Research article

Four new species of the *Hylomyscus anselli* group (Mammalia: Rodentia: Muridae) from the Democratic Republic of Congo and Tanzania

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Abstract. As in many other small mammal groups from the Afrotropics, the number of species recognized within the genus *Hylomyscus* has increased considerably over the past dozen years. The last comprehensive review (2005) of the genus recognized eight species. Since that time, nine additional species have been elevated from synonymy (n = 4) or described as new (n = 5). Here we describe four additional new species supported by morphological and molecular evidence, all collected by the late William Stanley. Two of the new taxa are sympatric and come from the poorly known left bank (direction source to mouth) of the Congo River. One of these (*Hylomyscus pygmaeus* sp. nov.) is easily recognized, as it is tiny and significantly smaller than any known species of the genus; the second new species (*Hylomyscus thornesmithae* sp. nov.) is also small, and syntopic with the first. The third new species (*Hylomyscus stanleyi* sp. nov.), from the SW corner of Tanzania, is quite large and had been previously included within the hypodigm of *Hylomyscus anselli* following its recognition from within the synonymy of *Hylomyscus denniae*. The fourth species (*Hylomyscus mpungamachagorum* sp. nov.) is from Mahale Mountains National Park, western Tanzania. Our study reveals a much higher species diversity of the genus than previously known, providing insights into additional Afrotropical and Afromontane centers of endemism that require further exploration.

Key words. Afrotropics, biodiversity, endemism, Murinae, molecular phylogeny, systematics, alpha-taxonomy, biogeography.

INTRODUCTION

Members of the genus *Hylomyscus* (wood mice) are widespread in the forests of sub-Saharan Africa, north of the Zambezi River. They are small (15–35 g), with tails longer than head and body and have skulls with a short upper tooth row and narrow zygomatic plates. Their short broad feet suggested to their describer that they were more arboreal than their relatives in the genus *Praomys* from which they were split (Thomas 1926). In 2005, Musser and Carleton recognized eight species within the genus: *Hylomyscus aeta* (Thomas, 1911); *H. alleni* (Waterhouse, 1838); *H. baeri* Heim de Balsac & Aellen, 1965; *H. carillus* (Thomas, 1904); *H. denniae* (Thomas, 1906); *H. grandis* Eisentraut, 1969; *H. parvus* Brosset et al. 1965; and *H. stella* (Thomas, 1911). Within one year, this

total increased to 12 (Carleton et al. 2006) with the description of *H. arcimontensis* Carleton & Stanley, 2005; and the elevation from synonymy of *H. anselli* (Bishop, 1979)*, H. vulcanorum* (Lönnberg & Gyldenstolpe, 1925), and *H. endorobae* (Heller, 1910). Since that time, one additional species has been elevated from synonymy (*H. simus* Allen & Coolidge, 1930) and four have been described as new: *H. heinrichorum* Carleton et al., 2015, *H. kerbispeterhansi* Demos et al., 2014, *H. pamfi* Nicolas et al., 2010 and *H. walterverheyeni* Nicolas et al., 2008, bringing the total to 17. Carleton et al. (2006), using phenetic characters, proposed six species groups within the genus ('*H. aeta*', '*H. alleni*', '*H. anselli*', '*H. baeri*', '*H. denniae*', and '*H. parvus*' groups). Eight characters were used to define the '*H. anselli*' group, four of which distinguished it from the '*H. denniae*' group with which it had been previously lumped: six mammae (instead of eight), shorter rostrum, shorter incisive foramina and a medium-sized subsquamosal foramen (compared to a tiny or absent subsquamosal foramen). Two species of the '*H. anselli*' group (*H. anselli* and *H. arcimontensis*) and three of the '*H. denniae*' group (*H. denniae, H. vulcanorum* and *H. endorobae*) were recognized at that time.

Today, the '*H. denniae*' group is restricted to the montane highlands of the Albertine Rift and the Kenya Highlands whereas the '*H. anselli*' group is distributed from the Kenya Highlands through the Eastern Arc and Southern Highlands of Tanzania (and northernmost Malawi), into the gallery forests of northern Zambia and the highland plateau of Angola. The other four species groups are confined to the tropical regions of the continent. Here we redefine this geographic pattern by describing four new species of the '*H. anselli*' group from a previously undocumented area of the Congo Basin and two isolated forests in western Tanzania.

MATERIAL AND METHODS

Specimens, morphology, morphometrics, collecting

Specimens are from the Field Museum of Natural History, Chicago (FMNH), National Museum of Zambia, Livingstone (NMZ) and British Museum Natural History, London (BMNH). Additional Zambian and Angolan records use the initials from their collectors (RS, R Sumbera) or country of origin (ANG, Angola) and are deposited in the Faculty of Sciences, University of South Bohemia (USB) in České Budějovice (carcasses) and in the Institute of Vertebrate Biology (IVB) of the Czech Academy of Sciences, Studenec (tissues and skulls), both in the Czech Republic. Field measurements, in millimeters, include: Total Length (TL), Tail vertebrae (TV), Hind foot length (HF), Ear length (EL), Weight (Wt, in grams); subtraction of TV from TL provides the head-and-body length (HB) unless measured separately in the

field. All external measurements were taken from original field data by respective collectors. Only two specimens of *H. heinrichorum* have weight recorded (both ANG). Length of hind foot includes the claw. Hind foot measurements of *Hylomyscus heinrichorum* from Angola and all *Hylomyscus anselli* from Zambia specified 'su' (sans unguinal). Accordingly, 1.0 mm was added to HF for missing claw length measurements. We employed the following 16 cranial measurements in millimeters (Carleton & Van der Straeten 1997): occipito-nasal length (ONL), condyle-incisive length (CI), greatest zygomatic breadth (ZB), breadth of the braincase measured across the parietal flanges behind the zygomatic arches (BBC), breadth across the occipital condyles (BOC), least interorbital breadth (IOB), length of nasals (LN), breadth of the rostrum (BR), post-palatal length (PPL), length of the bony palate (LBP), length of the incisive foramen (LIF), length of upper diastema (LD), breadth of the zygomatic plate (BZP), length of the auditory bulla, oblique to tooth row (LAB), coronal (rather than alveolar) length of the maxillary toothrow (CLM), and width of the first upper molar (WM1). We define rostral length as length of nasals divided by occipito-nasal length (LN/ONL). In order to estimate relative age and ontogenetic growth, we adopt dental wear stages from Verheyen & Bracke (1966). Specimens were measured and weighed, and either prepared as skins and skeletons or fixed in formalin and later transferred to 70% ethanol, and deposited at FMNH or USB. DRC refers to the Democratic Republic of Congo and TZ refers to Tanzania. An aliquot of tissue was taken from the specimen at the time of capture and preserved in ETOH until it was transferred to cryogenic storage at -180 °C at FMNH.

Principal components analysis (PCA) of 16 log-transformed cranio-dental variables based on a variance-covariance matrix was used to assess morphometric variation and visualize the morphometric distinctiveness of named and putative species for an eight species data set (159 specimens: *H. anselli*, *H. arcimontensis*, *H. heinrichorum*, *H. kerbispeterhansi*, *H.* sp. nov. 1 (pygmy *Hylomyscus* from DRC), *H.* sp. nov. 2 (small *Hylomyscus* from DRC), *H.* sp. nov. 3 (Mbizi *Hylomyscus* from Tanzania), *H.* sp. nov. 4 (Mahale *Hylomyscus* from Tanzania) and a four species data set (136 specimens: *H. arcimontensis*, *H. kerbispeterhansi*, *H.* sp. nov. 3 (Mbizi *Hylomyscus* from Tanzania) and *H.* sp. nov. 4 (Mahale *Hylomyscus* from Tanzania). Standard summary statistics were calculated from univariate measurements for 16 cranio-dental and six external characters. All statistical analyses were performed using the software PAST (Hammer et al. 2001).

Permission for the collection and export of specimens was provided by the Republic of Tanzania and the Democratic Republic of Congo. Approval for the import of specimens into the USA was provided by the US Fish and Wildlife Service. Relevant documents pertaining to

export and import are housed at FMNH under the following Accession Numbers: Z-20745, Z-20738, Z-19855, Z-19599. All euthanized specimens followed the protocol approved by the American Society of Mammalogists (Sikes et al. 2011). The study was approved by the Field Museum of Natural History Institutional Animal Care and Use Committee (09-3).

DNA extraction, amplification, and sequencing

Whole genomic DNA was extracted from tissue samples of *H. aeta* (n = 1, Uganda), *H. stella* (n = 1, Uganda), *H. heinrichorum* (n = 4, Angola), *H.* sp. nov. 1 (pygmy *Hylomyscus* from DRC, n = 1), *H.* sp. nov. 2 (small *Hylomyscus* from DRC, n = 5), *H.* sp. nov. 3 (Mbizi *Hylomyscus* from Tanzania, n = 5), *H.* sp. nov. 4 (Mahale Hylomyscus from Tanzania, n = 3) using the QIAGEN DNeasy Blood and Tissue Kit (Germantown, MD). An additional 34 *Hylomyscus* cytochrome-*b* (*Cytb*) sequences were downloaded from GenBank (Appendix 2). *Mastomys natalensis*, a close relative of *Hylomyscus* (Steppan & Schenk 2017), was chosen as an outgroup using a *Cytb* sequence downloaded from GenBank. In total, sequence data was generated or downloaded from GenBank for 16 of 18 currently recognized species (Mammal Diversity Database 2019) from all six *Hylomyscus* species groups. Frozen tissues and GenBank accessions were unavailable for *H. carillus* (Angola). Specimens were sequenced for *Cytb* using the primers L14723 and H159125 (Lecompte et al. 2002). PCR amplification was performed on 25 µL reactions using the following thermal conditions: an initial denaturation step at 94 °C for 3 min, followed by 38 cycles consisting of 30 s at 94 °C, 30 s at 50 °C, and 1 min at 68 °C, followed by a final extension step of 5 min at 68 °C. Amplified PCR products were purified using ExoSAP-IT (Thermo Scientific, MA, USA). Sequencing was carried out in both directions on an ABI 3100 thermocycler (Applied Biosystems, CA, USA) at the Pritzker Laboratory for Molecular Systematics and Evolution (FMNH). Chromatographs were checked manually and assembled and edited using Geneious 11.1.5 (Biomatters Ltd.). Sequences were aligned for *Cytb* using MUSCLE Alignment within the Geneious platform with default parameters. Sequence data from *Cytb* were translated into amino acids and the alignment was inspected for deletions, insertions, and premature stop codons to exclude possible nuclear pseudogenes.

Molecular data and phylogenetic analyses

The best supported model of nucleotide substitution for *Cytb* was determined using the BIC on the maximum likelihood topology inferred in jMODELTEST2 v.2.1.6 (Darriba et al. 2012) on CIPRES Science Gateway v.3.3 (Miller et al. 2010). Interspecific uncorrected sequence divergences (*p*-distances) were calculated in MEGA 7.0.26 (Kumar et al. 2016). Maximum likelihood inference of a *Cytb* gene tree was made using the program IQ-TREE v1.6.10 (Nguyen et al. 2015) on the CIPRES portal. We conducted analyses using the best-scoring ML tree search algorithm under the GTR+I+G model with 1,000 bootstrap replicates. Bayesian gene tree analyses were carried out using MRBAYES v.3.2.6 (Ronquist et al. 2012) on the CIPRES portal to infer a *Cytb* gene tree. Two replicates were run to facilitate proper mixing. Four Markov chains with default heating values were conducted for 10,000,000 generations and sampled every 1,000th generation. Stationarity of the MCMC chain was assessed using TRACER v.1.7.1 (Rambaut et al. 2018). The first 2,500 samples were discarded as burn-in and the remaining 7500 samples comprised the posterior probability (PP) distributions. A majority rule consensus tree was generated from the analysis. All newly generated sequences were deposited in GenBank with accession numbers MN857618–MN857637 (Appendix 2). We use these gene tree analyses to test the concordance of species limits inferred using morphological data with clades supported by genetic data, estimate support for monophyly of recognized and putative species, and assess phylogenetic relationships among them.

RESULTS

The specimens from the Congo basin (DRC) were clearly undescribed members of the *H. anselli* clade based on their morphological characters: short feet, teat formula (2+4 for *Hylomyscus* sp. nov., small *Hylomyscus*), short incisive foramen, thin stapedial strap and medium-size subsquamosal foramen. Their small size confirmed their unique status within the *H. anselli* clade. Subsequent genetic analyses were instrumental in revealing the existence of the two cryptic Tanzanian species.

Morphometrics

Two principal component analyses were performed on 16 log-transformed cranio-dental variables. The first included all eight putative species of the *H. anselli* group (Fig. 1); the second (Fig. 2) included those four species found east of the Albertine Rift Valley (Fig. 3). In the eight species PCA (Fig. 1), the small-sized Congo Basin taxa (*H.* sp. nov. 1, pygmy *Hylomyscus* from DRC and *H.* sp. nov. 2 (small *Hylomyscus* from DRC) are distinguished from all other species in the *H. anselli* group along the first axis and will not be discussed further. The Angolan taxon (*H. heinrichorum*) is distinguished along the second axis from the Zambian taxon (*H. anselli*).

In the four species PCA (Fig. 2), *H. kerbispeterhansi* and *Hylomyscus* sp. nov. 3 (Mbizi *Hylomyscus* from Tanzania) are readily distinguished along the second axis. *Hylomyscus* sp. nov. 3 (Mbizi *Hylomyscus* from
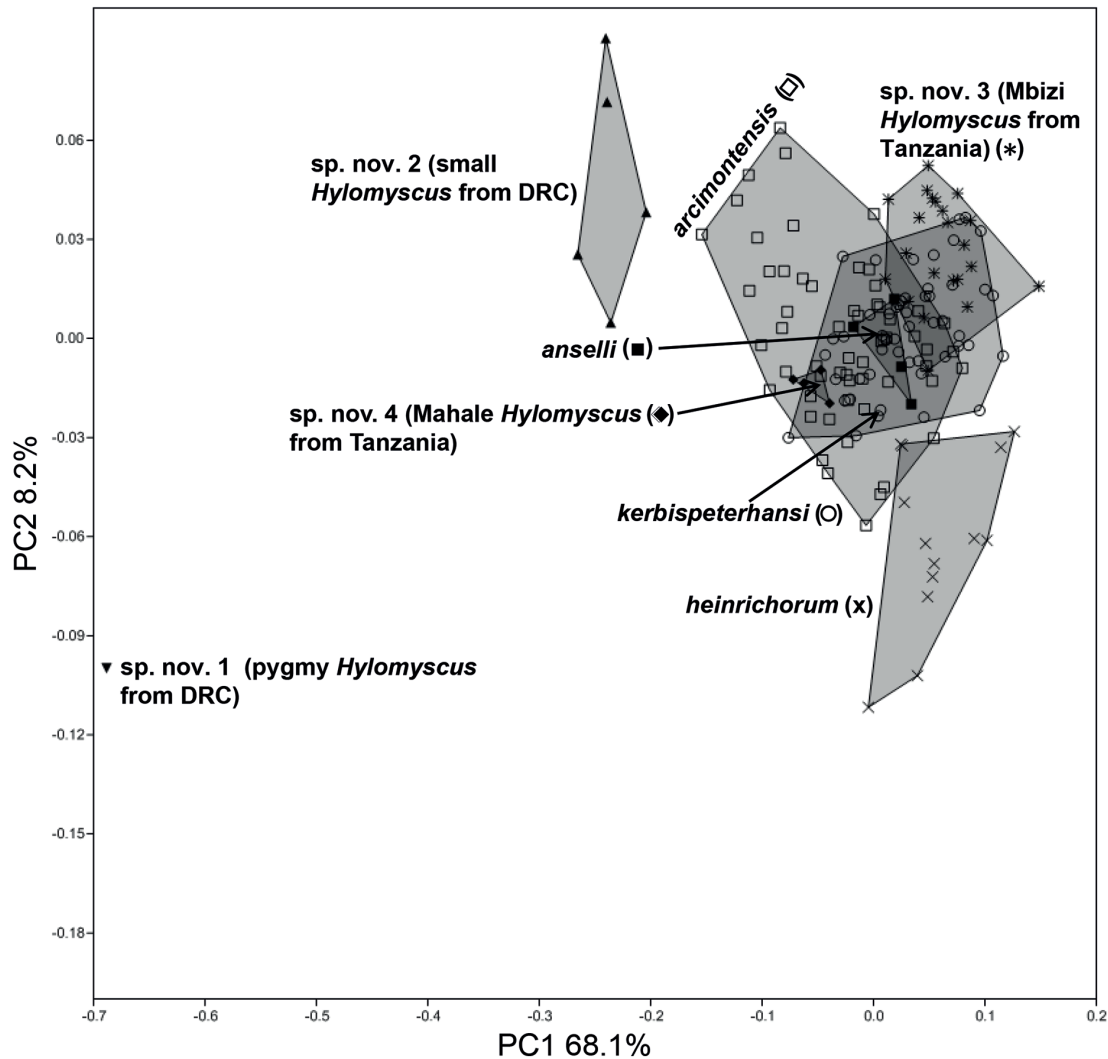
Fig. 1. Principle component analysis of cranial measurements of all eight members of the *Hylomyscus anselli* group.

Tanzania) has only modest overlap along the 1st and 2nd axes with *H. arcimontensis*, but *H. kerbispeterhansi* and *H. arcimontensis* show overlap along both principle components. *Hylomyscus* sp. nov. 4 (Mahale *Hylomyscus* from Tanzania) does overlap with *H. arcimontensis* in PCA multivariate space (Fig. 2) but they are allopatric and occupy different biogeographic regions: *Hylomyscus arcimontensis* is confined to the Eastern Arc montane archipelago while *Hylomyscus* sp. nov. 4 (Mahale *Hylomyscus* from Tanzania) is known only from the Albertine Rift; see Fig. 3).

In the eight species PCA, the first two principle components accounted for 76% of the cumulative variance (Table 1). The major contributing variables on PC1 were all correlated with the length of the rostrum: length of incisive foramen (LIF), length of nasals (LN) and length of

diastema (LD). On PC2 the major contributing variables were breadth of zygomatic plate (BZP), length of nasals (LN), and length of bony palate (LBP). In the four species PCA the first two principle components accounted for 64% of the cumulative variance (Table 2). The major contributing variables on PC1 were identical to PC1 on the eight species PCA: length of diastema (LD), length of incisive foramen (LIF) and length of nasals (LN). On PC2, the most important variables were breadth of zygomatic plate (BZP), length of bony palate (LBP) and crown length of molars (CLM).

Genetic analyses

The mtDNA gene tree (Fig. 4) supports the monophyly of the *Hylomyscus anselli* group minus *H.* sp. nov. 1

Table 1. PCA loadings from all eight members of the *Hylomyscus anselli* group.

Variable	Correlations	
	PC1	PC2
ONL	0.240	0.106
CI	0.253	0.095
ZB	0.192	0.102
BBC	0.138	0.040
BOC	0.143	-0.096
IO	0.152	-0.094
LN	0.359	0.427
BR	0.209	0.183
PPL	0.212	0.089
LBP	0.208	0.359
LIF	0.381	-0.220
LD	0.302	0.196
BZP	0.281	-0.636
LAB	0.234	-0.015
CLM	0.277	-0.208
WM1	0.267	-0.251
Cumulative % variance	68.1	76.3
Eigenvalue	0.0081	0.0010

Table 2. PCA loadings from four members of the *Hylomyscus anselli* group found east of the Albertine Rift.

Variable	Correlations	
	PC1	PC2
ONL	0.231	0.102
CI	0.267	-0.027
ZB	0.211	0.037
BBC	0.155	0.107
BOC	0.146	-0.006
IO	0.160	0.216
LN	0.314	0.327
BR	0.278	-0.131
PPL	0.260	0.044
LBP	0.208	0.392
LIF	0.325	-0.229
LD	0.340	-0.222
BZP	0.280	-0.546
LAB	0.298	-0.209
CLM	0.215	0.375
WM1	0.197	0.258
Cumulative % variance	52.6	64.3
Eigenvalue	0.0034	0.0008

(pygmy *Hylomyscus* from DRC; bootstrap [BS] = 99, posterior probability [PP] = 1.0). The new species, *Hylomyscus* sp. nov. 1 (pygmy *Hylomyscus* from DRC) from the western Congo basin, is highly divergent from other *H. anselli* group species (10.9–12.1% *Cytb* p-distance), and moderately well supported as sister to all other *H. anselli* group members (BS = 82, PP = 0.96). The new species *Hylomyscus* sp. nov. 2 (small *Hylomyscus* from DRC), *H.* sp. nov. 3 (Mbizi *Hylomyscus* from Tanzania) and *H.* sp. nov. 4 (Mahale *Hylomyscus* from Tanzania) are well supported clades (bootstrap = 100, posterior probability = 1.0). Carleton and Stanley (2005) and Carleton et al. (2006, 2015) assigned specimens from the Mbizi Mountains, Tanzania, to *H. anselli* based on similar phenetics and geographical proximity. However, our PCA (Fig. 1) shows little overlap between *H. anselli* and *H.* sp. nov. 3 (Mbizi *Hylomyscus* from Tanzania), although we had access to only four members of *H. anselli*. Further, our newly available genetic data indicate that this assignment was incorrect. The Mbizi *Hylomyscus* population is now assigned to distantly related *H.* sp. nov. 3 (Mbizi *Hylomyscus* from Tanzania, Fig. 4), illustrating how 'cryptic' these species are. *H. anselli* and *H.* sp. nov. 3 (Mbizi *Hylomyscus* from Tanzania) are not even sister; the genetic distance between them is 8.2% at *Cytb* (Table 3). *Hylomyscus* sp. nov. 3 (Mbizi *Hylomyscus* from Tanzania) + *H.* sp. nov. 4 (Mahale *Hylomyscus*

from Tanzania) + *H. kerbispeterhansi* form a distinct and highly supported East African clade (BS = 82, PP = 0.96) distributed in montane habitats in Kenya and Tanzania. These species exhibit allopatric distributions within the *H. anselli* group, although *H. kerbispeterhansi* is sympatric with *H. endorobae* (*H. denniae* group) on the Mau Escarpment in west-central Kenya (see Demos et al. 2014a, b; 2015). The relationship of *H. arcimontensis* from Tanzania is weakly supported (BS = 79, PP = 0.87) as sister to the aforementioned three East African *H. anselli* group species. *Hylomyscus* sp. nov. 2 (small *Hylomyscus* from DRC), also from the western Congo Basin, is strongly supported (BS = 92, PP = 1.0) as sister to the geographically distant and disjunct East African *H. anselli* group clade. *Hylomyscus anselli*, now restricted to Zambia on the basis of data from this study, is strongly supported (BS = 100, PP = 1.0) as sister to *H. heinrichorum* from Angola, and this clade (*H. anselli* + *H. heinrichorum*) is strongly supported (BS = 99, PP = 1.0) as sister to a clade that includes representatives of the *H. anselli* group from both East Africa and the western Congo Basin.

New taxa

All four new species (*Hylomyscus* sp. nov. 1, sp. nov. 2, sp. nov. 3, sp. nov. 4) described here nest within the *H. anselli* group. Of the characters suggested to define the *H.*
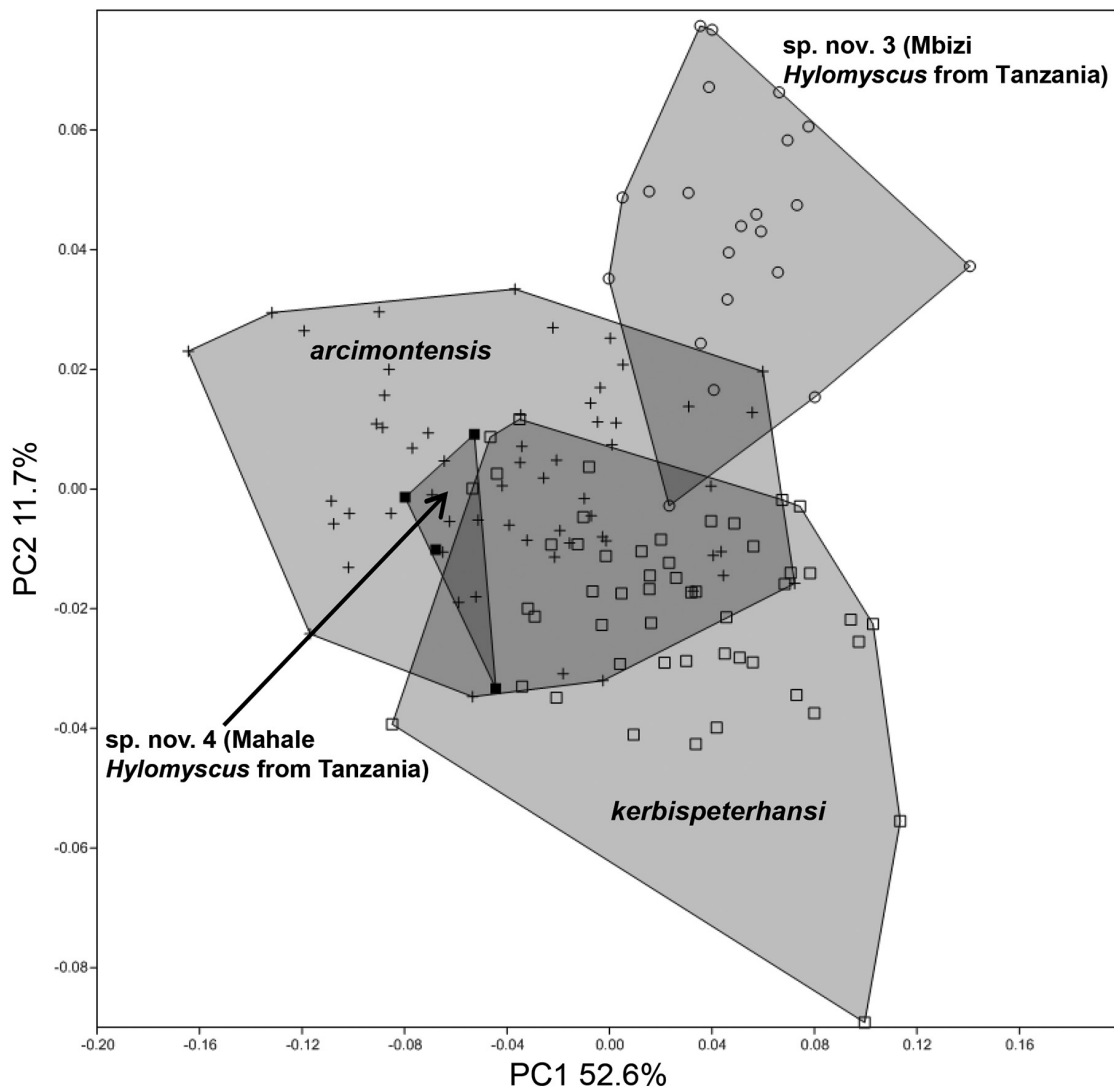
Fig. 2. Principle component analysis of cranial measurements of the four members of the *Hylomyscus anselli* group found east of the Albertine Rift.

anselli group (Carleton et al. 2006), the most reliable include abbreviated incisive foramina, the absence of pectoral mammae (total mammae = 2+4) and the thin, elongate hamular process providing for enlarged sub-squamosal foramina (discussed and illustrated in Carleton & Stanley 2005: fig. 6). These characters distinguish the *H. anselli* group from the *H. denniae* group, the only two groups with montane representatives to the east and south of the Congo Basin. All of the four new taxa described below possess these three characters; however, in *Hylomyscus pygmaeus* sp. nov. (pygmy *Hylomyscus* from DRC), teats are not visible, as the specimen is young.

***Hylomyscus pygmaeus* sp. nov.** Kerbis Peterhans, Hutterer & Demos
Dendromus sp. – Doty et al. (2017)

Holotype. Field Museum of Natural History, Division of Mammals number FMNH 219684 (field number WT Stanley 11,575; CDC 207), collected by W.T. Stanley, 13 June 2012 (listed in field notes as *Dendromus* sp.) during the first small mammal survey in the area. The specimen, consisting of a study skin and skull with carcass in alcohol, is a young adult female with first upper molar in early wear (stage IV of Verheyen & Bracke 1966). The basisphenoid-occipital suture is unfused. External mea-

Table 3. Uncorrected cytochrome-*b* *p*-distances (%) within (bolded numbers on diagonal) and between *Hylomyscus anselli* group species, calculated in MEGA 7.0.26 (Kumar et al. 2016).

Taxon	1	2	3	4	5	6	7	8
1 *anselli*	**1.1**							
2 *arcimontensis*	8.1	**1.5**						
3 *mpungamachagorum* sp. nov.	8.2	6.0	**0.0**					
4 *heinrichorum*	4.4	7.9	8.4	**0.3**				
5 *kerbispeterhansi*	8.1	6.6	4.7	8.0	**0.0**			
6 *stanleyi* sp. nov.	8.2	6.3	4.9	9.3	3.2	**0.0**		
7 *thornesmithae* sp. nov.	8.6	6.6	6.6	8.3	6.9	6.4	**0.0**	
8 *pygmaeus* sp. nov.	11.1	10.9	10.9	10.9	10.8	11.5	12.1	**na**
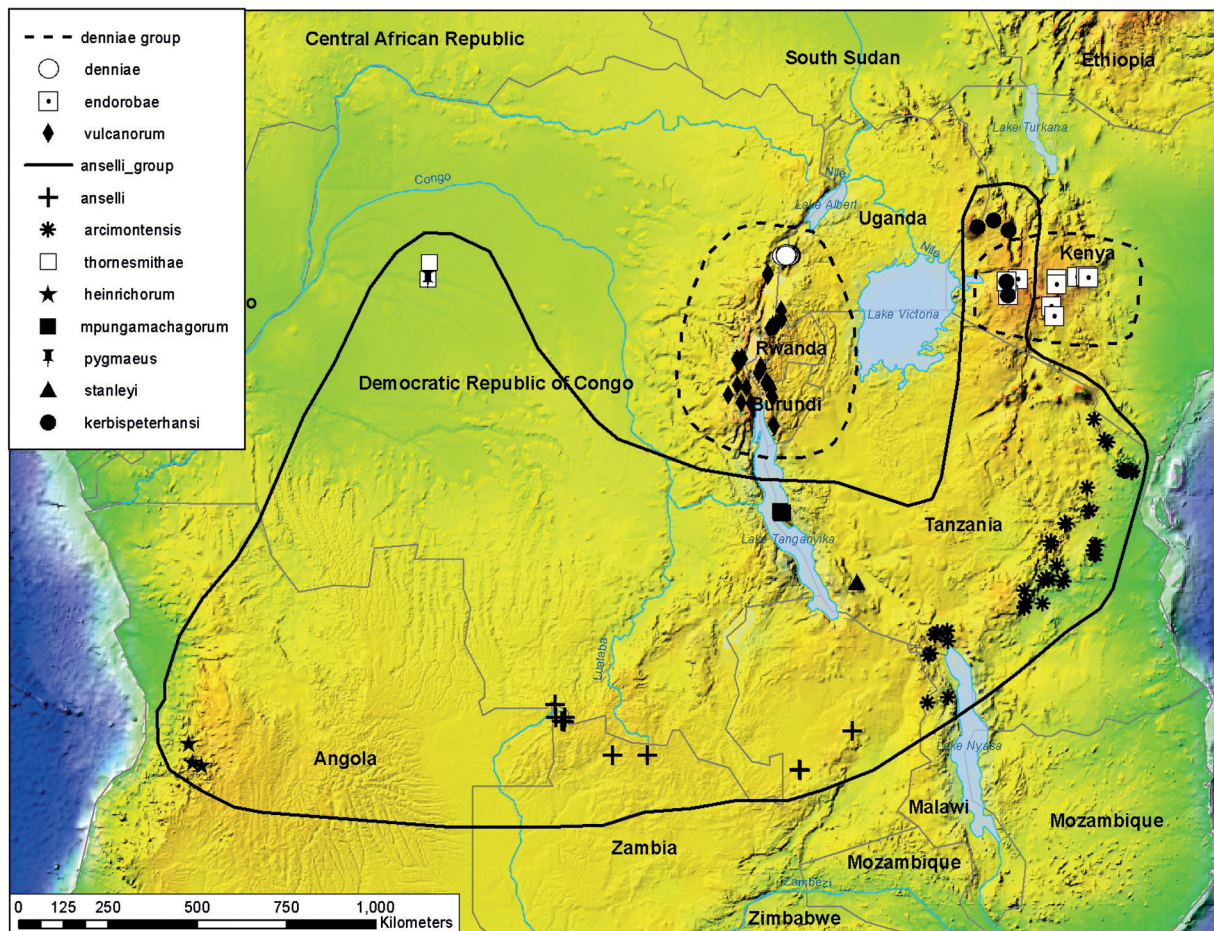
Fig. 3. Map of the distributions of members of the *Hylomyscus denniae* and *Hylomyscus anselli* groups.

surements were made in the field: TL 132, TV 76, HF 14, EL 12, Wt 5.8. Specimen caught in a pitfall trap (PF 4, Bucket 10).

Type locality. Democratic Republic of Congo, Tshuapa Province, 4 km N of Boende, Baliko (0.24127 S, 20.8833 E), right side Tshuapa River, elevation of 358 m.
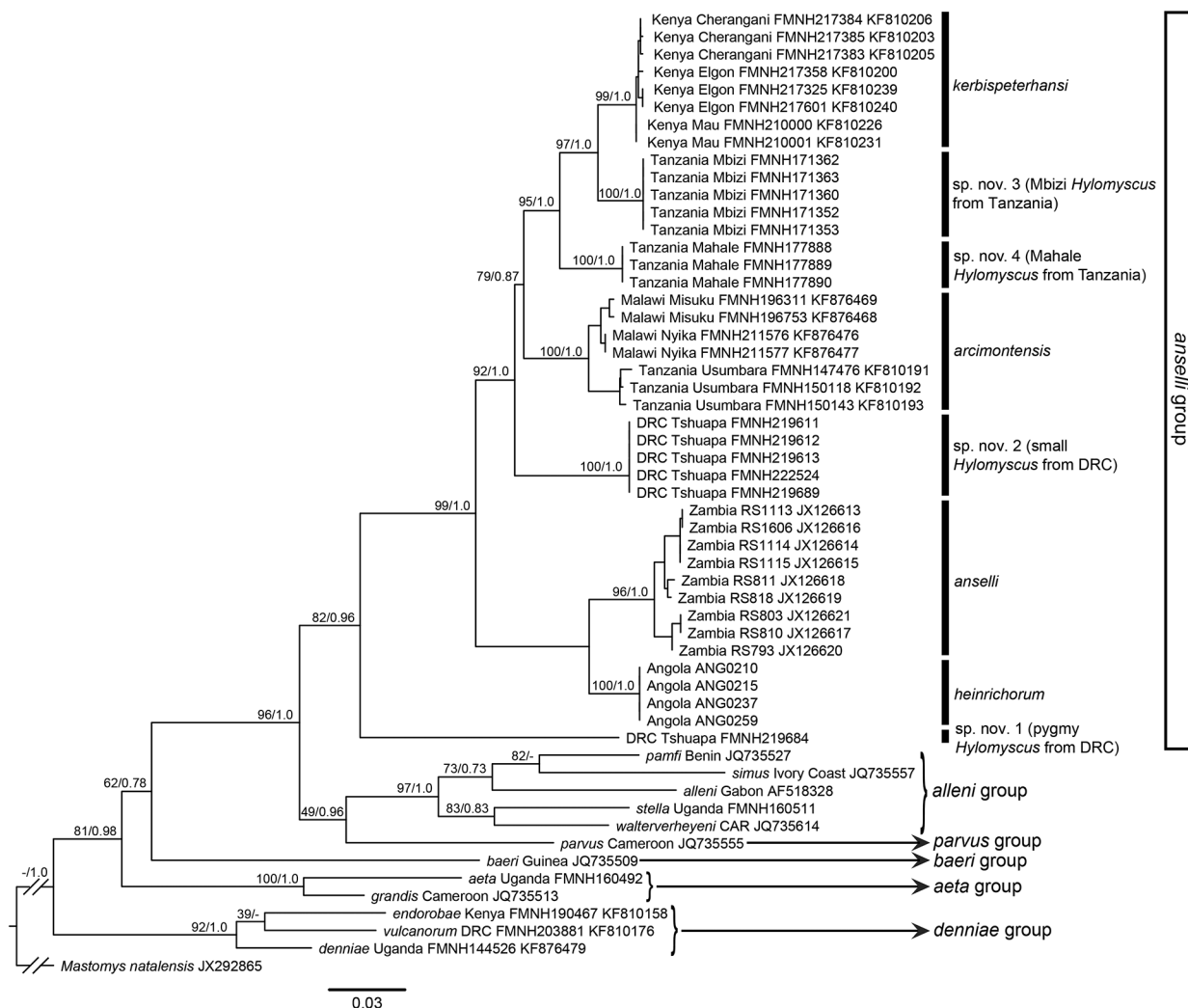
Fig 4. Phylogenetic tree, using cytochrome-*b*, of the genus *Hylomyscus* with focus on the *Hylomyscus anselli* group. Bootstrap values for maximum likelihood analysis followed by posterior probabilities for Bayesian analysis are indicated above branches.

Diagnosis. Easily recognized by its small size: HB 56, Wt 5.8, CI 15.9, CLM 2.6, WM1 0.8. All are significantly smaller than any other members of the *H. anselli* group (Figs 5a, c, 6a, c, e; Tables 4–5), or, for that matter, any member of *Hylomyscus*. Ears exceptionally long (Fig. 5c), 23% of HB. Incisors slightly pro-odont (Fig. 6e). Braincase inflated, round and bulbous (Figs 6a, e). Rostrum extremely short (Fig. 6a, LN/ONL = 26.7%).

Comparisons. This species is by far the smallest member of the *Hylomyscus anselli* group as reflected in Tables 4–5: e.g., crown length of upper molars 2.6, compared to 3.0–4.5; HB 56, compared to 76–109 for other members of the group.

Description. Size very small (HB 56, mass 5.8). Tail 36% longer than HB. Tail unicolor with 21–23 annulations per cm. Ears long, 23% of HB, 13 mm re-measured from dry study skin (vis a vis field notes = 12 mm). Belly hairs 3 mm, basal 50% slate grey, distal 50% slightly ochraceous. Dorsal hairs 4 mm, basal 2.5 mm slate grey, tipped with carmel brown. Dorsum of head appearing more grey, due to shorter ochraceous tips (perhaps in molt). Upper lip creamy white. Vibrissae 'long' – up to 25 mm in length –, ventral vibrissae white; dorsal vibrissae black and shorter. Young adult female with mammae not visible on dry skin. The number of fleshy pads on the hind foot are not determinable from the single study skin. The number of fleshy palatal ridges are not visible in the single cleaned skull.

Table 4. Craniodental measurements in millimeters (mean ± 1 SD and range) for eight species in the *Hylomyscus anselli* group. Abbreviated variables are defined in the text.

Variable	kerbispeterhansi (n = 51)	stanleyi (n = 22)	mpungamachagorum (n = 4)	arcimontensis (n = 53)	thornesmithae (n = 5)	anselli (n = 4)	heinrichorum (n = 13)	pygmaeus (n = 1)
ONL	26.36 ± 0.75 (24.68–27.96)	27.16 ± 0.56 (26.20–28.48)	25.25 ± 0.08 (25.17–25.36)	25.69 ± 0.69 (24.12–27.25)	22.84 ± 0.61 (22.09–23.39)	25.98 ± 0.30 (25.74–26.39)	26.73 ± 0.79 (25.52–28.12)	17.45
CI	24.73 ± 0.87 (22.66–26.53)	24.84 ± 0.56 (23.60–26.42)	23.34 ± 0.31 (22.95–23.70)	23.80 ± 0.70 (22.43–25.61)	21.42 ± 0.47 (21.06–22.08)	23.98 ± 0.57 (23.28–24.68)	24.77 ± 0.75 (23.68–26.18)	15.89
ZB	13.19 ± 0.42 (12.25–14.19)	13.35 ± 0.25 (12.86–13.95)	12.65 ± 0.12 (12.48–12.73)	12.85 ± 0.45 (11.91–13.89)	11.66 ± 0.10 (11.55–11.80)	12.84 ± 0.22 (12.53–13.05)	12.99 ± 0.38 (12.52–13.70)	9.68
BBC	11.81 ± 0.27 (11.25–12.51)	12.14 ± 0.24 (11.62–12.48)	11.65 ± 0.16 (11.51–11.83)	11.66 ± 0.34 (10.90–12.47)	11.07 ± 0.49 (10.64–11.62)	11.80 ± 0.39 (11.24–12.12)	11.81 ± 0.22 (11.55–12.29)	9.27
BOC	6.10 ± 0.18 (5.58–6.45)	6.11 ± 0.12 (5.93–6.32)	5.92 ± 0.11 (5.78–6.05)	6.12 ± 0.22 (5.55–6.54)	5.62 ± 0.17 (5.42–5.81)	6.18 ± 0.18 (6.00–6.40)	6.26 ± 0.12 (6.06–6.43)	4.94
IO	4.35 ± 0.10 (4.17–4.57)	4.60 ± 0.12 (4.46–4.91)	4.52 ± 0.21 (4.34–4.80)	4.36 ± 0.15 (4.09–4.66)	3.89 ± 0.08 (3.77–3.99)	4.41 ± 0.16 (4.20–4.57)	4.53 ± 0.08 (4.42–4.69)	3.74
LN	9.45 ± 0.46 (8.44–10.69)	10.14 ± 0.33 (9.26–10.61)	8.71 ± 0.07 (8.64–8.81)	9.19 ± 0.35 (8.44–9.76)	7.69 ± 0.31 (7.32–7.97)	9.13 ± 0.27 (8.81–9.38)	9.16 ± 0.49 (8.06–9.94)	4.66
BR	4.56 ± 0.27 (4.16–5.60)	4.55 ± 0.14 (4.27–4.97)	4.43 ± 0.11 (4.27–4.50)	4.45 ± 0.20 (4.08–4.96)	4.11 ± 0.20 (3.94–4.42)	4.59 ± 0.07 (4.48–4.63)	4.35 ± 0.24 (4.01–4.73)	3.23
PPL	9.03 ± 0.44 (8.12–10.32)	9.36 ± 0.27 (8.75–10.05)	8.98 ± 0.24 (8.69–9.28)	8.96 ± 0.31 (8.37–9.63)	8.62 ± 0.33 (8.23–8.94)	9.11 ± 0.24 (8.87–9.45)	9.40 ± 0.44 (8.58–10.20)	6.28
LBP	4.50 ± 0.18 (3.92–4.81)	4.76 ± 0.18 (4.36–5.09)	4.26 ± 0.06 (4.19–4.34)	4.42 ± 0.21 (3.95–4.83)	4.18 ± 0.14 (4.00–4.37)	4.79 ± 0.17 (4.60–4.93)	4.45 ± 0.20 (4.08–4.77)	2.91
LIF	5.59 ± 0.25 (5.02–6.06)	5.48 ± 0.16 (5.29–5.78)	5.09 ± 0.19 (4.89–5.34)	5.38 ± 0.30 (4.78–6.11)	4.38 ± 0.22 (4.10–4.67)	5.23 ± 0.22 (5.09–5.55)	5.84 ± 0.27 (5.33–6.33)	2.83
LD	7.82 ± 0.32 (7.25–8.62)	7.59 ± 0.17 (7.38–8.03)	6.95 ± 0.19 (6.74–7.20)	7.22 ± 0.25 (6.76–7.83)	6.55 ± 0.29 (6.14–6.82)	7.19 ± 0.19 (7.03–7.41)	7.47 ± 0.35 (7.05–8.15)	4.39
BZP	2.39 ± 0.12 (2.16–2.75)	2.28 ± 0.13 (2.07–2.57)	2.30 ± 0.05 (2.24–2.36)	2.31 ± 0.12 (2.01–2.54)	1.90 ± 0.09 (1.79–2.00)	2.34 ± 0.14 (2.17–2.47)	2.64 ± 0.17 (2.31–2.80)	1.76
LAB	4.59 ± 0.21 (4.26–5.23)	4.51 ± 0.12 (4.28–4.74)	4.23 ± 0.13 (4.04–4.34)	4.23 ± 0.12 (3.98–4.43)	3.86 ± 0.14 (3.73–4.05)	4.55 ± 0.07 (4.48–4.63)	4.45 ± 0.11 (4.23–4.61)	3.23
CLM	3.80 ± 0.07 (3.66–3.93)	4.13 ± 0.12 (3.97–4.51)	3.78 ± 0.05 (3.74–3.85)	3.85 ± 0.18 (3.40–4.17)	3.16 ± 0.09 (3.02–3.25)	4.10 ± 0.09 (3.97–4.18)	4.17 ± 0.14 (3.99–4.52)	2.60
WM1	1.20 ± 0.04 (1.12–1.29)	1.24 ± 0.04 (1.14–1.30)	1.13 ± 0.01 (1.12–1.13)	1.18 ± 0.05 (1.06–1.28)	0.95 ± 0.09 (0.86–1.06)	1.24 ± 0.04 (1.19–1.28)	1.28 ± 0.06 (1.17–1.34)	0.82

Skull tiny (ONL 17.45, CRM 2.6). Rostrum exceptionally short (LN/ONL = 26.7%) but this is expected to increase in older individuals. Inter-orbital region proportionately broad. Upper incisors slightly pro-odont. Incisive foramina fall short of upper tooth row. T3 on M^2 is present but a tiny vestige. Braincase bulbous and dorso-ventrally inflated. Hamular process of the squamosal long and thin, providing for a very large subsquamosal fenestra which is about 40% the size of the postglenoid foramen (see Carleton & Stanley 2005: fig. 6). Maxillo-palatal suture located at the rear third of the M^1 (Figs 6c, 8a). Post palatal foramina large, starting between M^1 and M^2 and extend back to middle of M^2 (Figs 6c, 8a). Fronto-parietal suture broadly U-shaped. Zygomatic plate narrow (1.34 mm) and without any sinuosity but gently sloping forward throughout. Mesopterygoid fossa rounded and open widely at rostral end.

As a divergent member of the *Hylomyscus anselli* group, some of the following characters contrast the Carleton et al. list of characters (2006: table 7) defining this group: 1) pectoral mammae unknown (not available as the holotype is a young adult), 2) upper incisors slightly pro-odont (Fig. 6e), whereas Carleton et al. (2006) characterized the *H. anselli* group as opisthodont, 3) T3 on M^1 is distinct and sub equal with t1 rendering it 'large' per Carleton et al. (2006); the anterior chevron is more or less symmetrical (Fig. 7g), whereas Carleton et al. (2006) characterized the '*H. anselli*' group as having a 'medium' sized t3 (e.g., smaller than t1), 4) t9 on M^1 is distinct (Fig. 7g), whereas Carleton et al. (2006) characterized the

Table 5. External measurements (mean ± SD, range, and sample size) of all eight members of the *Hylomyscus anselli* group. Measurements are in millimeters and mass is in grams. Abbreviated variables are defined in the text. *See text, totals have 1.0 mm added.

Variable	*kerbispeterhansi*	*stanleyi*	*mpungamachagorum*	*arcimontensis*	*thornesmithae*	*anselli*	*heinrichorum*	*pygmaeus*
TOT	230.2 ± 12.1 (201–260) 50	245.2 ± 7.1 (233–264) 32	234.3 ± 6.6 (230–244) 4	227.3 ± 12.5 (205–262) 50	204.4 ± 7.6 (193–212) 5	222.4 ± 13.4 (205–254) 16	233.3 ± 12.6 (207–255) 21	132 1
HB	92.6 ± 5.6 (80–103) 50	101.7 ± 3.8 (93–109) 32	97.8 ± 1.9 (95–99) 4	91.3 ± 5.6 (77–104) 50	83.2 ± 4.4 (76–87) 5	87.2 ± 6.4 (78–101) 16	94.8 ± 6.8 (82–106) 21	56 1
TAIL	137.6 ± 8.8 (117–158) 50	145.5 ± 5.1 (136–159) 32	138.3 ± 6.3 (132–147) 4	136.0 ± 9.0 (115–161) 50	121.2 ± 3.3 (117–125) 5	135.2 ± 9.2 (121–153) 16	138.5 ± 7.4 (121–150) 21	76 1
HF	20.4 ± 0.9 (19–22) 49	21.1 ± 0.8 (20–23) 32	20.3 ± 0.5 (20–21) 4	20.5 ± 1.0 (18–22) 50	18.0 ± 1.0 (17–19) 5	20.7* ± 0.5 (19.5–21.5)* 24	22.0* ± 0.9 (19.5–23)* 21	14 1
EAR	19.8 ± 1.0 (17.5–22) 47	19.9 ± 0.8 (18–21) 32	19.0 ± 0.0 (19) 4	18.2 ± 1.0 (17–21) 50	14.8 ± 0.8 (14–16) 5	18.0 ± 0.7 (16.5–19) 24	18.6 ± 1.0 (17–21) 21	13 1
Wt	24.9 ± 4.0 (17–39) 48	27.6 ± 3.1 (22–34.5) 31	21.8 ± 1.2 (20.5–23) 4	22.0 ± 3.7 (15–29.5) 50	13.9 ± 1.4 (11.5–15) 5	20.4 ± 4.0 (16–30.5) 15	NA	5.8 1
TAIL/HB	1.5 ± 0.1 (1.2–1.7) 50	1.4 ± 0.0 (1.4–1.5) 32	1.4 ± 0.1 (1.3–1.5) 4	1.5 ± 0.1 (1.2–1.7) 50	1.4 ± 0.1 (1.4–1.5) 5	1.6 ± 0.1 (1.4–1.8) 16	1.5 ± 0.1 (1.3–1.7) 21	1.4 1

'*H. anselli*' group as 'indistinct' 5) interorbital constriction is amphoral, whereas Carleton et al. (2006) characterized the '*H. anselli*' group as having a 'weak shelf, 6) rostral length is extremely short (Fig. 6a), whereas Carleton et al. (2006) characterized the '*H. anselli*' group with a 'medium' length rostrum, 7) incisive foramen is short, falling well short of the alveoli of M¹ (Figs 6c, 8a) as opposed to the Carleton et al. (2006) characterization as 'medium' (reaching anterior root of M¹), 8) the hamular strap is long and thin, subsquamosal foramen is large in size (see Carleton & Stanley 2005: fig. 6; Fig. 6e). In sum, several characters of this new species are unique or align more with the *Hylomyscus alleni* group than the *H. anselli* group: more proodont, distinct T9 on M¹, amphoral inter-orbital region, extreme shortening of the rostrum, and shorter incisive foramina. Perhaps these contrasts are not surprising given the basal position of this taxon.

Ecology. The habitat is seasonally flooded primary forest, 'edaphic forest' (Verhegghen et al. 2012). However, the pitfall line was set in a drier part of the forest and was less subject to flooding. The area supports two dry seasons (January to early March, and June to early September) with the rest being rainy averaging ca. 210 cm per year. Daily temperature average between 24 °C and 30 °C (Doty et al. 2017). Type specimen was caught in a generally dry area of the forest.

The vegetation of the Tshuapa region is mainly characterized by sempervirent or semi-sempervirent rain forests bound to hydromorphic soils, secondary forests and grassy vegetation (Evrard 1968). The sempervirent rain forests of terra-firma are distinguished by their structural density, distinct stratification and epiphytism (Lebrun & Gilbert 1954), while the upper stratum can reach 40–45 m in height. There are two types of forest bound to hydromorphic soils in swampy zones. These include periodically flooded forests (including where the type specimen was collected) comprising the following species: *Parinari congolensis, Guibourtia demeusei, Zeyrrhella longipedisellata* and swampy forests composed of *Entandrophragma palustre, Alstonia congolensis, Coelocaryon botryodes,* and *Sterculia tragacantha*. The second forest type is composed of bushy forests along the banks of large rivers including *Alchornea cardifolia, Lacosperma secundiflorum*; waterside forests with *Coelocaryon botryodes, Erispermum microspermum, Sclerosperma manirii,* and *Cleistanthus mycrophyllus*. Secondary forests are found around villages, roads and on former sites of forest extraction. Species frequently observed are *Musanga cecropioides, Harungana madagascariensis, Trema orientalis, Oncoba subtomentosa, Pycnanthus angolensis, Petersianthus macrocarpus, Ricinodendron heudelotii, Canarium schweinfurthii, Alstonia boonei*, and *Elaeis guineensis*. Grassy vegetation results from forest degradation and includes frequently burnt fallow fields, mainly with Graminaceae of the genera *Panicum, Pennisetum, Imperata, Serata*, and *Sorghum* (Evrard 1968).

Reproduction. The sole specimen is a young female with teats that are neither developed nor visible.

Fig. 5. Skins of two new species of the *Hylomyscus anselli* group from the Democratic Republic of Congo. (a) ventral and (c) dorsal views of *Hylomyscus pygmaeus* sp.nov., and (b) ventral and (d) dorsal views of *Hylomyscus thornesmithae* sp.nov.

Etymology. Named for its diminutive size. We recommend "pygmy wood mouse" as an English common name.

***Hylomyscus thornesmithae* sp. nov.** Kerbis Peterhans, Hutterer & Demos

urn:lsid:zoobank.org:act:DAE95BEF-D424-42C2-8415-A1805F494ADC

Hylomyscus sp. – Doty et al. (2017)

Holotype. Field Museum of Natural History, Division of Mammals number FMNH 222524 (field number WT Stanley 11,664; CDC 746), collected by W.T. Stanley, 27 June 2013 (originally listed as *Hylomyscus* sp.). The type specimen, consisting of an alcoholic carcass with skull removed, is an adult female with first upper molar in ear-

ly wear (advanced age stage IV) and large teats (2+4). The basisphenoid-occipital suture is fused. External measurements were made in the field: TL 210, TV 124, HF 18, EL 15, Wt 15. Specimen caught in a standard snap trap; apparently held by tail in trap as tail is broken ⅓ way down. Type specimen captured just behind camp in secondary growth forest on the edge of a forest that may occasionally be subject to flooding.

Type locality. Democratic Republic of Congo, Tshuapa Province, rt side Tshuapa River, 14 km north of Boende by road, Quatorz (0.16919° S, 20.92611° E) at an elevation of 322 m.
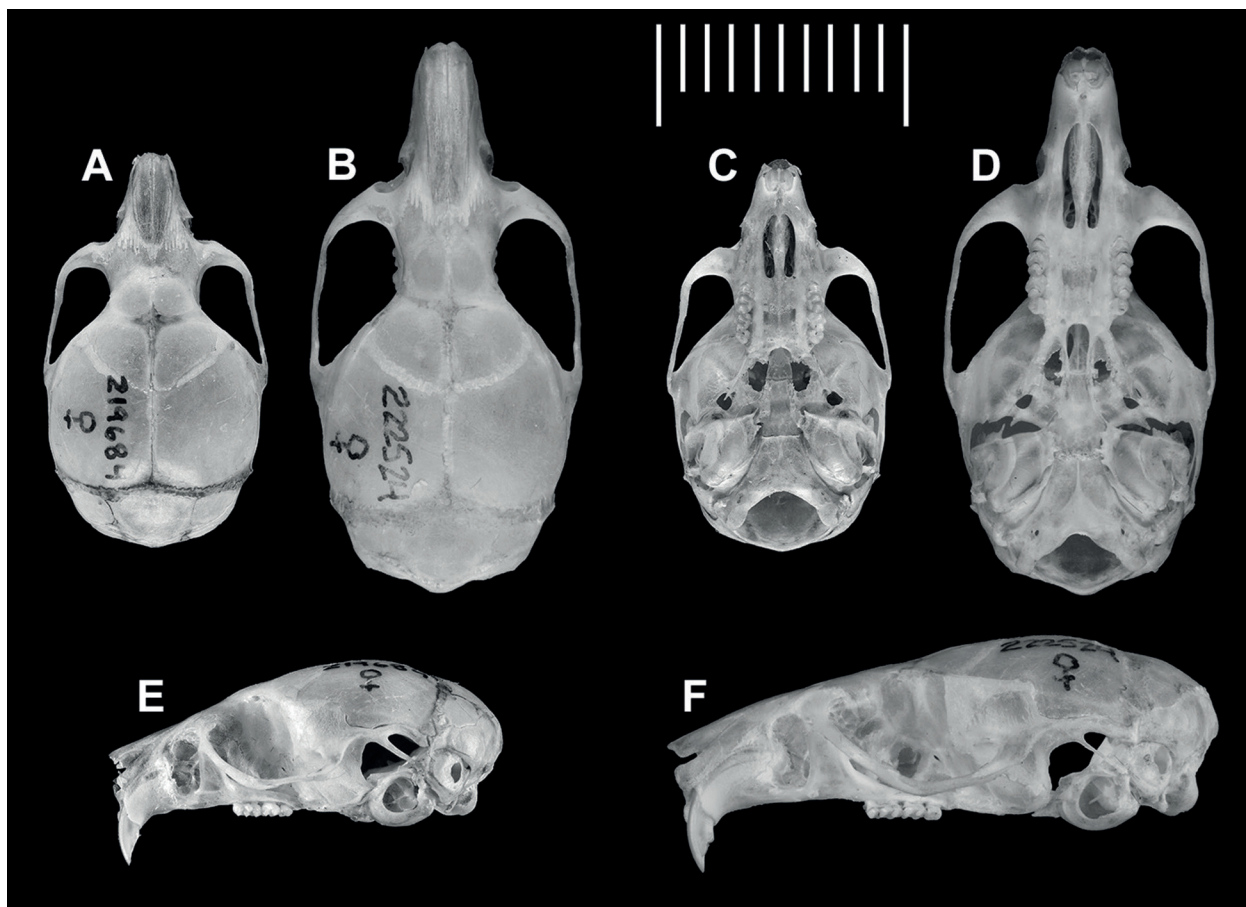
Fig. 6. Skulls of two new species of the *Hylomyscus anselli* group from the Democratic Republic of Congo. (a) Dorsal (c) ventral and (e) lateral views of *Hylomyscus pygmaeus* sp.nov. (b) Dorsal, (d) ventral and (f) lateral views of *Hylomyscus thornesmithae* sp. nov.

Paratypes (n = 4). All caught in conventional trap lines from Democratic Republic of Congo, Tshuapa Province, 4 km N of Boende, Baleko (0.24127° S, 20.8833° E) at an elevation of 358 m: FMNH 219611 (WTS 11471, CDC 103), alcoholic carcass with extracted skull, old scrotal male; FMNH 219612 (WTS 11592, CDC 224) alcoholic carcass with extracted skull, old female, teats 2+4; FMNH 2119613 (WTS 11594, CDC 226), alcoholic carcass with extracted skull, old scrotal male; FMNH 219689 (WTS 11481, CDC 113), skin and skull with carcass preserved in alcohol, old scrotal male, testes 10x5.

Diagnosis. Easily differentiated within the *Hylomyscus anselli* group by its small size (second smallest, but still much larger than preceding species): HB 83 (mean), Wt 13.9 (mean), ONL 22.8 (mean), CLM 3.2 (mean). All are significantly smaller than all other members of the *H. anselli* group (Tables 4–5), excepting the previously described species.

Comparisons. Upper incisors orthodont, contrasting with the proodont condition in *Hylomyscus pygmaeus*. Crown length of upper molars 3.0–3.25 mm, much larger than *Hylomyscus pygmaeus* (under 2.6 mm). External and cranio-dental measurements smaller than all other members of the *H. anselli* group (excepting *Hylomyscus pygmaeus*).

Description. Size very small (mean HB = 83, mean mass = 13.9). Tail 46% longer than HB, unicolor with ca. 18 annulations per cm. Ears of normal size, 18% of HB; ear color dark grey. Belly hairs 5 mm, basal 3 mm slate grey, distal 2 mm white. Dorsal hairs 7 mm, basal 5 mm slate grey, apical 2 mm orange, more bright orange towards flanks. Vibrissae up to 33 mm in length, mostly black but with 2–3 white hairs; upper lip with white fur patch behind vibrissae. Teats 2+4. The hind foot possesses the standard murine complement of 6 pads (see Ibe et al. 2014: fig. 2, II for reference); there is a single accessory pad on the 1st and 4th interdigital pads; the first is clear and well-defined while the 4th is larger and more integrat-
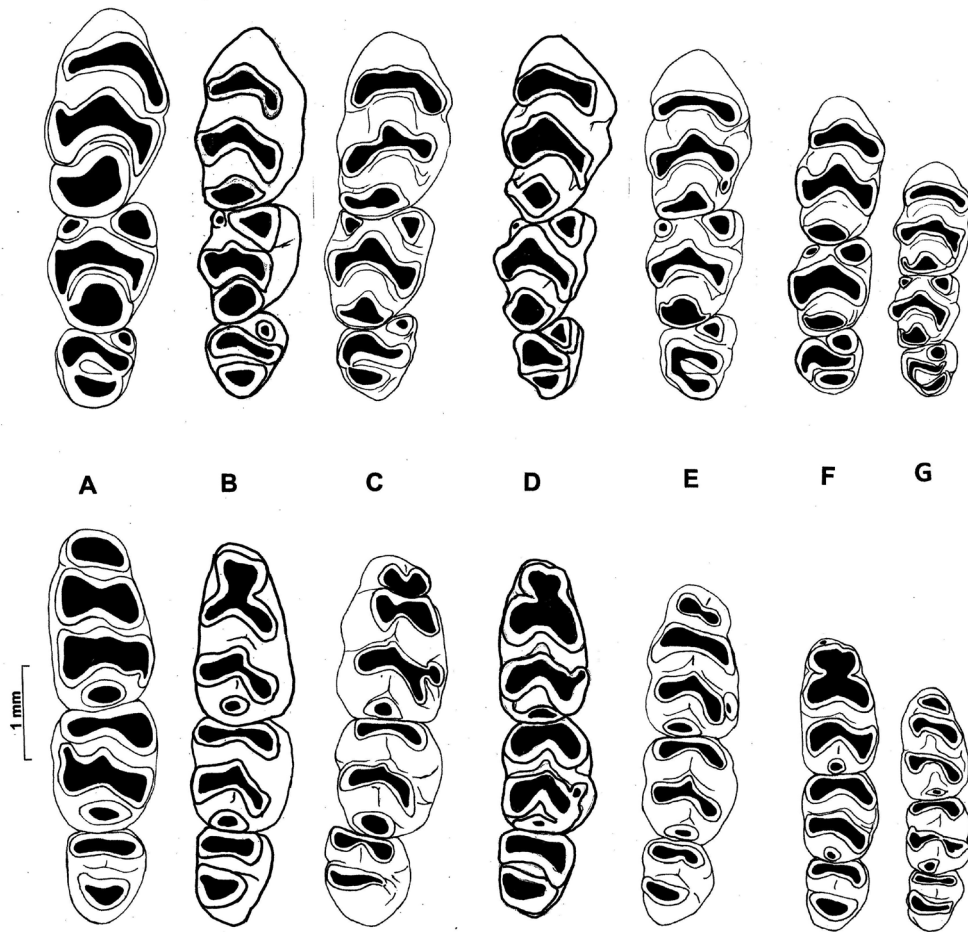
Fig. 7. Sketches of right upper (top row) and lower tooth rows (bottom row) of members of the *Hylomyscus anselli* group, including four new species described herein: (a) *H. stanleyi* sp. nov. (FMNH 171512), (b) *H. anselli* (BMNH 74.250), (c) *H. kerbispeterhansi* (FMNH 209995), (d) *H. mpungamachagorum* sp. nov. (FMNH 177889), (e) *H. arcimontensis* (FMNH 147271), (f) *H. thornesmithae* sp. nov. (FMNH 222524), (g) *H. pygmaeus* sp. nov. (FMNH 219684). Scale = 1 mm.
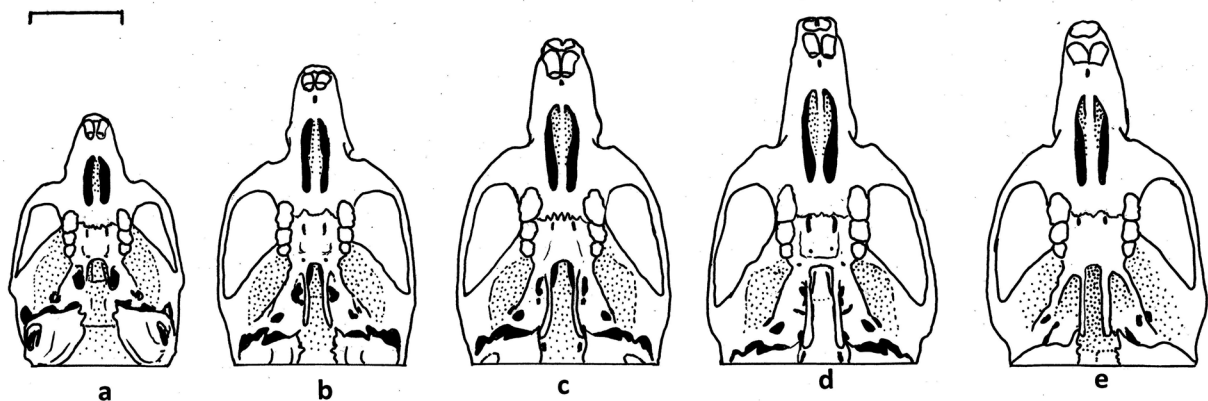

Fig. 8. Sketches of the bony palates of *Hylomyscus anselli* and the four new species of the *Hylomyscus anselli* group: (a) *H. pygmaeus* sp. nov. FMNH 219684, (b) *H. thornesmithae* sp. nov. FMNH 222524, (c) *H. mpungamachagorum* sp. nov. FMNH 177889, (d) *H. stanleyi* sp. nov. FMNH 171362, and (e) *H. anselli* BMNH 74.250. Scale = 5 mm.
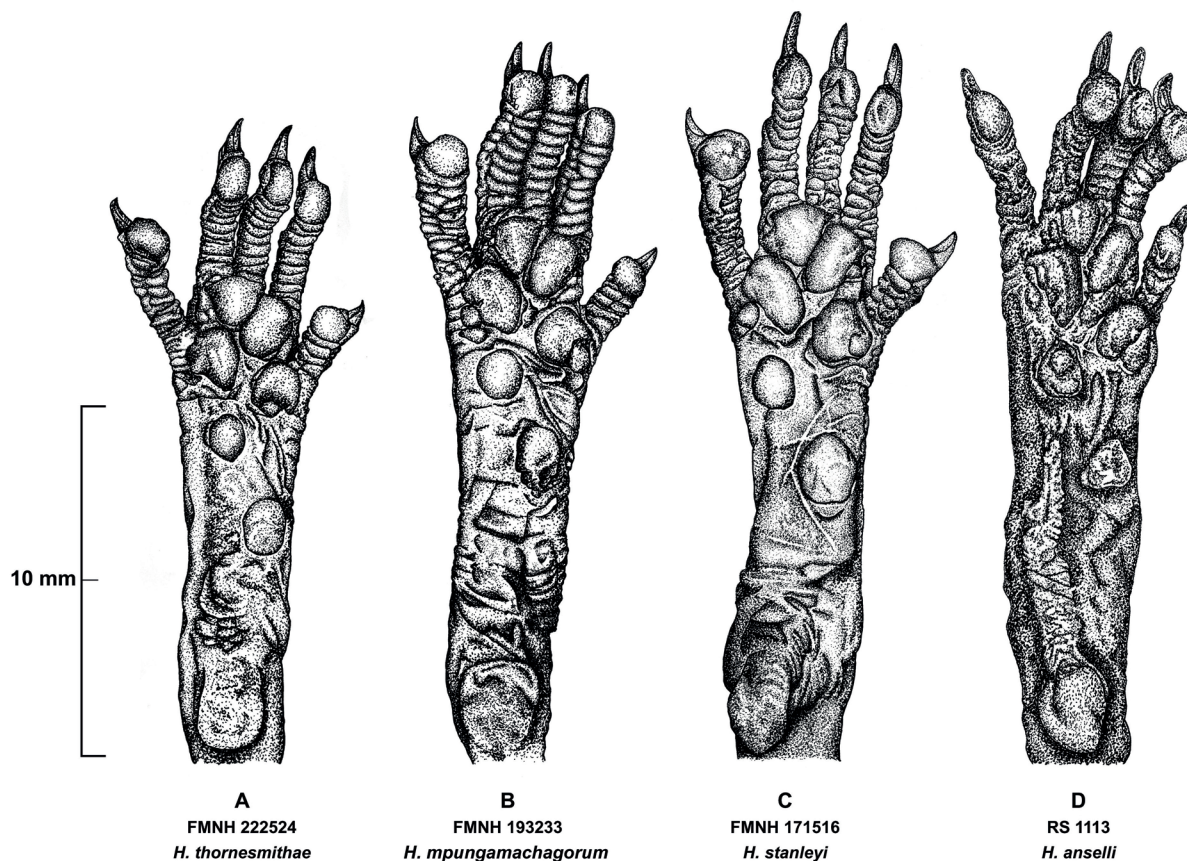
Fig. 9. Sketches of feet and plantar tubercles of four species of the *Hylomyscus anselli* group: (a) *H. thornesmithae* sp. nov., (b) *H. mpungamachagorum* sp. nov., (c) *H. stanleyi* sp. nov., and (d) *H. anselli*.

ed (Fig. 9a). The number of fleshy palatal ridges are not visible on any of the prepared skulls.

Skull small (mean ONL = 22.8, mean CRM = 3.2). Rostrum short, LN/ONL = 33.7%. Upper incisors orthodont. Incisive foramina fall well short of upper tooth row. T3 on M^2 is tiny. Braincase elongated. Hamular process of the squamosal long and thin, providing for a large subsquamosal fenestra which is about 35% the size of the post glenoid foramen (see Carleton & Stanley 2005: fig 6; Fig 6f). Maxillo-palatal suture zig-zags through the middle of the M^1 (Figs 6d, 8b). Post palatal foramina large, starting at rear 3rd of M^1 or between M^1 and M^2 and continues through to the 1st third of M^2. Zygomatic plate slightly sinuous. In aged individuals (FMNH 219611, FMNH 219612), the incisive foramina fall even shorter of the UTR, the maxillo-palatal suture is located more forward at the first half of M^1 and the post palatal foramina are more forward at the rear half of the M^1. Frontoparietal suture broadly rounded, U-shaped. Zygomatic plate narrow (1.9 mm) and virtually orthogonal to skull profile but gently sloping forward in lower third. Mesopterygoid fossa rounded at rostral end.

As a member of the *Hylomyscus anselli* group (sensu Carleton et al. 2006: table 7), the following characters are relevant: 1) mammae: 2+4, 2) upper incisors orthodont (Fig. 6f), 3) T3 on M^1 is 'medium' in size (smaller than t1), the anterior chevron is moderately asymmetrical (Fig. 7f), 4) T9 on M^1 is distinct but reduced (Fig. 7f), 5) interorbital constriction is amphoral in shape (Fig. 6b). 6) rostral length is short, LN/ONL = 33.7% (Fig. 6b), 7) incisive foramen is very short, falling short of the roots of M1 (Figs 6d, 8b), 8) the hamular strap is short but thin and delicate and allows for a large subsquamosal foramen, which is about 25% the size of the postglenoid foramen (Fig. 6f).

Distribution. Known only from two locations, both are ca. 250 km S of the Congo River, off the right bank of the Tshuapa River, Tshuapa Province, Democratic Republic of Congo. In addition to the type locality (n = 1), four paratypes are from 4 km N of Boende at Baleko (0.24127° S, 20.8833° E, elevation 358 m).

Ecology. Type specimen and 3 paratypes all caught in standard mammal snap traps while the fifth was caught

Fig. 10. Live photos of two new species of the *Hylomyscus anselli* group from Tanzania: (left) *H. stanleyi* sp. nov. and (right) *H. mpungamachagorum* sp. nov.

in a Sherman live trap. Type specimen captured in regenerating secondary forest on the edge of a seasonally flooded forest. One specimen captured in a trap line that was never flooded during heavy rain events while three came from a trap line that was prone to flooding.

Reproduction. All animals captured (n = 5) were adult. Type is adult female with swollen teats 2 + 4. A second female (FMNH 219612), despite having well-worn molars (beyond stage VII), had small teats that are difficult to decipher. Three adult males all with scrotal testes; testes of FMNH 219689 measured 10 × 5 in the field.

Etymology. Ellen Thorne Smith was a "professional volunteer" serving 2–3 days per week, sorting and organizing the bird collections at the Field Museum, and conducting original published research from the mid 1930's until the 1970's. During World War II with the museum's ornithologists away in Washington, she ran the Division of Ornithology. We recommend "Mother Ellen's wood mouse" as an English common name.

***Hylomyscus stanleyi* sp. nov.** Kerbis Peterhans, Hutterer & Demos
urn:lsid:zoobank.org:act:4512E5DE-2139-46CB-B2F9-823C9C3B1BAD
Hylomyscus anselli – Carleton & Stanley (2005); Carleton, Kerbis Peterhans & Stanley (2006); Demos, Agwanda & Hickerson (2014a); Carleton, Banasiak & Stanley (2015)
Hylomyscus cf. *anselli* – Nicolas et al. (2020)

Holotype. Field Museum of Natural History, Division of Mammals number FMNH 171362 (field number WT Stanley 4968), collected by Cosmos, 03 August 2001

(originally listed as *Hylomyscus* sp.). The specimen, consisting of a skin, skull and alcoholic carcass, is an adult pregnant female with first upper molar well worn (stage IV of Verheyen & Bracke 1966). Teats 2+4, large, embryos 4L, 1R (CR 14). The holotype was captured in a local snare baited with corn. The basisphenoid-occipital suture is fused. External measurements were made in the field: TL 256, HB 106, TV 154, HF 21, EL 20, Wt 29.

Type Locality. Tanzania, Rukwa Region, Sumbawanga District, Mbizi Forest Reserve, 0.5 km N, 4 km E of Wipanga, elevation 2200 m, 7.8639° S, 31.6694° E.

Paratypes (n = 32). Mbizi Forest Reserve, 0.5 km N, 4 km E of Wipanga, elevation 2200 m, 171357–171361, 171363–171367, 171517–171518 (6 m, 6 f), 7.8639° S, 31.6694° E; Mbizi Forest Reserve, 0.5 km S, 3 km E of Wipanga, 2300 m, 171342–171356, 171512–171516 (12 m, 8 f), 7.8639° S, 31.6694° E.

Diagnosis. UTR >3.97 mm, maxillo-palatal suture located at the rear third to the rear half of M^1 (Fig. 8d), rostrum elongate (LN/ONL= 37.33, LN>9.3; Fig. 12b, Table 4), very large posterior palatal foramen (ca. 0.7–0.9 mm) starting between M^1 and M^2 and extending into anterior half of M^2 (Figs 8d, 12d), very large sub-squamosal foramen (30–40% area of postglenoid foramen, Fig. 12f), fronto-parietal suture shallow V-shaped, zygomatic plate only slightly sinuous in lateral view, incisive foramina fall either just short of the alveoli of M^1 or barely reaching alveoli of M^1 (Figs 8d, 12d). T1 of M1 deflected far posteriorly (Fig. 7a).

Fig. 11. Skins of two new species of the *Hylomyscus anselli* group from Tanzania. (a) Ventral and (c) dorsal views of *Hylomyscus mpungamachagorum* sp. nov., (b) Ventral and (d) dorsal views of *Hylomyscus stanleyi* sp. nov.

Comparisons. One of the largest members of the *H. anselli* group with an upper molar crown length over 4.0, thereby needing comparison with only *Hylomyscus heinrichorum* and *H. anselli*. Compared to *H. heinrichorum*, *H. stanleyi* is typically orthodont vs. slightly opisthodont, see Carleton et al. 2015: fig. 7c (as *H. stanleyi*) vs. fig. 7b, has longer nasals (mean of 10.1 vs. 9.2; Ibid. 6c as H. anselli vs. 6b) with a more narrow zygomatic plate (Ibid. fig. 6c as *H. anselli* vs. fig. 6b, mean of 2.3 vs. 2.6) and with incisive foramina that do not penetrate the upper tooth row or alveoli (Ibid. fig. 6c *as H. anselli* vs. 6b). Since the sample size of available *H. anselli* is small (n = 4), we expect these differences may become more

ambiguous as older individuals and additional samples of *H. anselli* become available.

Description. Size large (mean HB = 102, mean mass = 27.5 g; Table 5). Tail 43% longer than HB. Tail uni-color with ca. 15 annulations per cm. Belly hairs ca. 9 mm, basal 6 mm slate grey, apical 3 mm white. Dorsal hairs ca. 11 mm, basal 6 mm slate grey, terminal 3 mm tipped with light brown. Dorsum of head same color as dorsum of body. Upper lip with whitish hairs but with grey roots. Ears with blackish skin, hairs barely visible. Vibrissae long, up to 35 mm, black in color. Pes dirty white in appearance due to white hairs overlaying darker skin. Manus white. The hind foot possesses the standard

Fig. 12. Skulls of two new species of the *Hylomyscus anselli* group from Tanzania. (a) Dorsal, (c) ventral and (e) lateral views of *Hylomyscus mpungamachagorum* sp. nov., (b) Dorsal, (d) ventral and (f) lateral views of *Hylomyscus stanleyi* sp. nov.

murine complement of 6 pads (see Ibe et al. 2014: fig. 2. II for reference); there is a single accessory pad on each of the 1st, 2nd and 4th interdigital pads; the first is larger and well-integrated into the 1st interdigital pad, the 2nd is small but distinct from the 2nd interdigital pad, while the 4th is smaller but distinctly separate from the 4th interdigital pad (Fig. 9c). There are seven fleshy palatal ridges: two are continuous and pre-dental, one is discontinuous and pre-dental, and the last four are discontinuous and inter-dental (Fig. 13).

Skull large (mean ONL = 27.2, mean CLM = 4.1, Table 4). Rostrum much longer than other members of the '*H. anselli*' group (LN/ONL = 37.3%), with nasals exceeding 9.3 mm (Table 4). Upper incisors generally orthodont, but a few slightly opisthodont. Incisive foramina fall short of upper tooth row crown but may reach alveoli. T3 on M^2 is large. Braincase elongate rather than rounded or globular. Hamular process of the squamosal thin, allowing for a large subsquamosal fenestra (ca. 30% of post glenoid foramen). Maxillo-palatal suture at third lamina of the M^1. Post palatal foramina large (0.7–0.9 mm), beginning between M^1 and M^2 and continuing through the 1st third or half of the M^2. Frontoparietal suture V-shaped.

Zygomatic plate narrow (mean breadth = 2.3 mm) and orthogonal to the long axis of the skull. Mesopterygoid fossa more rectangular at rostral end.

As a member of the *Hylomyscus anselli* group, the following characters are relevant: 1) mammary formula 2+4, 2) upper incisors orthodont with some individuals (5 of 33) slightly opisthodont, 3) T3 on M^1 is large and is more or less equal in size to T1, but T1 is deflected further posteriorly (Fig. 7a), 4) T9 on M^1 is distinct (Fig. 7a), 5) interorbital constriction has a weak shelf, 6) rostral length is long, LN/ONL = 37.3%, 7) incisive foramen is short, falling just short of the M^1 or barely meeting the beginning of the alveolus, 8) the hamular strap is thin allowing for well-developed subsquamosal foramen but which is proportionately smaller than in the two new DRC species (Figs 6e–f vs. Figs 12e–f).

Habitat. Mbizi is the largest area of montane cloud forest (ca. 2,000 ha) remaining on the denuded Ufipa Plateau. All of the extant forest is contained within the Mbizi Forest Reserve and is discontinuous with forest patches interspersed with grasslands. There is very little continuous canopy cover due to removal of commercially valuable
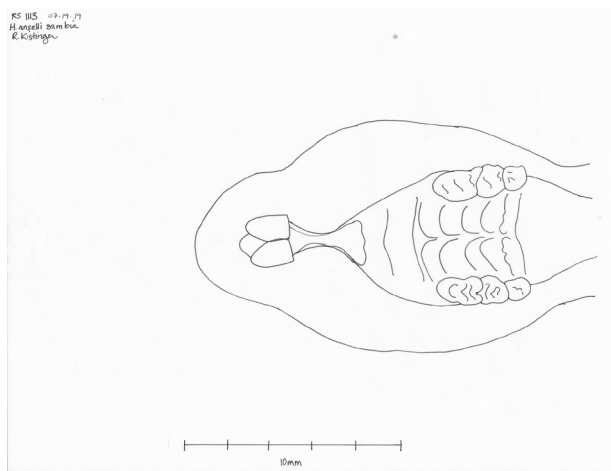
Fig. 13. Sketch of soft palate of *Hylomyscus anselli* from Zambia displaying the 2+(1+4) dental ridges format typical of the *Hylomyscus anselli* group: from tip of rostrum (to the left): 2 continuous pre-dental ridges, 1 discontinuous pre-dental ridge, 4 discontinuous inter-dental ridges.

timber species and exploitation for firewood and charcoal (Rodgers et al. 1984). The forest is on the eastern facing escarpment overlooking the Rukwa Trough. Surveys of the vegetation at Mbizi include those by Mtuy & Mkude (1974), Rodgers et al. (1984), and Rufo & Mabula (1987). The forest canopy reaches 25 m in places with dominant tree species being *Aguarista salicifolia, Allophyllus abyssinicus, Croton megalocarpus, Macaranga capensis, Neoboutonia macrocalyx, Olea chrysophylla, Olinia rochetiana,* and *Prunus africana* (Rodgers et al. 1984). The understory is between 8–20 m with the most commonly encountered tree species being: *Bersama abyssinica, Cathula edulis, Clerodendron sthulmanii, Bridelia brideliifolia, Polyscias fulva*, and *Rhus natalensis* (Rodgers et al. 1984, Rufo & Mabula 1987). The most striking aspect of Mbizi forest is scattered *Euphorbia amplophylla* that emerge above the canopy up to 35 m (Rodgers et al. 1984). Forest cover has been fragmented by past fires and smaller patches are now isolated on the periphery and in sheltered valleys. These are surrounded by species-rich grasslands maintained by nearly annual fires (Rufo & Mabula 1987). The central forest block is more or less continuous and covers an area of over 2000 ha. However, much of this is disturbed as the reserve is surrounded by villages and heavily exploited for firewood and charcoal. The area has many endemic plants (e.g., *Brillantaisia richardsiae, Glossostelma mbisiense, Pachycarpus pachyglossus, Spermacoce azurea, Sebaea perpava, Afrotysonia pilosicaulis*) and several undescribed plant species including a possible new species of *Ocotea* (Q Luke, pers. comm.).

Reproduction. Of the 33 examples of the new species collected (July–Aug 2001), there were 18 males and 15 females. All can be considered adult (3rd molars in advanced wear). Of the 15 females, 14 were inspected internally: 7 were pregnant, 7 were not. All pregnant females had either 4 or 5 embryos with an average crown rump length of 12–13 mm. The pregnant females averaged 28 g in weight while those that were not pregnant weighed an average of 25 g. All males were adult with scrotal testes. The entire population had well-worn molars, at least in advanced wear stage IV (Verheyen & Bracke 1966).

Distribution. Known only from two montane forest localities within Mbizi Forest, SW Tanzania: the type locality at ½ km S and 3 km E Wipanga, 2300 m (31.6667° E, 7.875° S) and a second locality ½ km N, 4 km E Wipanga, 2200 m (31.6694° E, 7.8639° S).

Etymology. Named for William T. Stanley (1957–2015) who directed the collection of all known specimens (n = 33) of this species from the Mbizi Mountains of Tanzania in 2001 as well as the type specimen of the other three species described in this manuscript (and many more). We recommend "Stanley's wood mouse" as an English common name.

***Hylomyscus mpungamachagorum* sp. nov.** Demos, Hutterer & Kerbis Peterhans
urn:lsid:zoobank.org:act:2831AD81-B8BF-41FC-82D3-35F2069C016A

Holotype. Field Museum of Natural History, Division of Mammals, FMNH 177889 (field number WT Stanley 5988), collected by WT Stanley, 25 Aug 2003 (originally listed as *Hylomyscus* sp.). The specimen, consisting of a study skin and skull with postcranial skeleton, is an adult scrotal male (testes 13 × 8 mm) with worn first upper molar (stage IV of Verheyen & Bracke 1966). The basisphenoid-occipital suture is fused. External measurements were made in the field: TL 244, HB 99, TV 147, HF 20, EL 19, Wt 20.5. The holotype was collected in a standard snap trap (Museum Special).

Type locality. Tanzania, Kigoma Region, Kigoma District, Mahale Mountains, Mahale National Park 2100 m, 0.5 km NW Nkungwe Hill summit (29.77895° E, 6.10433° S).

Paratypes (n = 11). Tanzania, Mahale National Park, Mahale Mountains, Mahale National Park 2100 m, 0.5 km NW Nkungwe Hill summit (29.77895° E, 6.10433° S) 178011, 177888, 177890–177892, 177911; Kabezi River, 1180 m, 193233 (29.8317° E, 6.1131° S); Mahale National Park, Mfitwa Mt, 2440 m, 193234, 193218 (29.7939° E, 6.1317° S); Mahale National Park, 0.5 km S of Pasagulu Hill, 1420 m (29.75353° E, 6.06618° S), 177886, 177887.

Diagnosis. A member of the *H. anselli* group with a short rostrum (nasals are 34.5% of ONL, Table 4), posterior palatal foramen located posteriorly (at the first lamina of M^2, Figs 8c, 12c), and maxillo-palatal suture located posteriorly – either between second and third lamina of M^1 or at level of third lamina of M^1 (Figs 8c, 12c). Zygomatic plate slightly sinuous in lateral view. Sub-squamosal fenestra moderate (ca. 25–30% of postglenoid foramen; i.e., Carleton & Stanley 2005: fig. 6; Fig. 12e). Incisive foramina penetrate the alveoli of the upper tooth row (Figs 8c, 12c). Frontoparietal suture shallowly U-shaped.

Comparisons. A mid-sized member of the *Hylomyscus anselli* group with an upper molar crown length ca. 3.8 mm, needing comparison only with *H. kerbispeterhansi* and *H. arcimontensis*. It is unique among these three in the location of its posterior palatal foramina, located at the beginning of the second molar (Figs 8c, 12c); in *H. kerbispeterhansi* it is located at the third lamina of the M^1, while in *H. arcimontensis* it is located between M^1 and M^2. The morphometrics of *H. mpungamachagorum* align closely with *H. arcimontensis*; indeed, it falls completely within its morphometric space (Figs 1–2). Compared to *H. kerbispeterhansi*, the skull is smaller (CI 23.3 vs 24.7, Table 4) and with shorter nasals (LN 8.7 vs 9.45) and diastema (LD 6.95 vs. 7.82) (Table 4).

Description. Size medium (mean HB = 98, CLM 3.74–3.85, mean mass = 22 g). Mean tail length 41% longer than HB. Tail unicolor with ca. 15 annulations per cm. Belly hairs 6 mm, basal 3 mm slate grey, distal 3 mm light brown. Dorsal hairs 10 mm, basal 8 mm slate grey, apical 2 mm light brown. Dorsum of head same color as back. Upper lip with white hairs, dark grey roots. Vibrissae long, black, up to 35 mm in length. Pes dirty white in appearance due to white hairs overlaying darker skin. Manus white. Ears black, hairs inconspicuous. The hind foot possesses the standard murine complement of 6 pads (see Ibe et al. 2014: fig. 2 II for reference); there is a single accessory pad on each of the 1st and 4th interdigital pads; the first is large and well-integrated into the 1st inter-digital pad, while the 4th is smaller and distinct from the 4th interdigital pad (Fig. 9b). There are seven fleshy palatal ridges: two are continuous and pre-dental, one is discontinuous and pre-dental, and the last four are discontinuous and inter-dental (as in Fig. 13).

Skull medium (mean ONL=25.25 mm, mean CLM = 3.8 mm). Rostrum moderate (nasals 34.5% GLS). Upper incisors orthodont but slightly opisthodont in younger individuals. Incisive foramina just reach the M^1 alveoli. T3 on M^2 is tiny but distinct as in the other species described here. Braincase elongated. Hamular process of the squamosal long and thin, allowing for a moderate subsquamosal fenestra (ca. 25% of postglenoid foramen). Maxillo-palatal suture either falling between 2nd and 3rd lamina of M1 or at 3rd lamina of the M1. Post palatal foramina small, lying level with 1st lamina of M^2. Zygomatic plate narrow (mean = 2.3 mm) and slightly sinuous. Mesopterygoid fossa rounded at rostral end.

In comparison with other members of the *H. anselli* group, the following characters are relevant: 1) mammary formula 2+4, 2) upper incisors orthodont but younger individuals (wear stage III and IV, i.e., FMNH 177890–1778892, 193218) slightly opisthodont, 3) T3 on M^1 is large, the anterior chevron more or less equal in size to T1 and T1 not as deflected far posteriorly as in *H. stanleyi* (Fig. 7d), 4) T9 on M^1 is distinct (Fig. 7d), 5) interorbital constriction has a weak shelf, 6) rostral length (LN/ONL) is moderate at 34.5%, 7) incisive foramen meets the beginning of the M^1 alveoli (in the four younger individuals the incisive foramina penetrate the upper tooth row crowns), 8) the hamular strap is long and thin and the subsquamosal foramen is well developed but proportionately smaller than in the new Congolese species (*H. pygmaeus*, *H. thornesmithae*) described above (Figs 12e).

Unlike other species described herein, several skulls of this taxon show anomalous patterns of the palate including extra post palatal foramen (FMNH 177887, 177888, 193218) and interrupted incisive foramina (FMNH 177886, 177887). One specimen (FMNH 193234) also displays a white tail tip.

Distribution. Known only from Mahale National Park, 1180–2440 m, western Tanzania.

Reproduction. Of the specimens collected, there were 7 males and 5 females. The reproductive condition of 4 females was inspected: females collected on Aug 25 & 28, 2005 had no embryos (FMNH 177888, 177890) but the former was lactating. Two others were in the early stages of pregnancy: FMNH 178011, collected on 25 Aug., 2003 (CR = 5 mm) and FMNH 193233, collected 9 Nov., 2005 (CR = 7 mm).

Habitat. The Mahale Peninsula is predominately covered with *Brachystegia* (Miombo) woodland, but higher elevations on the Mahale Ridge are covered in montane grasslands and forest (Itani 1990). Forest is also found on the western and southwestern slopes from the ridge at 2400 m down to lowland forests at 780 m on the shore of Lake Tanganyika. The montane forest vegetation is an outlier of the Albertine Rift forests. Over 1,170 plant species, of which 39 are Albertine Rift endemics, have been recorded at Mahale (Nishida & Uehara 1981; Nishida 1990; Plumptre et al. 2007).

One specimen was collected in riverine forest along the Kabezi River. This river and other smaller tributaries flowing down the Mahale and Kabezi ridges are lined with riverine forest surrounded by tall Miombo woodland with stands of solid-stemmed bamboo, *Oxytenanthera abyssinica*. Higher up on the Mahale Ridge, the Miombo gives way to tall montane grassland dominated

Fig. 14. Map of current biogeographic units and their possible barriers in eastern Africa as relevant to the *H. anselli* and *H. denniae* groups.

by *Hyparrhenia* spp., *Themeda triandra*, and *Festuca* sp., with scattered *Protea gauguedi, Erythrina abyssinica, Cussonia arborea* and isolated *Parinari curatellifolia*. The riverine forest canopy reaches 30 m in places and is dominated by *Newtonia buchannanii, Parinari excelsa, Bridelia micrantha,* and *Spathodea campanulata,* with occasional *Tabernaemontana stapfiana, Ficus sur, Ficus thonningii, Zanha golungensis, Prunus africana,* and *Myrianthus holstii*. The understory is dominated by woody shrubs and *Aframomum alboviolaceum* (Plumptre et al. 2003; Moyer 2006).

Two specimens originated in the Mfitwa Forest, on the SE side of the Mfitwa Peak (6°7'54" S, 29°47'38" S, 2440 m) which is surrounded by extensive areas of species-rich montane grasslands. The dominant species included *Festuca* sp., *Themeda triandra*, *and Hyparrhenia rufa*. Mature parts of Mfitwa forest in sheltered valleys reach a canopy height of 30 m. Dominate species include: *Polyscias fulva, Parinari curatellifolia, Agaurista salicifolia, Croton megalobostrys, Croton sylvaticus, Bersama abyssinica, Trichilia emetica, Ficus thonningii, Myrianthus arboreaus, Maesa lanceolata,* and *Syzygium caminnii*. The diverse forest understory is dominated by *Olyra latifolia, Dracaena laxissima, Mondia whitei, Renealmia engleri, Psychotria* sp., dense stands of bracken fern, *Pteridium aquilinum*, in light gaps and at the forest edge. Large areas of the forest are covered in nearly impenetrable monodominant stands of montane bamboo, *Oldeania alpina*, with very few other species penetrating this heavily shaded zone. Occasionally a forest tree emerges through the canopy in such stands; these areas are likely to be secondary, and at least some of them were under cultivation in the past (Itani 1990).

Etymology. The species is named for Noah E. Mpunga and Sophy J. Machaga, who run the Southern Highlands Conservation Program for the Wildlife Conservation Society. These leading conservationists have dedicated the last 20 years to helping describe, advocate for, and protect some of Tanzania's most threatened and iconic species. We recommend "Mahale wood mouse" as an English common name.

DISCUSSION

Comments on cryptic diversity

With the results presented here, the numbers of recognized species of *Hylomyscus* have increased from 8 to 21 since 2005. The 160% increase documented here over the past 14 years for *Hylomyscus* is an extraordinary number for a continental system; typically, sites of high increase in newly described species diversity are found on island systems (e.g., Madagascar, Goodman & Soarimalala 2018; Indonesia, Demos et al. 2016; Philippines, Heaney

et al. 2016). For *Hylomyscus*, such increases are due to the resurrection of synonymized taxa, new explorative surveys, and the recognition of cryptic species through genetic methods. Recently, based on molecular results, Nicolas et al. (2020) have shown that an additional 8–10 species remain undescribed from the genus, including potentially one more from the *anselli* group (figs 1–2: H. sp7). Accordingly, we predict a further increase of at least 30% over the next decade within the genus, because other species groups, especially those primarily distributed in the Congo Basin, have not yet been satisfactorily collected, documented or analyzed. We predict comparable increases will be attained in several other African small mammal groups including *Graphiurus*, *Dendromus*, *Crocidura* and various microbat species complexes currently being documented by Demos, Patterson, Esselstyn, Voelker, Kerbis Peterhans and colleagues (e.g., Demos et al. 2018, 2019a, 2019b; Patterson et al. 2019). Such cryptic, typically nocturnal, small mammal species that form the bulk of mammalian diversity (>70%), are often unrecognized by the scientific community. As an alternative, the work of Krásová et al. (2019) has taken a different approach in their review of the *Mus triton* complex; despite relatively important genetic multilocus differences among allopatric populations they have not split the complex into multiple species. Genetic analyses provided here are crucial in uncovering cryptic diversity within *Hylomyscus*. Although similar morphologically, *H. stanleyi* is only distantly related to true *H. anselli*, with which it had been co-mingled. Its close geographic proximity (ca. 400 km) and similar phenetics made it tempting to include the two as a single taxon (Carleton & Stanley 2005; Carleton et al. 2006; Demos et al. 2014a; Carleton et al. 2015; Nicolas et al. 2020).

Sadly, despite the lip-service, this is an era marked by declining resources and opportunities for field work and surveys, closure of dozens of natural history collections, a collapse in the number of trained alpha taxonomists and a lack of appreciation for the importance of biodiversity and the willingness to document it (Winker 1996; Tewksbury et al. 2014). Further, some conservation administrators feel it more important to protect individual organisms rather than entire ecosystems (Goodman & Lanyon 1994), a short-sighted strategy easily maintained by arm-chair 'conservationists'. Although this strategy may make sense among high profile taxa like gorillas or pandas, many ecosystems do not boast such charismatic species. The high fecundity of most small mammal species makes them quite resilient to collecting, but habitat loss reduces viable populations permanently. Further, integrative taxonomic revisions of small mammals can identify the regions with the highest (most valuable) evolutionary diversity and therefore provide straightforward suggestions for prioritization of conservation efforts.

Comments on biogeography

The *Cytb* data (Fig. 4) suggest that the once united clades of *H. anselli* and *H. denniae* (under *Hylomyscus denniae*) are not only distinct, reciprocally monophyletic, and not each other's sisters, but also have separate lowland forest origins. This answers the question posed by Carleton et al. (2006: 318) on whether or not these two montane species groups shared a recent common ancestor, relative to taxa from the Guineo-Congolian lowlands. The occurrence of two new members of the *H. anselli* group in the heart of the Congo Basin, including the first one to diverge, suggests a lowland origin for the group. Other members of core Congo Basin taxa (i.e., *H. alleni* and *H. parvus* groups) form a clade sister to the *H. anselli* group. In addition, within the *H. anselli* group, *H. pygmaeus* from the Congo Basin is sister to all other members. *Hylomyscus thornesmithae* from the Congo Basin is sister to our East Africa clade (Kenya, Tanzania and Malawi). Additional material from the Guineo-Congolian rainforest, especially from the left bank of the Congo/Lualaba River, may shed light on these biogeographic relationships, as would ancestral area reconstruction, which was not carried out in this study.

A significant phylogeographic break, shown here between the *H. anselli*/*H. heinrichorum* clade and the rest of the *H. anselli* clade (excepting *H. pygmaeus* and *H. thornesmithae* but including *H. kerbispeterhansi, H. stanleyi, H. mpungamachagorum,* and *H. arcimontensis*) has been depicted by Chapin (1932: fig. 18) in his delimitation of bird distributions. Chapin distinguishes a *Rhodesian Highland District* (= Zambian, including the ranges of *H. heinrichorum* and *H. anselli*; Chapin 1932: fig. 18, zone 14; see our Fig. 14) from an *East African Highland District* (zone 13, known known here as the *East African* clade), including the remaining taxa. It may be that these zones are separated by the Luangwa River Valley in northeastern Zambia as has been shown for the divide between *Praomys delectorum* of northern Malawi and *Praomys jacksoni* of NE Zambia (Ansell 1978: Map 187; Bryja et al. 2012: fig. 2c). The Luangwa River also seems to be the eastern limit in the distribution of *Hylomyscus anselli* (as '*Praomys denniae'* in Ansell 1978: Map 188; Bryja et al. 2012: fig. 2d). Further collecting on both sides of the upper Luangwa River is necessary to determine if this break holds for other small mammals. This biogeographic break, as well as additional potential barriers to extant small mammal distributions, are depicted in Fig. 14. Although not as strongly supported, the sister relationship of *H. arcimontensis* to other members of the *East African* clade (Fig. 4), demonstrates the long term isolation of the Eastern Arc Mountains from adjacent East African montane systems.

Mbizi Forest is, by definition, an Albertine Rift Forest, as it is adjacent to the SW end of Lake Tanganyika. It also lies ca. 200 km NW of the Southern Highlands of Tanzania and floristically is most closely related to these latter forests and the mountains around the northern end of Lake Malawi (Kerfoot 1964; White et al. 2001). There is no clear geographical barrier to montane forest species between Mbizi Forest and the forests around the northern end of Lake Malawi in the Southern Highlands. These areas are connected by high ground that could have supported montane forest in a wetter and colder period. However, there may have been a rain-shadow from the Southern Highlands that would have limited the extent of forest in this area (Moreau 1966).

Mbizi also contains elements of the forests of the Kenyan Highlands (Lovett 1990) as well as the Albertine Rift forests (30 of the 70 tree species are Albertine Rift endemics; Plumptre et al. 2007). Looking to the north, mixed affinities and disjunctions in distribution may be explained by the *Karema Gap* (Moreau, 1966), which forms an ecological barrier between Mbizi forest and the forested habitats of the Mahale Mountains (aka Kungwe Forest). This is a trough nearly 100 km wide extending from the shore of Lake Tanganyika southeast to the Rukwa Valley (further discussion below). Much of the terrain in the Karema Gap lies below 1000 m and forms a major biogeographical barrier to montane forest bird species distribution (Moreau 1966). It is apparent that this gap is also an important barrier for mammals.

Mbizi Forest is at the southern end of the postulated southwestern dispersal route for Guineo-Congolian forest species into the Eastern Arc (Lovett & Wasser 1993). However, Mbizi falls within the Lake Tanganyika climactic zone (Lovett 1990) and has notable faunistic differences. A number of neo-endemic and relictual forms of birds, reptiles, amphibians, and mammals are found in Mbizi with varying affinities to taxa in the Eastern Arc, Southern Highlands, Albertine Rift, and Guineo-Congolian forests (Vesey-Fitzgerald 1964; Moreau 1966; Britton 1980; Channing & Howell 2006; Plumptre et al. 2007). This is reflected in our phylogeny (Fig. 4) as the Mbizi population (*Hylomyscus stanleyi*) is sister to *H. kerbispeterhansi* from the Kenyan Highlands rather than the more proximate Mahale population (*H. mpungamachagorum*).

There are significant differences between the small mammal communities of Mbizi and the Southern Highlands: Mbizi is inhabited by *Praomys jacksoni* (Mizerovská et al. 2019), whereas the Southern Highlands are inhabited by the phylogenetically distant *Praomys delectorum* (Bryja et al. 2014; Sabuni et al. 2017). Though they are sister species, Mbizi houses the endemic *Lophuromys sabunii*, while Southern Highlands are inhabited by *Lophuromys machangui* (Verheyen et al. 2017; Sabuni et al. 2018). Finally, Mbizi is inhabited by *Crocidura montis* 1b, while Southern Highlands are inhabited by *Crocidura montis* 3 = '*luna*' (Sabuni et al. 2018: fig. 2b). On the other hand, the dry forest species living in woodland ecotones were able to disperse from northern part of South-

ern Highlands to the northwest along Lake Tanganyika (e.g., *Mus triton*, clade D, Krásová et al. 2019; *Grammomys surdaster*, clade su4, Bryja et al. 2017).

The montane forests of the Mahale Mountains are also an outlier of the Albertine Rift forests (Plumptre et al. 2007). To their south is the Karema Gap while to their north lies the 70 km. wide *Kigoma-Malagarasi River Gap*, separating Mahale from the Burundi Highlands (Moreau 1966). In an earlier, unfortunately overlooked paper, Moreau (1943) reviewed geological evidence for the origins of the Karema Gap and pointed to an ancient west to south-east trough of a geological age exceeding that of the Lake Tanganyika basin. On the west side of Lake Tanganyika, this trough is filled by the Lukuga River, which exits the lake at Kalemie (formerly Albertville). The age of this trough may explain why *Hylomyscus stanleyi* is more closely related to *Hylomyscus kerbispeterhansi* in southern Kenya (almost 1000 km to the northeast) than to the more proximate taxon, *Hylomyscus mpungamachagorum*, less than 300 km to the north. Moreau was convinced that Karema Gap is of much greater biogeographic significance than the Malagarasi River Gap.

On their western slope, Mahale forest cover is nearly continuous from the montane forests on the ridge at 2400 m down to lowland forests at 780 m on the shore of Lake Tanganyika. Only 39 of the 1,170 plant species recorded at Mahale are Albertine Rift endemics (Nishida & Uehara 1981; Plumptre et al. 2007). The lowland forests harbor mammal species more typical of the Guineo-Congolian lowland forests (Moyer 2006), including *Pan troglodytes schweinfurthii*, *Manis gigantea*, and *Protoxerus stangeri* ssp., as well as birds (e.g., *Phyllastrepus scandens*) and reptiles (e.g., *Dendroaspis jamesoni*). At least two small mammal species from the W.T. Stanley 2003 Mahale survey have an origin in the Southern Highlands of Tanzania (including Mt. Rungwe) with extensions into the Marungu Highlands of DRC. These are *Otomys lacustris* Allen & Loveridge, 1933 and *Rhynchocyon cirnei reichardi* Reichenow, 1886: see discussions in Taylor et al. (2009), Corbet & Hanks (1968), and Rathbun (2017: fig. 3). Small mammals originating in the Albertine Rift include *Grammomys* cf. *dryas*, *Praomys jacksoni* and *Sylvisorex* aff. *ruandae*. On the other hand, both new species of Tanzanian *Hylomyscus* described here (*H. mpungamachagorum, H. stanleyi*) are closely related to forms from the Kenyan Highlands and the Eastern Arc montane archipelago (Fig. 4). It is likely that when the ancestor of the Eastern Afromontane clade of *H. anselli* group dispersed from the Congo Basin, the Albertine Rift Mountains were already inhabited by the *H. denniae* clade. They were able to colonize the peripheral (southern) parts of these mountains, from where they colonized the Eastern Arc Mountains up to parts of the Kenyan Highlands. In both the Kenyan and Tanzanian Highlands, the *H. anselli* and *H. denniae* groups are typi-

cally mutually exclusive; only in the Mau Forest (Kenya) are both species groups found in sympatry.

Several other breaks in the distribution of the *Hylomyscus denniae* and *Hylomyscus anselli* clades, referenced in Figure 14 are worthy of mention. One of them is the restriction of *Hylomyscus denniae* to the Ruwenzori Mountains of western Uganda and eastern DRC as first demonstrated by Huhndorf et al. (2007) and subsequently by Demos et al. (2014a). This break is reinforced by the Semliki River to the south and the Victoria Nile to the north. Surveys of the Blue Mountains to the north of the Ruwenzoris would be enlightening in this regard. The arid corridor of northeastern Uganda, here called the Karamoja Gap (Fig. 14), further isolates species of *H. denniae* (sensu strictu) from other *Hylmomyscus* ssp. in western Kenya (e.g., Mt Elgon and Cherangani Hills; Demos et al. 2014a). Our collections and surveys have failed to detect members of the *Hylomyscus denniae* or *Hylomyscus anselli* groups in the Imatong Mountains of southern Sudan and their foothills in northern Uganda (i.e., Agora Agu Forest Reserve); only *Hylomyscus stella* has been recovered from these forests. Butynski (in litt.) believes that the primate communities (i.e., galagos and vervets) of Agora Agu/Imatong Forests are slightly more closely allied with the Albertine Rift forests than with the Kenya Highlands and further, that the Victoria Nile, despite its young age may have been a factor in isolating the chimpanzee (*Pan troglodytes*) to the Albertine Rift (although they have older mid-Pleistocene fossils in Kenya; McBrearty & Jablonski, 2005).

Another arid corridor, the Tsavo Gap (Fig. 14), separates the northernmost population of *Hylomyscus arcimontensis* (Taita Hills in SE Kenya) from another relative of the *Hylomyscus anselli* group in the Kenya Highlands (*Hylomyscus kerbispeterhansi*) as well as the more distantly related *Hylomyscus endorobae* (Mt. Kenya, the Aberdares and Mau Escarpment). It is curious that no *Hylomyscus* spp. have persisted in the Volcanic Highlands of northern Tanzania (Mt. Kilimanjaro, Mt. Meru, Arusha, Ngorongoro Crater) despite our collecting efforts in these areas. In this regard, specimens from northern Tanzania (Tengeru, Ngorongoro) referred to *Hylomyscus anselli* by Bishop (1979) in his seminal paper, were misidentified.

The distribution of *Hylomyscus arcimontensis* (indeed the genus *Hylomyscus*) comes to an abrupt end in Mwenembwe Forest, Nyika National Park, northern Malawi. This gap, called here, the central Malawi Gap, at about 12° south, lies 'between Nyika and Mount Ntchisi within the central highlands of Malawi' (Kaliba 2014: 213 in his discussion of bird and mammal distributions; see his fig. 6.1). In her review of avian biogeography in Malawi, Dowsett-Lemaire (1989) pinpoints the major Malawi avian break slightly further south, at 14°.

These biogeographic factors have received little attention since Moreau's (1966) discussion of their impacts on

bird distributions. The biotic impacts of these isolating mechanisms must be considered in future conservation management decisions. Given this faunal mosaic, the discovery of pockets of endemism, and the likelihood of discovering further unknown biodiversity, we call for new surveys of the virtually undocumented highlands of the Albertine Rift along the shores of Lake Tanganyika including the Marungu Highlands of southeastern Democratic Republic of Congo (not surveyed since 1884 by Richard Böhm; Noack 1887) and Gombe Mountain NP, well known for its chimpanzees but little else.

Key to Afromontane *Hylomyscus* (excepting W Africa) plus all members of the *H. anselli* group

1. Supra-orbital shelf strongly beaded ....
   ....*H. aeta* (Thomas, 1911)
2. Supra-orbital shelf not beaded 3
3. Sub-squamosal foramen tiny/absent, hamular process short & thick (*H. denniae* group) 5
4. Sub-squamosal foramen large, hamular process long & thin 9
5. Only found in Ruwenzori montane forests, size large ONL 25.6–27.8 ....*H. denniae* (Thomas, 1906)
6. Found in other East African montane forests 7
7. Size large, CI 26.8–28.6, Kenya only: Mt Kenya, Aberdares & Mau forests ....
   ....*H. endorobae* (Heller, 1910)
8. Size small, CI 24–26 mm, Albertine Rift S of Ruwenzoris (not including Tanzania) ....
   ....*H. vulcanorum* (Lönnberg & Gyldenstolpe, 1925)
9. Teats 4+4, incisors orthodont ....
   ....*H. stella* (Thomas, 1911)
10. Teats 2+4, incisors proodont, orthodont or weakly opisthodont (*H. anselli* group) 11
11a.Crown length of upper tooth row under 3.3 (Congo Basin, small) 13
11b.Crown length of upper tooth row 3.3–4.0 (Afromontane, medium) 15
11c.Crown length of upper tooth row over 4.0 (Afromontane, large) 19
13. Crown length of upper tooth row under 1.8, slightly proodont .... *H. pygmaeus* (sp. nov.)
14. Crown length of upper tooth row 3.0–3.25, orthodont ....*H. thornesmithae* (sp. nov.)
15. Post palatal foramina at rear (3rd lamina) of M1, LD and NL longer, Table 4 (montane Kenya only) ....
   ....*H. kerbispeterhansi* Demos et al., 2014
16. Post palatal foramina between M1 and M2 or at beginning of M2, LD and NL shorter, Table 4 17
17. Post palatal foramina between M1 and M2, incisive foramina fall just short of upper molar alveoli, upper incisors orthodont (Eastern Arc only) ....
   .... *H. arcimontensis* Carleton & Stanley, 2005
18. Post palatal foramina at beginning of M2, incisive foramina reach upper molar alveoli, upper incisors

typically opisthodont (Mahale Mts only) ....
   .... *H. mpungamachagorum* (sp. nov.)
19. Incisive foramina penetrate CLM, slightly opisthodont (Angola only) ....
   ....*H. heinrichorum* Carleton et al., 2015
20. Incisive foramina do not penetrate CLM 21
21. Occipito-nasal length under 26.4, nasal length under 9.4 (Zambia only) ....*H. anselli* (Bishop, 1979)
22. Occipito-nasal length over 26.3, nasal length over 9.3 (Mbizi Mts only) ....*H. stanleyi* (sp. nov.)

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APPENDIX 1

Specimens examined in this study (n = 199). Specimens included in the morphometric analyses only are in standard type, those included in both morphometric and molecular analyses are in boldface type, and those included in the molecular analyses only are indicated with an asterisk (*). All specimens include Field Museum of Natural History (FMNH) catalogue numbers except for the *Hylomyscus anselli* type series from the British Museum of Natural History (BMNH), National Museum of Zambia (NMZ), Specimens from the Czech Republic located at the University of South Bohemia and at the Institute of Vertebrate Biology have the following acronyms: ANG for specimens from Angola and RS for specimens from Zambia.

Hylomyscus aeta (1): **Uganda**, Nteko Parish, edge of Bwindi-Impenetrable NP, 1600 m: 160492*.

Hylomyscus anselli (19): **Zambia**, Mwinilunga Dist.: Jimbe Stream, BMNH 74.250 (TYPE), NMZ 3639, NMZ 3808; Kasombu Stream ('Isombu', see Ansell, 1978), NMZ 3631; Nyanjowe Stream ('Nyansowe', Ansell 1978), BMNH 74.251, NMZ 3638; Sakeji Stream (Sabeji, Sekezhi; see Ansell, 1978), BMNH 61.944; Mpika Dist., Danger Hill, Lubikila Stream ('Lubikila', 'Luitikila'; see Ansell 1978) BMNH 73.142, NMZ 2764–2767, NMZ 2769–2781; Kasanka National Park, pontoon, RS 1113–1115; Kasanka National Park, Fibwe, RS 1606–1607; Zambezi source, RS 803, 810, 811; Kifubwa Rock Shelter Stream, RS 818; Nchila Wildlife Reserve, RS 793.

Hylomyscus arcimontensis (58): **Malawi**, Misuku Hills, Mughese Forest, 1625 m: 196303, 196311*, **196753**, 196754–196759, 196761**;** Misuku Hills, Mughese Forest, 1890 m: 196762–196769**;** Nyika National Park, Mwenembwe Forest**,** 2233m: 211576*, 211577*; **Tanzania**, Mt Rungwe, Rungwe FR, 5 km E Ilolo, 1870 m: 163584–163588, 163590–163595; Mt Rungwe, Rungwe FR, 6 km E, 1.2 km N of Ilolo, 2140 m: Mt Rungwe, Rungwe FR, 7 km E, 2.5 km N of Ilolo, 2410 m: 163598–163600; East Usambara Mts, 4.5 km ESE Amani, Monga Tea Estate, 870–900 m: 150120, 150121, 150123, 150124, 150125, 150142, 150143*, 150146, 150147, 150149, 150150,

150153, 150430; East Usambara Mts, 4.5 km WNW Amani, Monga Tea Estate, 870–900 m, 150119, 151251; East Usambara Mts, 4.5 km NW Amani, Monga Tea Estate, 1100 m, 147291, 147476*; East Usambara Mts, 6 km NW Amani, Monga Tea Estate, 1100 m, 150118*; West Usambara Mts., 12.5 km NW Korogwe, Ambangu-lu Tea Estate, 1300 m, 150130, 150135, 150136, 150138, 150154, 150156, 150159.

Hylomyscus denniae (1): **Uganda**, Rwenzori Mts NP, Mubuku R, rt bank, Nyabitaba Hut , 2667 m: 144526*.

Hylomyscus thornesmithae (5): **Democratic Republic of Congo**, 14 km N of Boende, Quartorze, 326 m: **222524** (TYPE); 4 km N of Boende, Baliko, 358 m, **2119611-219613**,**219689**.

Hylomyscus endorobae (1): **Kenya**, Aberdare Range, 3.8 km W & 2.5 km S of Gatarakwa, 2700 m: 190467*.

Hylomyscus heinrichorum (25): **Angola**, Mt Moco, 83793, 83795, 83796 (TYPE), 83797, 83799, 83801–83807, 83895; Mt Soque, 83783–83792; Namba Village, ANG 210, ANG 215, ANG 237, ANG 252, ANG 259.

Hylomyscus kerbispeterhansi (55): **Kenya**, Cherangani Hills, Kipkunnur Forest, 2740 m: 217377, 217381–217382, 217383*, **217384**, 217385*, 217386, 217390, 217394–217395, 217408, 217422, 217605–217610, 217612–217614; Kapenguria, 153250, 2100 m; Mau Forest, 15.5 km N, 16.4 km E Bonet, 2350 m: 209997,

210000, 210001*, 210017 (TYPE), 210018, 210023, 210042; Mau Forest, 8.5 km N & 18.4 km E of Kericho, 2320 m: 210061–210063, 210065, 210069, 210071, Mt Elgon National Reserve, nr. Kimothon Gate, 2530 m: 217325*, 217327–217333, 217340–217342, 217345, 217354, **217358**, 217597–217600, **217601**, 217602, 217604.

Hylomyscus mpungamachagorum (6): **Tanzania**, Mahale Mts NP, Mahale Mts, 0.5 km NW of Nkungwe Summit, 2100 m: 177911, **177888**, **177889** (TYPE), **177890**; Mahale Mts NP, Mahale Mts, 0.5 km S of Pasagulu Hill, 1420 m: 177886–177887.

Hylomyscus pygmaeus (1): **Democratic Republic of Congo**, Baleko, 358 m, **219684** (TYPE).

Hylomyscus stanleyi (25): **Tanzania**, Mbizi Forest Reserve, 0.5 km N, 4 km E of Wipanga, 2200 m: 171357–171359, **1171360**, 171361, **171362** (TYPE), **171363**, 171364–171367; Mbizi Forest Reserve, 0.5 km S, 3 km E of Wipanga, 2300 m: 171343, 171344, 171346–171348, 171350, 171351, **171352**, **171353**, 171354–171356, 171512, 171513.

Hylomyscus stella (1): **Uganda**, Bwindi-Impenetrable NP, Buhoma, 1500 m: 160511*.

Hylomyscus vulcanorum (1): **Democratic Republic of Congo**, Itombwe Forest, 1.5 km S Lusasa, 2050 m: 203881*.

APPENDIX 2

List of GenBank sequences.

Taxon	Voucher No.	GenBank No.	Country
Hylomyscus aeta	FMNH 160492	MN857618	Uganda
Hylomyscus alleni		AF518328	Gabon
Hylomyscus anselli	RS1113	JX126613	Zambia
Hylomyscus anselli	RS1114	JX126614	Zambia
Hylomyscus anselli	RS1115	JX126615	Zambia
Hylomyscus anselli	RS1606	JX126616	Zambia
Hylomyscus anselli	RS810	JX126617	Zambia
Hylomyscus anselli	RS811	JX126618	Zambia
Hylomyscus anselli	RS818	JX126619	Zambia
Hylomyscus anselli	RS793	JX126620	Zambia
Hylomyscus anselli	RS803	JX126621	Zambia
Hylomyscus arcimontenisis	FMNH 196753	KF876468	Malawi
Hylomyscus arcimontenisis	FMNH 196311	KF876469	Malawi

Taxon	Voucher No.	GenBank No.	Country
Hylomyscus arcimontenisis	FMNH 211577	KF876477	Malawi
Hylomyscus arcimontenisis	FMNH 147476	KF810191	Tanzania
Hylomyscus arcimontenisis	FMNH 150118	KF810192	Tanzania
Hylomyscus arcimontenisis	FMNH 150143	KF810193	Tanzania
Hylomyscus baeri		JQ735509	Guinea
Hylomyscus denniae	FMNH 144526	KF876479	Uganda
Hylomyscus endorobae	FMNH 190467	KF810158	Kenya
Hylomyscus grandis		JQ735513	Cameroon
Hylomyscus heinrichorum	ANG0210	MN857622	Angola
Hylomyscus heinrichorum	ANG0215	MN857623	Angola
Hylomyscus heinrichorum	ANG0237	MN857624	Angola
Hylomyscus heinrichorum	ANG0259	MN857625	Angola
Hylomyscus kerbispeterhansi	FMNH 217383	KF810205	Kenya
Hylomyscus kerbispeterhansi	FMNH 217384	KF810206	Kenya
Hylomyscus kerbispeterhansi	FMNH 217385	KF810203	Kenya
Hylomyscus kerbispeterhansi	FMNH 217325	KF810239	Kenya
Hylomyscus kerbispeterhansi	FMNH 217358	KF810200	Kenya
Hylomyscus kerbispeterhansi	FMNH 217601	KF810240	Kenya
Hylomyscus kerbispeterhansi	FMNH 210000	KF810226	Kenya
Hylomyscus kerbispeterhansi	FMNH 210001	KF810231	Kenya
Hylomyscus stanleyi	FMNH 171352	MN857627	Tanzania
Hylomyscus stanleyi	FMNH 171353	MN857628	Tanzania
Hylomyscus stanleyi	FMNH 171360	MN857629	Tanzania
Hylomyscus stanleyi	FMNH 171362	MN857630	Tanzania
Hylomyscus stanleyi	FMNH 171363	MN857631	Tanzania
Hylomyscus pamfi		JQ735527	Benin
Hylomyscus parvus		JQ735555	Cameroon
Hylomyscus pygmaeus	FMNH 219684	MN857626	DR of Congo
Hylomyscus simus		JQ735557	Ivory Coast
Hylomyscus mpungamachagorum	FMNH 177888	MN857619	Tanzania
Hylomyscus mpungamachagorum	FMNH 177889	MN857620	Tanzania
Hylomyscus mpungamachagorum	FMNH 177890	MN857621	Tanzania
Hylomyscus stella	FMNH160511	MN857632	Uganda
Hylomyscus thornesmithae	FMNH 219611	MN857633	DR of Congo
Hylomyscus thornesmithae	FMNH 219612	MN857634	DR of Congo
Hylomyscus thornesmithae	FMNH 219613	MN857635	DR of Congo
Hylomyscus thornesmithae	FMNH 222524	MN857636	DR of Congo
Hylomyscus thornesmithae	FMNH 219689	MN857637	DR of Congo
Hylomyscus vulcanorum	FMNH 203881	KF810176	DR of Congo
Hylomyscus walterverheyeni		JQ735614	Central African Republic