatedly acknowledge their important field work in Africa conducted in the middle 1900s. Notwithstanding the enduring scientific relevance of their bird and mammal collections, these museum expeditions—to Angola (1953–1955, 1957–1958), Tanzania (1961–1963), and South Africa (1963)—unfolded as a means to an end, that end being to afford Heinrich yet another opportunity to pursue his zoological first love, the natural history and taxonomic diversity of parasitic wasps or ichneumon flies (Insecta: Hymenoptera: Ichneumonidae). While just a teenager, Heinrich devoted himself to understanding this exceedingly diverse, systematically intractable family, and it remained a lifelong passion, somehow sustained during, between, and after the World Wars that sundered normalcy in Europe. He opportunistically promoted his service as professional collector, obtaining vertebrate specimens under the auspices of large, well funded museums in order to visit exotic faraway geographies and collect never-before-seen ichneumons. His body of publications and prolific taxonomic descriptions were foundational for understanding major groups of Ichneumonidae over vast areas of their distribution (e.g., G. Heinrich, 1934, 1938, 1961–1962, 1967–1968). For more about Gerd Heinrich, his scientific contributions and improbable life, readers should consult Weems (1986), B. Heinrich (2007), and Collar (2009).

Although Gerd Heinrich's personal energy in the field surpassed indefatigable, the successes of his many expeditions owed as much to the abilities and equally unflagging dedication of his female companions. Prior to World War II, his wife Anneliese Machatchek and her younger sister Liselotte accompanied him to Sulawesi (1930–1932) and Myanmar (1937–1938), laboring as indispensable field assistants. After emigrating to the U.S. following World War II, Heinrich resumed fieldwork in Mexico (1952–1953) and those various countries of Sub-Saharan Africa (1953–1963), where he was joined by his second spouse Hildegarde (Hilde) Buruvna, who shared in all aspects of camp maintenance, data collection, and specimen preparation. Gerd Heinrich's efforts as mammal collector have been individually recognized for his earlier fieldwork in Sulawesi (*Hyosciurus heinrichi* Archbold and Tate, 1935; *Rattus penitus heinrichi* Tate and Archbold, 1935 [= *Bunomys andrewsi* J. A. Allen]) and Myanmar (*Callosciurus griseimanus heinrichi* Tate, 1954 [= *C. phayrei* Blyth]). Our specific patronym acknowledges both Gerd and Hilde and their complementary roles in generating these significant African collections. The species name *heinrichorum* thus combines the family surname Heinrich, a proper noun, and the Latin genitive plural suffix -orum.

Discussion

Taxonomic remarks. Had the Angolan form been described in the latter 1900s, a new subspecies would have been the preferred taxonomic rank to convey the subtle, nearly imperceptible differences in pelage color and cranial size that we document here. Indeed, Bishop in 1979 had named *anselli* as a third subspecies of *Praomys* (*Hylomyscus*) *denniae*, along with the nominate race and *vulcanorum*. Instead, *Hylomyscus* "*denniae*" sensu Allen (1939), Bishop (1979), and others (Honacki *et al*., 1982; Corbet & Hill, 1991; Musser & Carleton, 1993; Dieterlen, 2013) has been revealed as a composite construct, now partitioned into 7 species (Fig. 4), each endemic to a particular mountain system and apportioned between two species groups according to current understanding (Carleton & Stanley, 2005; Carleton *et al.*, 2006; Demos *et al.*, 2014b).

FIGURE 9. Gerd and Hildegarde (Hilde) Heinrich pictured in a camp setting labeled as Mount Moco. After emigrating to the U.S. following World War II, the couple undertook several prolonged collecting trips within North America and Africa, including the 1953–1955 expedition to Angola, during which the sample of *Hylomyscus heinrichorum*, new species, was procured. Hilde was cradling an orphaned monkey, while Gerd attended the final steps of specimen preparation. Photograph by anonymous; reproduced with permission of Bernd Heinrich.

The singular covariation patterns recovered for *Hylomyscus heinrichorum* in comparison with *H. anselli*, *H. arcimontensis*, and *H. kerbispeterhansi* (Figs. 1A, 2C, 3) assume significance in light of the genetic differentiation that has been recently documented between such cohesive craniodental morphologies. Evidence of genetic divergence consistent with specific distinctiveness generally has accompanied the demonstration of well delineated morphometric footprints for several genera of African murines (e.g., Kennis *et al.*, 2011; Nicolas *et al.*, 2005;

Verheyen *et al*., 2002, 2003, 2007), including among lowland species of the *Hylomyscus alleni* species group (Nicolas *et al*., 2008, 2010). Directly pertinent to our taxonomic subject is the recent study by Demos *et al.* (2014b), whose gene-sequencing results have supported the specific recognition of two members of the *H. anselli* group, *H. anselli* and *H. arcimontensis* as defined by Carleton & Stanley (2005), and justified the description of a third, *H. kerbispeterhansi*, from the Kenyan Highlands. Such findings reinforce the thesis developed by Voss and colleagues (Voss *et al*., 1990; Voss & Marcus, 1992), who demonstrated that covariation patterns commonly distilled from ordination of muroid craniodental measurements relate to underlying ontogenetic trajectories that account for such conserved patterns of size and shape and, by inference, to pronounced genetic divergence between the sampled populations. Of course, independent genetic evaluation of the specific status and relationship of *H. heinrichorum* is highly welcomed. In the meanwhile, we regard the morphological and morphometric evidence presented here as sufficient to advance a hypothesis of specific divergence of our Angolan samples, not intraspecific variation.

The number of species circumscribed by *Hylomyscus* totals 16, counting *H. heinrichorum* and other recently diagnosed species and taxa resurrected from synonymy (Carleton & Stanley, 2005; Carleton *et al*., 2006; Nicolas *et al*., 2008, 2010; Demos *et al*., 2014b). This total doubles the number recognized just 10 years ago (Musser & Carleton, 2005), and more species surely await description (e.g., see discussions or results in Carleton *et al*., 2006; Nicolas *et al*., 2010, 2012; Bryja *et al*., 2012). This body of research accordingly portrays the *Hylomyscus* clade as a modest radiation in Sub-Saharan Africa, second to *Praomys* Thomas among the genera of Praomyini (sensu Lecompte *et al*., 2008). Among the species complexes in *Hylomyscus*, the *H. anselli* group is noteworthy for the diversity so recently uncovered, given the prior acceptance of this variation as indicative of a single, widely ranging montane species, *H. denniae*, an errant view that prevailed over the 1900s and into the early 21st century (e.g., Musser & Carleton, 2005). Even with the advantage of hindsight, we find it remarkable that so morphometrically and genetically distinctive forms as *vulcanorum* Lönnberg & Gyldenstope (1925) and *anselli* Bishop (1979), as disclosed by recent studies (Carleton & Stanley, 2005; Carleton *et al*., 2006; Demos *et al*., 2014b), were actually named as subspecies. Over this era, nevertheless, the biological species concept exerted a pervasive influence over taxonomic description and revision, leading systematists to interpret slight but consistent interpopulation differences as worthy, at most, of subspecific recognition and effectively suppressing the appreciation of species diversity and levels of endemism.

Biogeographic perspectives. Mt Moco and/or Mt Soque, the localities where the Heinrichs obtained the samples of *Hylomyscus* herein described as a new species, have been specifically mentioned in many avifaunal studies as Angolan mountains that harbor vestiges of moist montane forest (Moreau, 1966; Dean, 2000; Mills *et al*., 2011). Angolan highlands were not initially included among the seven "islands" of Afromontane forest delineated by White, a phytogeographer who opined (1978: 480), "In Angola well-developed Afromontane vegetation is apparently absent." He (1978, 1981) did characterize certain taxa (*Ficalhoa*, *Myrsine*, *Podocarpus*) that occur in western Angola as Afromontane elements, but considered such populations or species as incidental outliers within plant formations otherwise composed of lowland floral elements. Recognition of the Angolan Highlands as an important biogeographic isolate of moist montane forest has coalesced from extensive syntheses of avian distribution and endemism, beginning with Moreau (1966) and continuing through the present (e.g., Diamond & Hamilton, 1980; Crowe & Crowe, 1982; Dowsett, 1986; Prigogine, 1987; Stuart *et al*., 1993; de Klerk *et al*., 2002; Fjeldså & Bowie, 2008). Within East African highlands, geographic hubs of avian diversity and endemism usefully mirror metrics of biodiversity in other vertebrate groups (Burgess *et al*., 2000; Brooks *et al*., 2001; Levinsky *et al.* 2013). Whether the presence of *H. heinrichorum* in westcentral Angola represents an as yet unappreciated guild of mammalian Afromontane endemics cannot be assessed in view of the coarse taxonomic and distributional understanding of so many small mammals that occur in the country. Crawford-Cabral (1986) stressed this point and discussed 11 of 42 nominal muroid species that needed taxonomic refinement before any meaningful biogeographic synthesis of Angolan mammals could be attempted; "*Praomys*" *carillus*, the only species of *Hylomyscus* he then recognized, was not included among those 11 problematic species-group taxa. Crawford-Cabral's own lifelong contributions, especially as summarized in his monograph (1998) on "The Angolan rodents of the Superfamily Muroidea," have substantially improved the taxonomic foundation needed to elevate biogeographic insights. Naturally, more basic systematic research of this kind is needed.

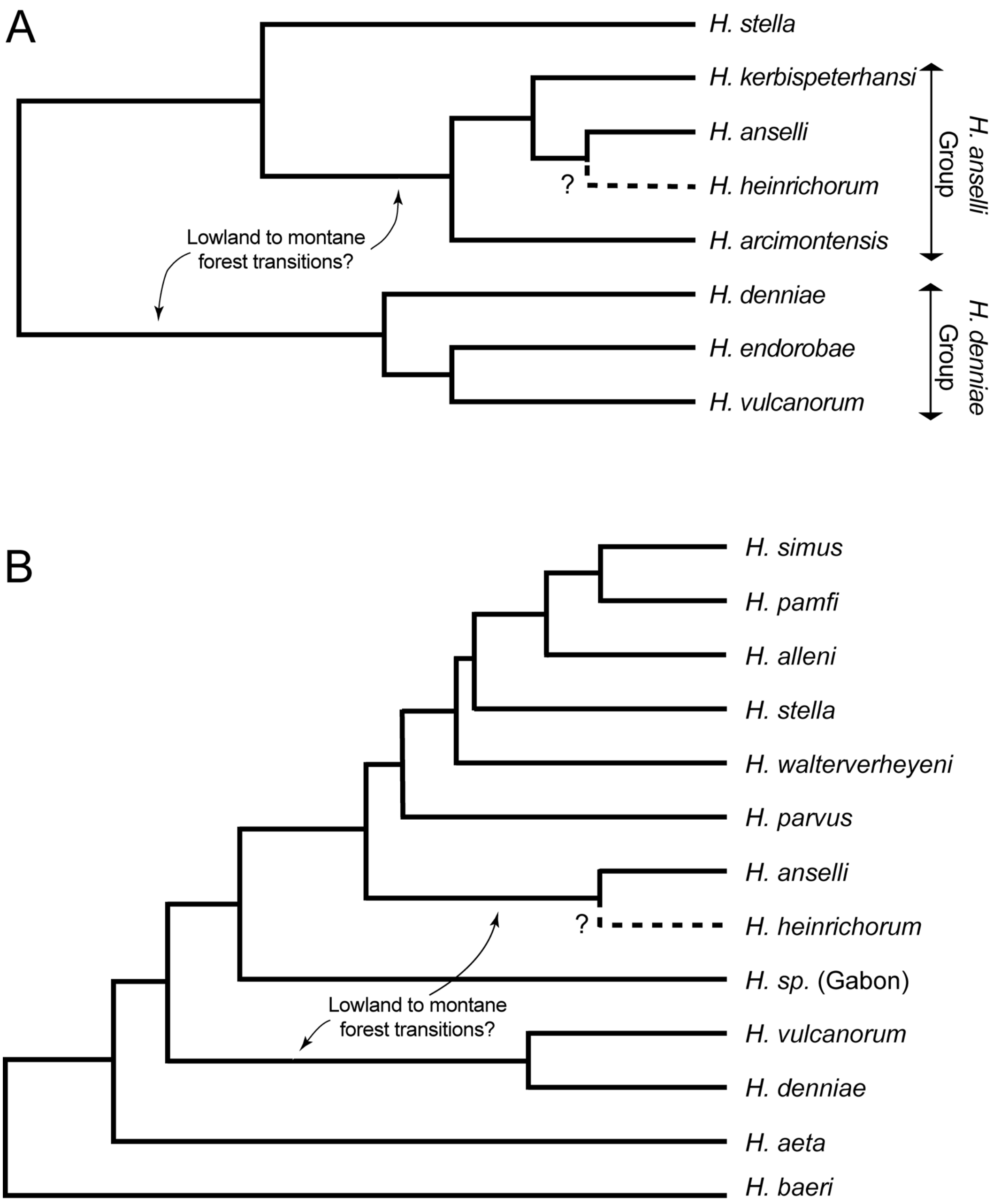

FIGURE 10. Cladograms of *Hylomyscus* species adapted from recent gene-sequencing results (terminal specimen branches collapsed to species recognized), with hypothesized relationship of *H. heinrichorum* indicated within the *H. anselli* species group. A) Multilocus gene tree reported by Demos *et al.* (2014b: Fig. 7). B) Maximum likelihood cytochrome-*b* tree (most indeterminate taxa pruned) reported by Bryja *et al.* (2012: Fig. 3c). Phylogenetic relationships depicted in both studies intimate the independent evolutionary transition of *Hylomyscus* into the Afromontane Biotic Zone from ancestral stocks distributed in Guineo-Congolian lowland rainforest.

The Afromontane Biotic Zone of Sub-Saharan Africa is by its nature highly fragmented, consisting of discontinuous mountain landscapes isolated by lowland rainforest and/or expansive savannas. White (1978, 1981) aptly characterized these patchily distributed mountain groups, each with their own crown of moist forest and stenotopic biota, as the "Afromontane archipelago." Seven physiographic groups are conventionally recognized within the region (we here use the terminology of Fjeldså & Bowie, 2008); the Angolan Highlands and Cameroon Highlands are the most isolated among these. Moreau (1966) noted that montane high forest in Angola is distantly removed from similar forest associations found elsewhere in Africa, separated by approximately 1900 km (1200 mi) from the Cameroon Highlands to the north and by approximately 1700 km (1050 mi) from the Albertine Rift upland forests to the east. Some 990 km (615 mi) of predominantly Miombo woodlands separate the localities of

Hylomyscus heinrichorum in westcentral Angola from the nearest records of *H. anselli* in northwestern Zambia (Fig. 4). No members of the *H. anselli* species group, or of the *H. denniae* species group, have been as yet documented from the Cameroon Highlands.

Many taxa in the Angolan Highlands are more closely related to species that occur in forested highlands far to the east—the Albertine Rift, Kenyan Highlands, and/or Eastern Arc Mts—instead of congeners that inhabit neighboring lowland forest. The comprehension of some historical link between the Angolan Highlands and these eastern mountains is supported not only by patterns of faunal similarity (White, 1981; Dowsett, 1986; Stuart *et al.*, 1993), but also by phylogeographic studies that integrate interspecific or intraspecific relationships and species distributions (Njabo *et al.*, 2008; Voelker *et al.*, 2010). Three observations invoke a similar biogeographic explanation for the derivation of *H. heinrichorum*: its close phenetic similarity to *H. anselli*; the latter's annectant distribution in mountains of northern Zambia and westcentral Tanzania (Fig. 4), to the south of the Congo forest block; and the phylogeographic logic whereby montane sister species have been demonstrated to occur on geographically approximate but spatially separated mountain systems (e.g., Voelker *et al.*, 2010). Those Zambian mountains where *H. anselli* occurs are not formally identified as part of the Afromontane biotic region sensu Moreau (1966) or White (1978). Miombo woodlands form the dominant arborescent cover over much of the country, and montane forest associated with the southern Albertine Rift is confined to extreme northeastern Zambia (Bryja *et al.*, 2012). Nonetheless, some Zambian mountain ranges do receive moderately high annual rainfall (≥ 1120 mm) and are sufficiently high to support submontane and montane forest. Populations of *Hylomyscus anselli* and *Praomys jacksoni* de Winton commonly co-occur in these forests (Ansell, 1978; Bryja *et al.*, 2012), and Ansell (1978: 82) considered the latter species to be "virtually confined to montane forest and forest edge."

The moist evergreen forests inhabited by members of the *Hylomyscus anselli* and *H. denniae* species groups are found in mountains that fringe the eastern and southern periphery of the Congo Basin and its expansive stands of lowland rainforest (Fig. 4). The *H. anselli* group ranges from the Kenyan Highlands (*H. kerbispeterhansi*), through the Eastern Arc Mountains (*H. arcimontensis*) and highlands in northern Zambia (*H. anselli*), to the remote Angolan Highlands (*H. heinrichorum*). The *H. denniae* group is more localized within East Africa, distributed in the Kenyan Highlands (*H. endorobae*) and Albertine Rift (*H. denniae* and *H. vulcanorum*). In spite of the resurgence of biotic surveys in Afromontane forest, no member of the *H. anselli* or *H. denniae* species group has been as yet documented from the high volcanoes in northern Tanzania—Mt Kilimanjaro, Mt Meru, and Ngorongoro Crater (Carleton & Stanley, 2005, 2012; Demos *et al.*, 2014b)—but this apparent biogeographic discontinuity warrants additional verification. As specific ranges are presently understood, both species groups are known to cohabit only the Kenyan Highlands (Fig. 4); their co-occurrence in these Highlands was long obscured by simple specimen misidentification (either as *endorobae* or as *denniae*; see Carleton *et al.*, 2006, and Demos *et al.*, 2014b, respectively).

Taxonomically and geographically synoptic ornithological investigations have highlighted these mountain groups for their high peaks of endemism and as "hotspots" of Plio/Pleistocene speciation (Fjeldså & Lovett, 1997; Roy *et al.*, 1997; de Klerk *et al.*, 2002; Fjeldså *et al.*, 2007; Fjeldså & Bowie, 2008). Comparable tallies of species richness and endemism have been recorded for small mammals in many of these same Afromontane regions (e.g., Brooks *et al.*, 2001; Carleton *et al.*, 2006; Plumptre *et al.*, 2007; Carleton & Stanley, 2012); in general, mammalian studies to date lack such a taxonomically robust phylogenetic foundation to illuminate deep versus shallow patterns of historical genesis. As one notable exception, Demos *et al.* (2014a, 2014b) placed the divergence between the *H. anselli* and *H. denniae* lineages within the late Miocene (ca. 7.4 mya) and estimated the cladogenesis among species of the *H. anselli* group to have transpired within the middle Pleistocene (ca. 1.84–0.83 mya).

Carleton *et al.* (2006: 317) questioned whether the *H. anselli* and *H. denniae* species groups shared a recent common ancestor or whether they independently radiated into highland forest settings from different Guineo-Congolian ancestral stocks. The presence of the two groups in the same biotic zone, distributed across more or less contiguous mountain systems, and their former classification as races of the single species *H. denniae* plausibly favor the former interpretation; nevertheless, recent gene-sequencing studies have yielded phylogenies that convincingly support the latter interpretation (Fig. 10). Independent radiation into Afromontane forest is equivocal based on the multilocus tree obtained by Demos *et al.* (2014b: Fig. 7) because only a single lowland species (*H. stella*) was included. However, the denser geographic and taxonomic sampling used to generate the cytochome-*b* phylogeny reported by Bryja *et al.* (2012: Fig. 3c) represented all six species groups, as provisionally defined by Carleton *et al.* (2006), and four of these (*aeta*, *alleni*, *baeri*, and *parvus*) are principally distributed within sectors of lowland rainforest in West and Central Africa. Interspecific relationships depicted in this tree parsimoniously argue for at least two evolutionary dispersions into Afromontane forest from Guineo-Congolian progenitors (Fig. 10B). *Hylomyscus grandis* Eisentraut, described from Mount Oku, Cameroon, at 2100 m and considered an inhabitant of montane forest (e.g., Hutterer, 2013), may represent a third evolutionary instance of lowland to montane forest transition within the genus, in this case presumably involving the *H. aeta* species group (the relationships of *H. grandis* invite reevaluation). That such broad-scale ecological parallelism may have accompanied cladogenesis within *Hylomyscus* is hardly unusual; for example, montane distributions among African forest robins (*Sheppardia* Haagner) are inferred to have evolved four times from ancestors that occur in lowland forest habitats (Voelker *et al*., 2010).

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APPENDIX

Listed below are adult specimens of *Hylomyscus anselli*, *H. arcimontensis*, and *H. kerbispeterhansi* used to conduct morphological comparisons, compute sample statistics (Table 6), and perform morphometric analyses (Figs. 1–3). Localities are listed only to mountain system or reserve name for *H. arcimontensis*; full locality data and geographic coordinates are provided in Carleton & Stanley (2005).

Hylomyscus anselli. Tanzania: Rukwa Region, Mbizi Mts, Mbizi FR, 2200 m (FMNH 171358, 171359, 171364, 171367) and 2300 m (FMNH 171342, 171345, 171346, 171349, 171350, 171352–171354). Zambia: Mpika District, Danger Hill, Luitikila Stream (BMNH 73.142); Mwinilunga District, Sakeji Stream (BMNH 61.944); Solunezi District, Nyansule Stream (BMNH 74.251).

Hylomyscus arcimontensis. All OTUs fromTanzania.

(OTU 1) Kilimanjaro Region, South Pare Mts, Chome FR, 1100 m (FMNH 151253) and 2000 m (FMNH 153946, 153947, 153949–153951).

(OTU 2) Tanga Region, Korogwe District, West Usambara Mts, 1250 m (FMNH 147278–147280, 147282–147284, 147286–147288) and 1300 m (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).

(OTU 3) Tanga Region, Muheza District, East Usambara Mts, 900 m (FMNH 150121–150124, 150140–150142, 150144–150146, 150148–150150, 150152, 150153, 150433, 151248, 151250–151252) and 1100 m (FMNH 147290, 147291, 150118, 150119, 150139).

(OTU 4) Tanga Region, Handeni District, Nguu Mts, Nguru North FR, 1180 m (FMNH 168175) and 1430 m (FMNH 168176); Morogoro Region, Morogoro District, Nguru Mts, Manyangu FR, 1000 m (FMNH 161270, 161271); Morogoro Region, Morogoro District, Nguru Mts, Nguru South FR, 1500 m (FMNH 161272).

(OTU 5) Morogoro Region, Kilosa District, Ukaguru Mts, Mamiwa-Kisara FR, 1840 m (FMNH 166923–166925) and 1900 m (FMNH 166916–166922).

(OTU 6) Morogoro Region, Morogoro District, Uluguru Mts, Uluguru North FR, 1345 m (FMNH 158343–158353, 158495, 158500, 158573) and 1535 m (FMNH 158355, 158505).

(OTU 7) Morogoro Region, Kilombero District, Udzungwa Mts, Udzungwa Scarp FR, 910 m (FMNH 155555–155563), 1460 m (FMNH 155390, 155564–155570), and 2000 m (FMNH 155392, 155571–155573).

(OTU 8) Mbeya Region, Rungwe District, Mt Rungwe, Rungwe FR, 1870 m (FMNH 163584–163593), 2140 m (FMNH 163594–163597), and 2410 m (FMNH 163598–163600).

Hylomyscus kerbispeterhansi. Kenya, Guas Ngishu Plateau, 30 mi N Pain (USNM 163349); Rift Valley, Nakuru District, 4 mi E Molo (USNM 437428, 437468); Mt Elgon NP, Chepnyali Waterfall, 6 km from Chorlim Gate (USNM 589874, 589879, 579880); Mt Elgon NP, 5 km from Chorlim Gate (USNM 589876); Mt Elgon NP, 15 km from Chorlim Gate, towards Koitobos Peak (USNM 589881).