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RESEARCH PAPER

Phylogenetic relationships and biogeography of the *Hybomys* division (Muridae: Murinae: Arvicanthini), rodents endemic to Africa's rainforests

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Abstract. The *Hybomys* division (Muridae: Murinae: Arvicanthini) consists of four genera (*Hybomys*, *Typomys*, *Dephomys*, and *Stochomys*) endemic to the Guineo-Congolian rainforests of central Africa. Based on sequences from two mitochondrial (Cyt*b*, 12S rRNA) and two nuclear (*Rbp3*, *Ghr*) genes, we present a fossil-calibrated molecular phylogeny of the *Hybomys* division, based on wider taxon and geographic sampling than previously published phylogenies. Species of *Typomys* formed a clade that was sister to a clade containing *Hybomys* and the sister genera *Dephomys* and *Stochomys*. *Hybomys basilii* and *Hybomys lunaris* were recovered as monophyletic, whereas *Hybomys univittatus* was recovered as polyphyletic and likely consists of at least three species. The divergence between the East African taxon *H. lunaris*, and the West and Central African taxa of *Hybomys* is estimated at 3.1 Mya. Based on molecular phylogenies and genetic distances, we infer that forms of *Hybomys* from both the highlands and lowlands of the Cameroon Volcanic Line, except for *H. basilii*, should be considered a single species for which *Hybomys rufocanus* is the oldest available name. As proposed, *H. rufocanus* would include the named forms *badius* and *eisentrauti* as synonyms, as well as populations north of the River Sanaga previously recognized as *H. univittatus*. Material from nearest the type locality of *H. univittatus* is sister to *H. rufocanus*, whereas other specimens currently recognised as *H. univittatus* from south of the River Ogooue and in the Congo Basin are sister to this *H. rufocanus* + true *H. univittatus* clade. Dating estimates place the origin and early diversification of the *Hybomys* division in the late Miocene, slightly preceding the radiation of most arvicanthine genera that inhabit savannah biomes. The historical biogeography of the *Hybomys* division appears to be congruent with hypothesized forest refugia, savannah barriers, and aridification cycles of the Neogene and Pleistocene.

Key words: Afromontane, Bioko, Dahomey Gap, Guineo-Congolian Region, Miocene refugia, *Hybomys univittatus* complex

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Introduction

The *Hybomys* division (Murinae: Arvicanthini) was coined by Musser & Carleton (2005) to circumscribe three genera of murid rodents – *Dephomys*, *Hybomys*, and *Stochomys* – all confined to rainforest landscapes of Sub-Saharan Africa (Fig. 1B). *Stochomys* and *Dephomys* contain one and two species, respectively, but the oldest named taxon *Hybomys* is more speciose, with six or seven valid species in recent taxonomic synopses (Musser & Carleton 2005, Carleton 2013, Denys et al. 2014, 2017). The generic limits of *Hybomys* were debated soon after Thomas's (1910) original description (type species – *Mus univittatus* Peters, 1876), which was based on a species from north-western Gabon. One year later, Thomas (1911) named the genus *Typomys* (type species – *Mus trivirgatus* Temminck, 1853) to embrace a morphologically distinctive taxon from Ghana. Notwithstanding Thomas's diagnoses as separate genera, the subsequent taxonomic history of *Hybomys* and *Typomys* has been closely intertwined; systematists have supported their synonymy, with or without explicit retention of *Typomys* as a subgenus (Ingoldby 1929, Ellerman 1941, Rosevear 1969, Van der Straeten & Verheyen 1982, Carleton & Robbins 1985, Musser & Carleton 2005, Carleton 2013, Aplin 2017, Denys et al. 2017).

In a pivotal morphometric study, Van der Straeten (1984) revived the issue of *Hybomys* and *Typomys* as distinct genera. His multivariate analyses of craniodental dimensions disclosed a stronger similarity of *Hybomys* (*Hybomys*) to samples of *Dephomys* than to those of *Hybomys* (*Typomys*), a phenetic relationship that persuaded him to recognize *Typomys* as a valid genus. While acknowledging Van der Straeten's (1984) results and taxonomic recommendation, Musser & Carleton (2005) enumerated many qualitative morphological characters shared by *Hybomys* and *Typomys* that jointly set them apart from *Dephomys*. They elected to maintain *Typomys* as a well-defined subgenus, while advising broader surveys of character variation among murids indigenous to Africa's rainforests to better illuminate the most appropriate taxonomic rank accorded *Typomys*. Recent molecular studies, incorporating a combination of mitochondrial and nuclear genes, have grouped species of *Hybomys* with those of *Stochomys* and *Dephomys* in a strongly defined clade (Lecompte et al. 2008, Schenk et al. 2013, Missoup et al. 2016, Steppan & Schenk 2017, Missoup et al. 2018, Rowe et al. 2019, Mikula et al. 2021). Although such molecular results lend support to the recognition of a *Hybomys* division within Arvicanthini, the conspicuous absence of members of *Typomys* sensu stricto from most of these studies left unresolved the questions of its phyletic kinship and correlative taxonomic status.

Missoup et al. (2018) first reported the paraphyly of the genus *Hybomys* in their molecular phylogeny including members of the subgenera *Hybomys* and *Typomys*, resolving the debate of the status of *Typomys* and demonstrating that it warrants generic status. *Hybomys* and *Typomys* were not recovered as sister taxa but rather *Typomys* was recovered as sister to a clade containing *Hybomys*, *Dephomys* and *Stochomys* (Missoup et al. 2018). These relationships were also recovered from recent analyses of multilocus nuclear data and mitogenomes (Mikula et al. 2021). Unfortunately, discussion by Missoup et al. (2018) of the morphological context and biogeographic implications of this result were brief. This study also raised questions regarding the validity of the montane endemic species, *Hybomys eisentrauti* and *Hybomys badius*, which were recovered in a clade with *Hybomys rufocanus* and all three showed little genetic differentiation. This *eisentrauti/badius/rufocanus* group was recovered as sister to *Hybomys univittatus*. However, the analyses conducted by Missoup et al. (2018) were based on genes sequenced from a single specimen of each taxon and did not include sequences available in GenBank for additional specimens of the *Hybomys* division. Although clear from their results, that the *eisentrauti/badius/rufocanus* group likely represented a single species, the relationships with populations in the *H. univittatus* species complex necessitates further investigation, particularly in the context of biogeography.

The phylogenetic reality of a *Hybomys* division and interrelationships among its constituent genera hold significance in view of the climatic history of the Guineo-Congolian rainforests inhabited by these rodents. Biogeographers have divided Africa's Guineo-Congolian Region into several major forested blocks (Fig. 1A) and identified biogeographic zones within each block based on major river barriers and savannah intrusions, notably the Dahomey Gap (Booth 1958, Happold 1996). Climatic fluctuations have certainly affected expansion and contraction of Guineo-Congolian rainforests (Plana 2004) and left their imprint on the evolutionary histories of faunas that are reliant

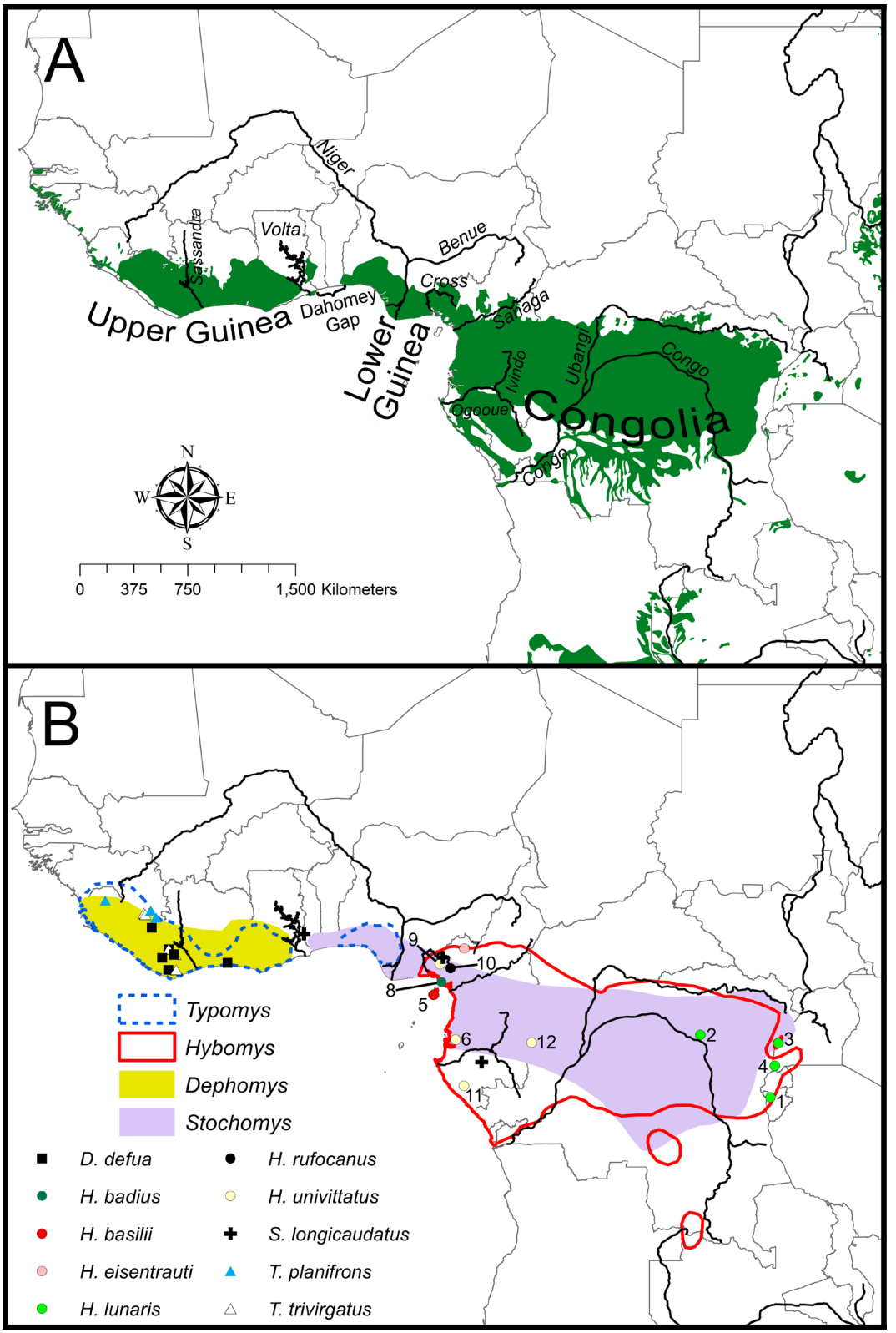

Fig. 1. The Guineo-Congolian Region, sensu White (1983), and distribution of the *Hybomys* division, tribe Arvicanthini. A) Current extent of Guineo-Congolian rainforests (green – range shapefiles imported from White 1983). Major forest subdivisions of the Guineo-Congolian Region follow Hardy et al. (2013), who defined the frontier between Upper Guinea and Lower Guinea at the Dahomey Gap and between Lower Guinea and Congolia along the drainage of the Congo-Ubangi rivers. Other major rivers of biogeographic significance include the Cross and Niger. B) Distribution of genus-group taxa currently assigned to the *Hybomys* division (range shapefiles acquired from Terrestrial Mammal dataset, IUCN Red List – http://www.iucnredlist.org/technical-documents/spatial-data). Since their descriptions, most systematists have maintained *Typomys* Thomas, 1911 as a valid subgenus of *Hybomys* Thomas, 1910. Collecting localities of taxa of the *Hybomys* division are shown and those of the genus *Hybomys* are identified with numbers and described in more detail in Table 1.

upon them, as reflected by the speciation patterns hypothesized for a wide variety of rainforest mammals (Carleton & Robbins 1985, Quérouil et al. 2003, Gaubert et al. 2004, Bohoussou et al. 2015) and birds (Mayr & O'Hara 1986, Fjeldså & Bowie 2008). In light of this engaging body of research, we note that the four genus-group taxa of interest here – *Dephomys*, *Hybomys*, *Stochomys*, and *Typomys* – exhibit discrete distributions within various subregions of the Guineo-Congolian Region (Fig. 1B).

In this study, we developed a robust molecular phylogeny, employing two mitochondrial (Cyt*b* and 12S rRNA) and two nuclear (*Rbp3* and *Ghr*) genes, to investigate the systematics of the *Hybomys* division, tribe Arvicanthini. Our study provides a wider geographic sampling of taxa of the *Hybomys* division than used in previous molecular studies (Lecompte et al. 2008, Schenk et al. 2013, Missoup et al. 2016, 2018, Steppan & Schenk 2017, Mikula et al. 2021) and includes sequence data from all named taxa with the exception of *Dephomys eburneae* and *Typomys pearsei*, which is currently recognized as a synonym of *Typomys trivirgatus.* The specific objectives of this study are: 1) to evaluate the evolutionary history of the genera within the *Hybomys* division sensu Musser & Carleton (2005) in the context of broader arvicanthine evolution; 2) to assess relationships within the genus *Hybomys*; and 3) to relate the phylogeographic pattern and divergence age of taxa within the *Hybomys* division to influential Neogene climatic events.

Material and Methods

Specimens, taxonomic sampling, and abbreviations

Fresh tissues of *Stochomys longicaudatus*, *Dephomys defua*, *Typomys planifrons*, and *T. trivirgatus* were acquired through expeditions to Ghana (in 1999; Decher et al. 2021), Côte d'Ivoire (in 2002; Decher et al. 2005), Guinea (in 2003 and 2008; Norris 2006), Sierra Leone (in 2006; Decher et al. 2010), and Liberia (in 2010). Tissues of *Hybomys basilii* were obtained from the Field Museum of Natural History (FMNH), Chicago, Illinois, and those of *H. univittatus* from the Muséum National d'Histoire Naturelle (MNHN), Paris, France. Voucher specimens are deposited in the U. S. National Museum of Natural History (USNM), Smithsonian Institution, Washington, D. C., in the FMNH or in the MNHN (Table S1); tissues of the USNM vouchers are maintained at the University of Vermont Natural History Museum. Gene sequences for all genera and species of the *Hybomys* division sensu Musser & Carleton (2005) other than *D. eburneae* were obtained either from these tissues or from accessions downloaded from GenBank (Table S1). Mitogenomes assembled as by-products of sequence data obtained by anchored hybrid enrichment by Mikula et al. (2021) were used to obtain sequences for two mitochondrial genes (Cyt*b* and 12S rRNA) from six taxa of the *Hybomys* division (Genbank Accession numbers MN807597-MN807602). The quality of the Cyt*b* sequences obtained from these mitogenomes were assessed by Kimura-2-parameter distance (Kimura 1980) and amino acid p-distance intraspecific comparisons using MEGA6.0 (Tamura et al. 2013). Sampling localities of sequences of the *Hybomys* division used in this study are shown in Fig. 1B.

Musser & Carleton (2005) did not recognize formal tribes of the Murinae (see Discussion) but allied the 126 murine genera they considered valid into 29 divisions, including the *Hybomys* division. Rowe et al. (2019) subsequently refined this number to 33 divisions, excluding 12 extant and extinct genera, which Rowe et al. (2019) considered *incertae sedis*. To inform selection of sister groups and second-order outgroups, we relied upon hierarchical relationships divulged by recent, taxonomically broad molecular phylogenies of Murinae and accompanying tribal reclassifications (Lecompte et al. 2008, Schenk et al. 2013, Missoup et al. 2016, Steppan & Schenk 2017, Rowe et al. 2019). Thus, we included an exemplar of Deomyinae (*Acomys*) as sister-group to Murinae and selected generic representatives of several murine tribes (Apodemini, Millardini, Murini, Otomyini, Phloeomyini, and Rattini) as potential outgroups to Arvicanthini, all based on sequences obtained from GenBank (Table S2). We underscore that the tribe Arvicanthini, which includes the genera of the *Hybomys* division (Lecompte et al. 2008), the hypothesized ingroup, is well covered among our genetic samples and numbers 49 species representing 19 arvicanthine genera (Table S1, Table S2).

Morphological terms used to describe cranial and dental features of murine rodents, as mentioned in the Discussion, are defined and/or illustrated in Rosevear (1969) and Carleton & Robbins (1985). We abbreviated the International Code of Zoological Nomenclature, 4th edition (International Commission on Zoological Nomenclature 1999),

to the "Code" and abbreviated its authorship as ICZN, together with the year and relevant article.

DNA extraction, sequencing, and alignment

DNA extraction was carried out using the Gentra Puregene Mouse Tail Kit (QIAGEN). Approximately 5-10 mg of liver or other tissue stored in 95% ethanol was soaked briefly in sterile distilled water (Kilpatrick 2002) before being ground to a fine powder in liquid nitrogen and incubated overnight at 55 °C in 300 µl cell lysis solution and 1.5 µl Proteinase K. Extracted DNA was air dried overnight and rehydrated with 50 µl of sterile water. The quantity and quality of the extracted DNA was assessed on a NanoDrop 1000 (Thermo Scientific) spectrophotometer.

Cytochrome *b* (Cyt*b*) was sequenced in three parts with the primer pairs Cyt*b* A and Cyt*b* E, Bath3 and 752R, and Ru13 and End2 or Cyt*b* G and Cyt*b* J (Table S3). Primers 12S-1S and 12S-3'GW were used to sequence the entire 12S rRNA or 12S-1S and 12S-2'NS, and 12S-2NS and 12S-3'GW were used to sequence in two parts (Table S3). Interphotoreceptor retinoid-binding protein (*Rbp3*) was sequenced with the primer pair IRBP119A2 and IRBP8F and growth hormone receptor exon ten (*Ghr*) was sequenced in two parts with primer pairs GHREXON10 and GHR8, and GHR7 and GHR2 (Table S3). Cyt*b* and 12S rRNA were amplified with 35 cycles with denaturation at 94 °C for 1 min, annealing at 50 °C for 1 min and extension at 72 °C for 1 min. *Rbp3* and *Ghr* were amplified with 40 cycles with denaturation at 94 °C for 1 min, annealing at 58 °C for 1 min and extension at 72 °C for 1 min.

Amplification reactions were conducted in 25 µl volumes with PuRe Taq Ready-To-Go PCR Beads (GE Healthcare Life Sciences). PCR products were visualized with ethidium bromide after gel electrophoresis on 1.2% agarose gels. ExoSAP (Exonuclease and Shrimp Alkaline Phosphatase) (ThermoFisher Scientific) was used to purify the PCR products. A few amplifications were conducted in 25 µl reactions using Titanium® Taq (Takara Bio USA) following the manufacturer's protocol. Sequencing reactions (15 µl) were conducted with 1-2 µl of ExoSAP product, 1 mM primer (forward or reverse), nuclease free water and fluorescent tagged terminator (BigDye v3.1; Applied Biosystems). Sephadex columns were used to purify the products of the sequencing reaction before they were fractionated on an Applied Biosystems 373 automated DNA sequencer. Some of the later sequences were obtained in 16.4 µl reactions containing 1.5 µl of a 1:10 to 1:20 dilution of the ExoSAP product, 1.6 µl of 2 mM primer and purified with the BigDye X Terminator (Applied Biosystems) reactions. Chromatograms were visualized and edited in Chromas 2.6.2 (Technelysium: http://technelysium.com.au/wp/chromas/).

Two mitochondrial (Cyt*b* and 12S rRNA) and two nuclear (*Rbp3* and *Ghr*) genes were included in the analyses. Cyt*b* (1,140 bp), *Rbp3* (1,236 bp) and *Ghr* (921 bp) were aligned using ClustalW (Thompson et al. 1994) in Mesquite 2.75 (Maddison & Maddison 2011); whereas, 12S rRNA (1,094 bp) was aligned in two steps, first using MAFFT (Katoh & Standley 2013) and then adjusted by eye.

Genetic distance, phylogenetic analyses, and divergence times

Kimura 2-parameter genetic distances (K2P; Kimura 1980) between genera and within species were estimated using MEGA6.0 (Tamura et al. 2013), based on Cyt*b* alignments of individuals in Table S1. To calculate genetic distances, species were grouped into their respective species as currently recognized (i.e. Happold 2013, Missoup et al. 2016, 2018) and by sampling localities (Fig. 1B).

The concatenated data set of sequences in Table S1 and Table S2 was divided into four individual partitions *a priori* with each gene (Cyt*b*, 12S rRNA, *Rbp3*, *Ghr*) treated as a single partition. Partition finder 2.1.1 (Lanfear et al. 2016) was used to determine the best partitioning scheme and best model for each partition based on the AIC criterion under a likelihood framework using PhyML (Guindon et al. 2010) and the greedy algorithm (Lanfear et al. 2012).

Maximum likelihood (ML) analysis was conducted with RA×ML (Stamatakis 2014) for the concatenated sequences with 1,000 bootstrap replicates using the GTR+I+G model on all partitions. The majority rule consensus tree (MRC) of bootstrap results was constructed in Mesquite. A partitioned Bayesian analysis was conducted on the CIPRES portal (Miller et al. 2010) using the GTR+I+G for the concatenated dataset in MrBayes 3.2.3 (Ronquist & Huelsenbeck 2003). Two simultaneous runs of 10,000,000 generations with sampling every 1,000 generations were carried out. The MrBayes

log files for both runs were examined in Tracer 1.6 (Rambaut et al. 2014) and a burn-in of 2,500,000 generations was set for each run. The runs were combined after discarding the burn-in and the MRC tree with posterior probability (PP) values was constructed in Mesquite.

Timing of divergence among clades was estimated using the Bayesian relaxed-clock model implemented in BEAST 1.8.4 (Drummond & Rambaut 2007) using the concatenated dataset with four partitions. Three calibration points from Kimura et al. (2017) and Aghová et al. (2018) were used: crown Murinae (lognormal prior distribution; mean: 3.2; Log(Stdev): 1.0; offset: 13.24; median: 15.2 million years before present (mya); 95% interval: 13.5-27.0 mya), *Arvicanthis*/*Mus* (lognormal prior distribution; mean: 4.0; Log(Stdev): 1.0; offset: 10.47; median: 12.9 mya; 95% interval: 10.8-27.7 mya), and Arvicanthini/Otomyini/Millardini (lognormal prior distribution; mean: 4.6; Log(Stdev): 1.0; offset: 8.52; median: 11.3 mya; 95%: 8.9-28.3 mya).

Aghová et al. (2018) also calibrated their analysis by applying a date at a stem position for the clade containing all extant *Arvicanthis* (lognormal prior distribution; mean: 5.5; Log(Stdev): 1.0; offset: 5.34; median: 8.7 mya; 95% interval: 5.8-29.0 mya) based on the Lemudong'o Formation, Kenya (Ambrose et al. 2007, Deino & Ambrose 2007, Manthi 2007). Because *Lemniscomys* is recovered as a well-supported sister taxon to *Arvicanthus* (Aghová et al. 2018), their approach effectively uses these fossils to establish a calibration at *Arvicanthis*/*Lemniscomys*. In addition to *Arvicanthis*, Manthi (2007) also identified material that he assigned to *Lemniscomys* with the same age at the Lemudong'o Formation, but Aghová et al. (2018) excluded these from consideration due to the absence of the first upper molar (M1). *Aethomys* is also present at Lemudong'o (Manthi 2007, Aghová et al. 2018). Mikula et al. (2021) opted against applying the Lemudong'o *Arvicanthis* to set a minimum age for the *Arvicanthis*/*Lemniscomys* divergence, but instead used it to establish a minimum age for *Arvicanthis*/*Aethomys*, which is a much more basal node. Under this scenario, they recovered an *Arvicanthis*/*Lemniscomys* date (~3 mya) that is considerably younger than the Lemudong'o Formation (~6 mya). A literal interpretation of Manthi (2007) indicates that the date associated with Lemudong'o should be applied to the *Arvicanthis*/*Lemniscomys* divergence, but the results of Mikula et al. (2021) suggest otherwise. Pending a more detailed evaluation of the Lemudong'o fossils in the context of arvicanthine morphological evolution, we chose to analyse our data both with and without this calibration at a stem *Arvicanthis* position.

The BEAST analysis was run for 100,000,000 generations, sampling trees and parameters every 5,000 generations. The BEAST log file was examined in Tracer 1.6 (Rambaut et al. 2014) and a burn-in of 10,000,000 generations was set. TreeAnnotator (Drummond & Rambaut 2007) was used to generate a maximum clade credibility tree by discarding the first 10,000,000 generations. Geological time elapsed since a most recent common ancestor is expressed either in million years ago (= mya – Miocene, Pliocene, and Pleistocene) or in years before present (= yr BP – Holocene). Posterior age estimates from BEAST analyses are expressed with associated 95% highest posterior densities (= 95% HPD). African rainforest classification follows Hardy et al. (2013).

Results

Intraspecific comparison of the Cyt*b* sequences recovered from the mitogenomes assembled by Mikula et al. (2021) for *D. defua* (MN807600) and *Stochomys longicaudus* (MN807599) had a mean K2P distance of 0.0886 (range 0.0841-0.0969) and 0.0882 (range 0.0863-0.0893) respectively. The mean intraspecific amino acid divergence for these two Cyt*b* sequences were 0.015 (range 0.0074-0.0215) and 0.0296 (range 0.024-0.038), respectively. Both the Cyt*b* and 12S rRNA sequences recovered from these two assembled mitogenomes were excluded from our analyses due to the large amount of noise that appeared to be present. The K2P distance for the remaining Cyt*b* sequences recovered from the mitogenomes for *Typomys* (MN807601 and MN807602) and *Hybomys* (MN807598 and MN807597) were < 0.018 for intraspecific comparisons and thus the Cyt*b* and 12S sequences from these mitogenome assemblages were included in our analyses.

Molecular definition of the tribe Arvicanthini based on the four genes sequenced herein received convincing support (ML = 86, PP = 1.00) and concurred with the generic contents identified by Lecompte et al. (2008) (Fig. S1; Fig. S2). Maximum likelihood and Bayesian phylogenetic analyses recovered the *Hybomys* division, sensu Musser

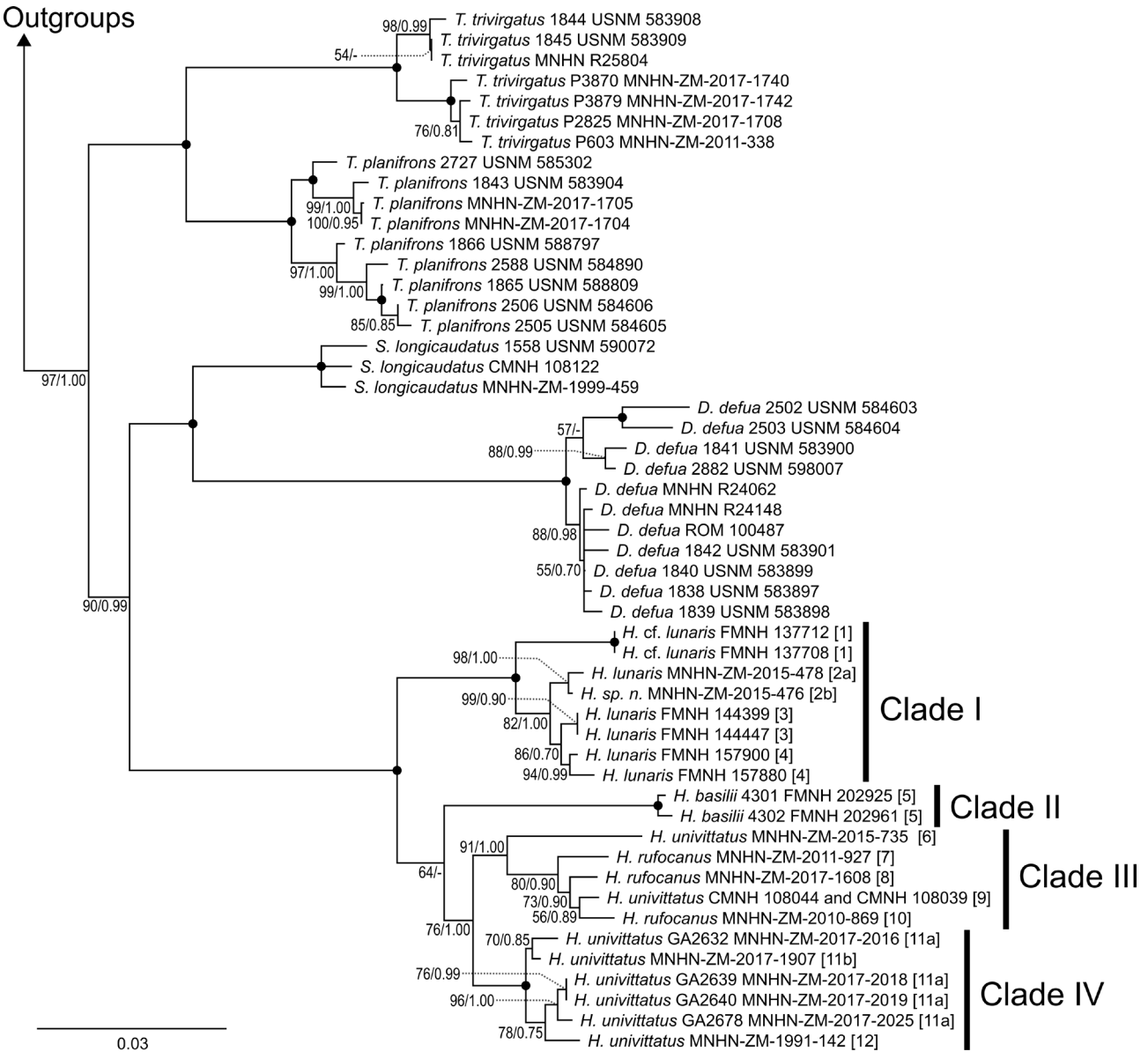

Fig. 2. Maximum Likelihood Majority rule consensus tree of the *Hybomys* division based on concatenated sequences of two mitochondrial (Cyt*b*, 12S rRNA) and two nuclear (*Ghr*, *Rbp3*) genes. Numbers in parenthesis following the individuals of *Hybomys* refer to the locality from which they were collected (Fig. 1B, Table 1). Nodal support is provided as Maximum Likelihood bootstrap (1,000 replicates) and Bayesian posterior probability values (ML/PP: only if > 50%). A solid black circle identifies nodes with fully realized support (ML = 100 and PP = 1.00). Full Maximum Likelihood and Bayesian Majority rule consensus tree presented in Fig. S1 and Fig. S2 respectively.

& Carleton (2005), as monophyletic, strongly supported by bootstrap and posterior probability metrics (ML = 97, PP = 1.00) and nested within the large clade of arvicanthine rodents (Fig. 2). Inclusion of the stem *Arvicanthis* calibration (Manthi 2007) yielded divergence estimates that were markedly older than the analysis where they were excluded. For example, the most recent common ancestor of the *Hybomys* division was estimated as dating to 8.0 (7.0-9.3 HPD) mya with the stem *Arvicanthis* calibration (Fig. S3) but 7.4 (6.2-8.7 HPD) mya without (Fig. S4). Pending a detailed re-evaluation of the phylogenetic position of Lemudong'o fossils, we have chosen to focus on the dates yielded by the BEAST analysis where the stem *Arvicanthis* calibration is excluded.

Although the four genus-group taxa of the *Hybomys* division formed a monophyletic group, the nominal subgenera *Hybomys* and *Typomys* were not recovered as sister taxa in the consensus tree (Fig. 2), which aligns with Missoup et al. (2018) in contrast to historical hypotheses that united these forms into a single genus (e.g. Ingoldby 1929, Rosevear 1969, Van der Straeten & Verheyen 1982, Carleton & Robbins 1985, Musser & Carleton 2005, Denys et al. 2017). Both species of *Typomys* were indisputably allied (ML = 100,

Table 1. Sampling localities, voucher identifications and taxonomic hypotheses of taxa of *Hybomys*.

Sample Number	Taxon Designation Musser & Carleton (2005)	Vouchers	Country	Locality	Coordinates	Current Taxon Designation	Reference
1	*H. univittatus*	FMNH 137708	Burundi	Kibira NP, 2.9 km N and 1.4 km W Teza, 2,450 m	3.186 S, 29.548 E	*H.* cf. *lunaris*	Huhndorf et al. (2007)
		FMNH 137712		Kibira NP, 3.5 km S and 2.6 km W Teza, 2,160 m	3.23 S, 29.545 E		
2a	*H. univittatus*	MNHN-ZM 2015-478	DRC	Bangole (shown)	0.88 N, 25.15 E	*H. lunaris*	Missoup et al. (2018),
				Reported as Masako in MNHN data base	0.6 N, 25.22 E		this study
2b	*H. univittatus*	MNHN-ZM 2015-476	DRC	Masako	0.6 N, 25.22 E	*H.* sp. n. *(*cf. *lunaris)* *H. lunaris*	Mikula et al. (2021) this study
3	*H. lunaris*	FMNH 144399 FMNH 144447	Uganda	Ruwenzori Mt. NP, Nyabitaba Camp, 2,500 m	0.367 N, 29.983 E	*H. lunaris*	Huhndorf et al. (2007)
4	*H. univittatus*	FMNH 157880 FMNH 157900	Uganda	Bwindi-Impenetrable NP, Ruhiza, 2,300 m	1.033 S, 29.767 E	*H. lunaris*	Huhndorf et al. (2007)
5	*H. basilii*	FMNH 202925	Equatorial	Bioko Island, Lake Biao	3.35 N, 863 E	*H. basilii*	this study
		FMNH 202961	Guinea	Bioko, Moka Wildlife Sanctuary	3.36 N, 866 E		
6	*H. univittatus*	MNHN-ZM-2015-735	Gabon	Mvoum	0.58 N, 9.88 E	*H. univittatus*	Missoup et al. (2018), this study
7	*H. eisentrauti*	MNHN-ZM-2011-927	Cameroon	Mount Oku	6.22 N, 10.53 E	*H. rufocanus*	Missoup et al. (2018)
8	*H. badius*	MNHN-ZM-2017-1608	Cameroon	Mount Cameroon	4.14 N, 9.13 E	*H. rufocanus*	Missoup et al. (2018)
9	*H. univittatus*	CMNH 108044	Cameroon	Southwestern Province, Mana River Bridge	5.25 N, 9.033 E	*H. rufocanus*	this study
10	*H. rufocanus*	MNHN-ZM-2010-869	Cameroon	Mount Bakossi	5.00 N, 9.68 E	*H. rufocanus*	Missoup et al. (2018)
11a	*H. univittatus*	MNHM-ZM-2017-2016 MNHM-ZM-2017-2018 MNHM-ZM-2017-2019 MNHM-ZM-2017-2025	Gabon	Moneva	2.28 S, 10.51 E	*H.* sp.	this study
11b	*H. univittatus*	MNHN-ZM 2017-1907	Gabon	Mt. Doudou	2.33 S, 10.38 E	*H. univittatus* *H.* sp.	Mikula et al. (2021) this study
12	*H. univittatus*	MNHN 1991-142	Congo	M'Béna	0.40 N, 14.7 E	*H.* sp.	this study

Table 2. Mean genetic distances (Kimura 2-Parameter) based on Cytb within (along diagonal) and between species of the *Hybomys* division. All sampes of *H. univittatus* treated as a single taxon.

Taxon	*H. univittatus*	*H. rufocanus*	*H. lunaris*	*H.* cf. *lunaris*	*H.* sp. n.	*H. basilii*	*T. planifrons*	*T. trivirgatus*	*D. defua*	*S. longicauda*
H. univittatus	0.0510 (n = 8)	0.0836	0.1132	0.1094	0.1232	0.0863	0.1856	0.1607	0.1844	0.1563
H. rufocanus		0.0312 (n = 3)	0.1259	0.1104	0.1291	0.0829	0.1975	0.1795	0.1819	0,1528
H. lunaris			0.0173 (n = 5)	0.0582	0.0201	0.1222	0.1785	0.1589	0.1632	0.1354
H. cf. *lunaris*				0.0000 (n = 2)	0.0558	0.1324	0.1779	0.1700	0.1715	0.1335
H. sp. n.					nc (n = 1)	0.1407	0.1927	0.1629	0.1719	0.1554
H. basilii						0.0071 (n = 2)	0.1975	0.1863	0.1842	0.1628
T. planifrons							0.0365 (n = 8)	0.1411	0.2147	0.1809
T. trivirgatus								0.0182 (n = 8)	0.2087	0.1879
D. defua									0.0275 (n = 11)	0.1758
S. longicaudus										0.0274 (n = 3)

PP = 1.00) and diverged in a basal lineage to all other members of the division, the derivative sister clade hierarchically arranged as (*Hybomys* (*Dephomys* + *Stochomys*)). The union of *Stochomys* and *Dephomys* attained very strong support (ML = 100, PP = 1.00). The taxa of *Hybomys* sensu stricto were recovered in a well-supported (ML = 100, PP = 1.00) monophyletic clade composed of four subclades (clades I-IV, ML = 91-100, PP = 1.00; Fig. 2). The sister taxon relationship between *Hybomys* sensu stricto and a *Dephomys-Stochomys* clade (Fig. 2) also attained strong support (ML = 90, PP = 0.99). A hierarchical arrangement of the genera of the *Hybomys* division as (*Typomys* (*Hybomys* (*Dephomys* + *Stochomys*))) has been recovered by analyses of mitochondrial and nuclear sequence data by Missoup et al. (2018), Mikula et al. (2021) and this study.

Our sequencing data convincingly ratify the specific distinction and close relationship of *T. planifrons* and *T. trivirgatus*, despite the past confusion over their taxonomic status and genus-group affinity (see Carleton & Robbins 1985). Genetic distance between the two species is substantial (K2P = 0.1411) and approximates that derived between some species of *Hybomys*, such as *Hybomys lunaris* and *H. rufocanus* (K2P = 0.1259; Table 2). Mean genetic distances obtained within species of the *Hybomys* division are minimal (Table 2), falling comfortably within the range of intraspecific variation summarized for Rodentia (Baker & Bradley 2006); apart from *H. univittatus*, which exceeds 0.05. In addition, our sampling of *H. univittatus* and *S. longicaudatus* insufficiently represents the broad geographic distribution of these taxa.

Analyses of sequence data available from taxa of *Hybomys* sensu stricto (see Table 1 and Fig. 1B for localities) identified four distinct clades (Fig. 2). Clade I (ML = 100, PP = 1.00) contains *H. lunaris*, *H.* cf. *lunaris*, and a specimen designated as *H.* sp. n. by Mikula et al. (2021). Clade II (ML = 100, PP = 1.00) contains *H. basilii*, and clade III (ML = 91, PP = 1.00) contains *H. rufocanus*, including samples that were previously recognized as *H. badius* and *H. eisentrauti*, and specimens of *H. univittatus* from Mvoum, Gabon (Fig. 1B, locality 6) and the Southwestern Province of Cameroon (Fig. 1B, locality 9). Clade IV (ML = 100, PP = 1.00) contains specimens of *H. univittatus* from Moueva and Monts Doudou, Gabon (Fig. 1B, locality 11) and M'Bena, Congo (Fig. 1B, locality 12). Majority rule

consensus trees derived from ML and Bayesian methods resulted in incongruent placement of clades I and II within the *Hybomys* sensu stricto clade (Figs. S1 and S2). In the ML MRC tree clade II (*H. basilii*) was found sister to clade III + IV (ML = 64), whereas in the Bayesian MRC tree clade I (*H. lunaris* – *H.* cf. *lunaris*) was sister to clades III + IV (PP = 0.58). The time calibrated tree from BEAST agreed with the topology of the ML tree in regard to the placements of clade II as sister to clades III + IV (Fig. S4).

The specimen designated as *H.* sp. n. by Mikula et al. (2021) was recovered within a *H. lunaris* clade (Fig. 2) and demonstrated mean K2P distances ranging from 0.000 to 0.024 from other *H. lunaris* populations sampled (Table 3). The *H. lunaris* – *H.* cf. *lunaris* (clade I) diverged about 3.1 (95% HPD = 2.7-4.3) mya (Fig. S4), followed by *H. basilii* (clade II) at 2.0 (95% HPD = 1.5-2.5) mya, whereas clades III and IV diverged about 1.6 (95% HPD = 1.2-2.1) mya. Among those species represented by sequences from multiple individuals *H. lunaris*, *H.* cf. *lunaris*, and *H. basilii* formed well supported (ML = 82-100, PP = 1.00) monophyletic subclades, whereas *H. univittatus* was polyphyletic (Fig. 2). The sample of *H. univittatus* (Fig. 1B, locality 9) from north of the River Sanaga in Cameroon (Table 3) was recovered as the sister taxon of a specimen of *H. rufocanus* from Mount Bakossi (Fig. 1B, locality 10) with little support (ML = 56, PP = 0.89). However, these two specimens were recovered in a moderately well-supported clade (ML = 80, PP = 0.90) containing other samples of *H. rufocanus* from Mount Cameron (Fig. 1B, locality 8) and Mount Oku (Fig. 1B, locality 7). The mean genetic distance (Cyt*b* K2P) between this sample of *H. univittatus* (Fig. 1B, locality 9) and *H. rufocanus* is 0.029 (Table 3). The sample of *H. univittatus* from Mvoum, Gabon (Fig. 1B, locality 6), a location between the Sanaga and Ogooue rivers, was the sister taxon to the two taxon clade described above (Fig. 2) but with little support (ML = 91, PP = 1.00). In addition, these two samples of *H. univittatus* recovered in this clade from localities 6 and 9 have a K2P distance of 0.088 (Table 3) and the Cyt*b* sequence from locality 6 demonstrates a mean K2P distance of 0.090 from samples of *H. rufocanus*. The samples of *H. univittatus* from the Congo (Fig. 1B, locality 12) and Moueva, Gabon (Fig. 1B, locality 11), were recovered in a well-supported clade (ML = 100, PP = 1.00) that is sister to the previous *H. univittatus* – *H. rufocanus* clade (Fig. 2). This south-eastern clade of *H. univittatus* shows considerable

Table 3. Mean Cyt*b* K2P distances between and within sampling localities (Table 1, Fig. 1B) of *Hybomys univittatus*, *H.* sp. n. (Mikula et al. 2021) and other named taxa of *Hybomys*. Intra-populational distance marked with an asterisk.

Taxon	Sample Location	Sample Size	Region	*H. lunaris* (3-4)	*H. u.* (6)	*H. u.* (9)	*H. u.* (11)	*H. u.* (12)	*H.* sp. n. (2b)
H. cf. *lunaris*	1	n = 2	Albertine Rift South	0.058	0.100	0.103	0.111	0.100	0.055
H. lunaris	2a	n = 1	Northeastern Congo Basin	0.024	0.112	0.115	0.106	0.094	0.000
H. lunaris	3-4	n = 4	Albertine Rift North	0.013*	0.104	0.114	0.111	0.100	0.024
H. basilii	5	n = 2	Boiko Island	0.116	0.089	0.089	0.093	0.086	0.104
H. rufocanus	7, 8, 10	n = 3	Cameroon Volcanic Line	0.120	0.090	0.029	0.107	0.103	0.123
H. univittatus	6	n = 1	Between Sanga and Ogooue rivers		nc	0.088	0.088	0.088	0.112
H. univittatus	9	n = 1	North of the River Sanga			nc	0.107	0.103	0.115
H. univittatus	11	n = 5	South of the River Ogooue				0.015*	0.021	0.106
H. univittatus	12	n = 1	Western Congo Basin					nc	0.094
H. sp. n.	2b	n = 1	Northeastern Congo Basin						nc

genetic differentiation (Cyt*b* K2P) from the other populations of this species that were sampled with values of 0.088 and greater (Table 3).

The divergence of the *Hybomys* division from other arvicanthine genera (excluding *Golunda* and *Oenomys*) is estimated to be 8.1 (95% HPD = 6.9-9.4) mya, an origin set within the late Miocene (Fig. S5). After the Miocene origination of the division, successive phylogenetic splits led to the generic diversification within the *Hybomys* division (Fig. S4), beginning with the divergence of *Typomys* (7.4; 95% HPD = 6.2-8.7 mya), followed by *Hybomys* proper (6.7; 95% HPD = 5.6-8.1 mya), and lastly *Dephomys* and *Stochomys* in the early Pliocene (4.8; 95% HPD = 3.5-6.2 mya). Species of *Typomys* (*T. trivirgatus* and *T. planifrons*) diverged around 4.3 (95% HPD = 3.2-5.4) mya and those of *Hybomys* begin to diverge around 3.1 (95% HPD = 2.4-4.0) mya (Fig. S4).

Discussion

The *Hybomys* division, tribe Arvicanthini

Musser & Carleton (2005) classified the genus-group taxa *Dephomys*, *Hybomys* (*Hybomys*), *Hybomys* (*Typomys*), and *Stochomys* within the *Hybomys* division, a grouping that was convincingly supported as monophyletic based on the four genes used to generate our phylogeny (Fig. 2). Musser & Carleton (2005) refrained from specifying formal tribes within Murinae when they formulated their family-group classification of Muroidea. At the time (editorial deadline: June 2003), no taxonomically dense, synthetic molecular studies addressed the Murinae and illuminated its major lineages, in contrast to the substantial literature then available for other murid subfamilies and ample evidentiary bases for delineating formal tribes (e.g. see their introductory commentary to the subfamilies Arvicolinae, Neotominae, Sigmodontinae, and Gerbillinae). Rather than burden systematists with a word-scrabble of newly named tribes and complicate future nomenclatural issues, they elected to borrow a generic aggregative term from the classical literature on murid rodents, this being the "division" of Misonne's (1969) African and Indo-Australian Muridae (Musser & Carleton 2005: 1,248). The division per se is not specifically governed by the Code (International Commission of Zoological Nomenclature 1999), which expressly denotes family-group ranks (Article 35.1) and their prescribed endings (Article 29.2) – i.e. the superfamily (-oidea), family (-idae), subfamily (-inae), tribe (-ini), and subtribe (-ina).

Taxonomically and geographically inclusive molecular studies have proliferated since 2005 and immensely improved our understanding of inter-generic relationships within Murinae. The innovative contribution by Lecompte et al. (2008) is especially relevant in this regard given its emphasis on African genera and murine tribal assemblages. According to their phylogenetic perspective, a view repeatedly corroborated by others (Fabre et al. 2013, Missoup et al. 2016, 2018, Steppan & Schenk 2017, Rowe et al. 2019, Mikula et al. 2021, this study), the *Hybomys* division of Musser & Carleton (2005) hierarchically corresponds to a sub tribal rank within the tribe Arvicanthini (see Table S4, footnote [a]). Should systematic mammalogists ultimately determine that these lesser clades within Arvicanthini deserve formal names, then proper definitions, designation of type genera, and circumscription of generic contents must ensue, a purpose beyond the scope of our investigation. In the meanwhile, the following discussion continues to employ "division" in the non-binding nomenclatural sense intended by Musser & Carleton (2005).

The monophyletic (ML = 97, PP = 1.00) *Hybomys* division is a part of a large clade that includes the core Arvicanthini (minus *Golunda* and *Oenomys*). The *Hybomys* division represents the earliest diverging clade within this group, though this position receives only poor support (ML < 50, PP = 0.80). Within the *Hybomys* division, our results corroborate certain generic relationships reported in past molecular studies, which depicted *H. univittatus* as sister group either to *Stochomys* (Lecompte et al. 2008, Schenk et al. 2013, Bryja et al. 2017) or to *Dephomys* and *Stochomys* (Missoup et al. 2016, Steppan & Schenk 2017). With addition of samples of *Typomys*, the molecular analyses of Missoup et al. (2018), Mikula et al. (2021), and this study recovered four well defined subclades within the *Hybomys* division; however, the phylogenetic structure inferred from these data failed to portray *Typomys* as a subgenus and junior synonym of *Hybomys*, the generic construct long accepted as valid (Ellerman 1941, Rosevear 1969, Musser & Carleton 2005, Carleton 2013, Aplin 2017). On this basis, Missoup et al. (2018) proposed that *Typomys* be recognized as a genus distinct from *Hybomys* s.s., a taxonomic recommendation also adopted by Burgin et al. (2018), supported by Mikula et al. (2021) and one with which we are entirely in agreement.

Although they provided ample discussion of taxonomic and genetic components, Missoup

et al. (2018) provided only a brief discussion of the morphological context of their result and we expand on that here. Morphological contrasts between species of *Hybomys* and *Typomys* are numerous and substantial as so far documented (here consolidated from Thomas 1911, Ingoldby 1929, Rosevear 1969, Carleton & Robbins 1985 and Carleton 2013). Species of *Typomys* lack the pectoral pair of mammae (0 + 2 = 4); those of *Hybomys* possess a pectoral pair (1 + 2 = 6). The t9 (metacone) in the upper molars of *Typomys* is diminutive in size, usually absent in the M2; a well-defined t9 occurs on both the M1 and M2 in nearly all specimens of *Hybomys*. Accessory cusps (anteromedian, anteorlingual, posterolingual) irregularly occur along the m1 cingula in examples of *Typomys*; such supplementary enamel structures commonly embellish the m1 cingula in members of *Hybomys*. The upper and lower first molars in *Typomys* are anchored by three and two roots, respectively, a formula interpreted as the ancestral character state in Muroidea; accessory rootlets uniformly occur in samples of *Hybomys*, the M1 4- or 5-rooted and the m1 4-rooted. Most examples (< 7%) of *Typomys* lack an alisphenoid strut; this strut, a bridge of the alisphenoid bone dividing the masticatory-buccinator foramen and foramen ovale accessorius, is present in most *Hybomys* (> 90%). The optic foramen is large, approximating the size of the sphenoidal fissure, in examples of *Typomys*; the optic foramen is smaller, noticeably less than the area of the sphenoidal fissure, in *Hybomys*.

Specimens of *Typomys* and *Hybomys* differ in their cranial architecture, displaying visually obvious shape contrasts that were captured in Rosevear's (1969) characterization of the "*Typomys*-type" *vs.* "*Hybomys*-type" skull. Key shape features involve the development of the incisive foramina (relatively shorter but wider in *Typomys*; long and narrow in *Hybomys*), zygomatic plate (narrower, anterior edge slanted, forming a shallow zygomatic notch in *Typomys*; wider, anterior edge vertical, incising a deep zygomatic notch in *Hybomys*), interorbital region (broader with amphoral supraorbital borders in *Typomys*; narrower with cuneate borders in *Hybomys*), and mandible (gracile and slender, with deep angular notch in *Typomys*; robust and deeper, with shallow angular notch in *Hybomys*). Predictably, such conspicuous shape differences would find quantitative rigor in variable loading coefficients derived in traditional morphometric investigations, in which the first factor extracted, whether in principal component or discriminant function analyses, sharply segregated specimens of *Typomys* and *Hybomys* without overlap in multivariate space (Van der Straeten & Verheyen 1982, Van der Straeten 1984, Carleton & Robbins 1985).

Hybomys and *Typomys* may also be distinct in their chromosomal complement based on the species karyotyped to date (Carleton & Robbins 1985). Karyograms of *Typomys* are characterized by lower diploid (2n) of 35-43 and fundamental numbers (FN) of 40-43 compared with the higher figures reported for populations of *Hybomys* (2n = 44-48, FN = 46-48).

In summary, the phylogenetic, genetic, morphological, morphometric, and chromosomal data currently marshalled, unambiguously reinforce one another and advise recognition of *Typomys* Thomas, 1911, as a genus distinct from *Hybomys* Thomas, 1910, bringing the number of genera in the *Hybomys* division to four (Table S4).

Systematics of the taxa of the genus *Hybomys*

In this study, representatives of all six of the described species of *Hybomys* sensu stricto were included. *Hybomys badius* Osgood, 1936; *H. basilii* Eisentraut, 1965; *H. lunaris* (Thomas, 1906); and *H. univittatus* (Peters, 1876) are currently considered valid species (Aplin 2017), whereas *H. eisentrauti* Van der Straeten & Hutterer, 1986 is considered a synonym of *H. badius*, and *H. rufocanus* (Tullberg, 1893) a synonym of *H. univittatus* (Musser & Carleton 2005, Carleton 2013). Aplin (2017) referred to recently collected molecular data showing a close relationship between material referable to *H. badius* and *H. rufocanus*. Missoup et al. (2018) reported close affinities among *H. badius*, *H. eisentrauti*, and *H. rufocanus* and proposed that *H. badius* and *H. eisentrauti* were junior synonyms of *H. rufocanus*. Our phylogenetic analyses recovered all species of *Hybomys* in a single well supported clade (ML = 100, PP = 1.00) containing four subclades (Fig. 2).

Thomas (1906) described *lunaris* as a subspecies of *H. univittatus* from specimens collected from Mubuku, Ruwenzori East, in Uganda at an elevation of 6,000 ft. Van der Straeten et al. (1986) concluded that *lunaris* was a distinct species and expanded its range to include specimens from eastern Democratic Republic of the Congo (DRC) and Rwanda. However, their analysis in 1986 did not include specimens from the type locality or any

other parts of Uganda. While the morphometric analyses of Van der Straeten et al. (1986) failed to examine the type and holotypes of *H. lunaris*, the body measurements of the type were within the ranges reported for the specimens examined from Rwanda and the DRC. In most recent revisions (Musser & Carleton 2005, Dieterlen 2013, Taylor 2017), the distribution of *H. lunaris* has been restricted to the Rwenzori Mountains of Uganda. However, Musser & Carleton (2005) noted that two specimens from Kanyawara, Uganda, matched Thomas's (1906) description of the type specimen has a small, delicate form and differ from the larger and more robust forms from Rwanda. Huhndorf et al. (2007) expanded the range to the montane forest along the Albertine Rift north of the Virunga Volcanoes and demonstrated substantial genetic differentiation with the populations to the south in Burundi (*H.* cf. *lunaris*). Sequences from specimens of *H. lunaris* from Uganda and the eastern DRC, previously reported by Huhndorf et al. (2007) and Missoup et al. (2018) respectively, along with sequences from *H.* cf. *lunaris* reported by Huhndorf et al. (2007) and *H.* sp. n. reported by Mikula et al. (2021) were recovered in a well-supported (ML = 100, PP = 1.00) clade (Fig. 2, clade I). The mean genetic distance (K2P) observed between the *H. lunaris* subclade samples and the *H.* cf. *lunaris* subclade samples for Cyt*b* was 0.0580, whereas the intraspecific differentiations were 0.0180 and 0.000, respectively. Our analyses support a broader geographic range for *H. lunaris* than described by Huhndorf et al. (2007), as the specimen from Bangole in the DRC (recorded as Masako, DRC in the MNHN database) and the specimen identified as *H.* sp. n. (recorded as *H. lunaris* from Masako, DRC in the MNHN database) are recovered in the clade with samples from the type locality of *H. lunaris*. The Cyt*b* K2P distance of 0.022 between these specimens and those sampled in the Rwenzori Mountains, suggest that the range of *H. lunaris* extends at least 550 km to the NW into north-eastern portion of the DRC. This *H. lunaris* species complex of central Africa is estimated to have diverged about 3.1 mya from other forms of *Hybomys* (Fig. S4). More complete molecular and morphological analyses are needed to better define the geographic range of *H. lunaris* and to further test the hypothesis of Huhndorf et al. (2007) of an unnamed species occurring in Burundi.

Hybomys univittatus is distributed in the rainforest of the Congo Basin and from the River Niger to the Albertine Rift and the shores of Lake Victoria (Carleton 2013, Aplin 2017). Considerable morphological variation has been reported among populations of this taxon (Rosevear 1969, Carleton & Robbins 1985) leading Musser & Carleton (2005) to suggest that *H. univittatus* consists of several morphologically similar species. In addition, three different karyotypes with diploid numbers of 44, 46, and 48 have been reported (Carleton & Robbins 1985, Verheyen & Van der Straeten 1985) among populations in Cameroon and Gabon. Our phylogenetic analyses of sequence data recovered *H. univittatus* sampled from locality 9 (Fig. 1B) north of the River Sanaga in Cameroon, locality 6 between the Sanaga and Ogooue rivers in Gabon, locality 11 south of the River Ogooue in Gabon, and locality 12 from the Congo (Table 3, Fig. 1B) as polyphyletic (Fig. 2). The sample from north of the River Sanaga from the Southwestern Province of Cameroon (Fig. 1B, locality 9) was recovered within a well-supported (ML = 80, PP = 0.90) *H. rufocanus* clade. The mean level of genetic differentiation (Cyt*b* K2P) between this *H. univittatus* sample and samples of *H. rufocanus* was 0.029 (Table 3), lower than the level for interspecific differentiation reported by Baker & Bradley (2006). These results suggest that populations currently recognized as *H. univittatus* from Southwestern Cameroon are part of the *rufocanus-badius-eisentrauti* lineage. Low levels of genetic differentiation among *rufocanus*, *badius* and *eisentrauti* based on a somewhat larger sampling of these taxa was reported by Missoup et al. (2018) to range between 0.010 and 0.028. Our analyses not only support the conclusion of Missoup et al. (2018) that *H. badius* and *H. eisentrauti* should be considered as synonyms of *H. rufocanus* (Tullberg, 1893) but provide data to support their suggestion that populations from lowland forest north of the River Sanaga previously reported as *H. u. univittatus* (Eisentraut 1968, 1973, Denys et al. 2009) should be included within this taxon. Eisentraut (1963) and Sanderson (1940) had noted the similarity of the lowland forms of *H. univittatus* north of the Cameroon Mountains in size with *H. badius* and further noted that these two taxa were only differentiated by colour.

The sequence data from Missoup et al. (2018) from a specimen of *H. univittatus* from Mvoum (Fig. 1B, locality 6), between the Sanaga and Ogooue rivers and only 15 km NE of Dongila (type locality of *univittatus*), was recovered in our analyses as sister to the *H. rufocanus* clade with strong support (ML = 91, PP = 1.00). However, this specimen from locality 6, which we assume to represent true

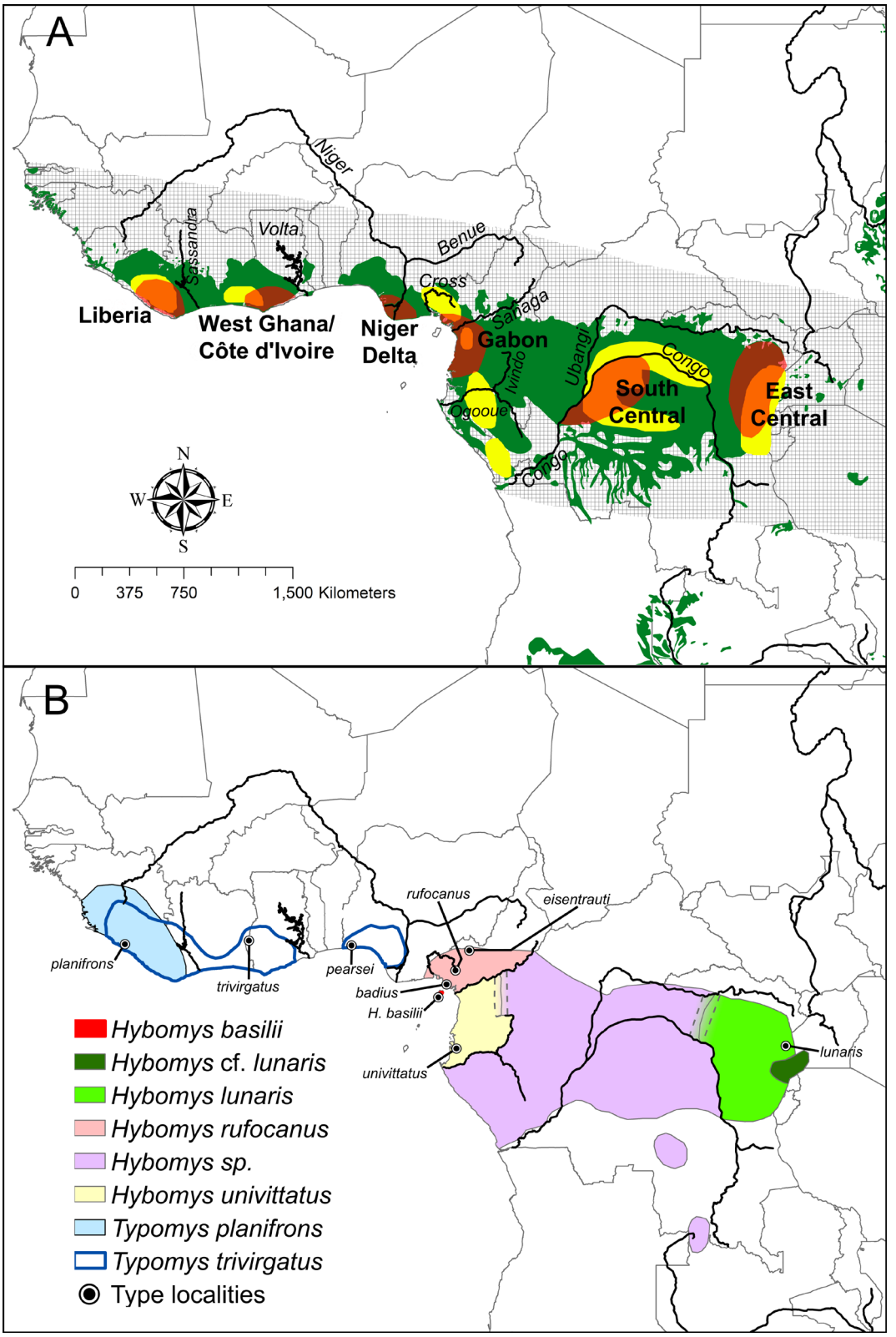

Fig. 3. The Guineo-Congolian Region, sensu White (1983), and specific distributions of the genera *Hybomys* and *Typomys*, *Hybomys* division. A) Current extent of Guineo-Congolian rainforests (green – range shapefiles imported from White 1983) compared with the hypothesized maximal extent of rainforests during wet periods of the Early Pliocene (chequered, following Hardy et al. 2013). Also depicted are hypothesized Late Quaternary rainforest refugia (yellow, after Maley 1996) and centres of endemism (red, after Happold 1996), which substantially overlap in their geographic location (orange). B) Distributions of currently recognized species of *Hybomys* and *Typomys* (range shapefiles acquired from Terrestrial Mammal dataset, IUCN Red List – http://www.iucnredlist.org/technical-documents/spatial-data) and modified with the results of this study. Type locality shown with a dot within a circle.

univittatus as it was collected near the type locality for this taxon, demonstrates considerable genetic differentiation from the taxa of its sister clade to the north (Table 3) with a mean Cyt*b* K2P = 0.087 and a range of 0.079-0.094. We hypothesize that additional sequences from samples between the Sanaga and Ogooue rivers would result in a distinct clade, representing true *univittatus*, sister to the *H. rufocanus* clade.

Our phylogenetic analyses recover the remaining samples of *H. univittatus*, from Gabon south of the River Ogooue (Fig. 1B, locality 11) and from the Congo (Fig. 1B, locality 12), in a well-supported clade (ML = 76, PP = 1.00) that is sister to the *H. rufocanus* – true *H. univittatus* clade. This latter *H. univittatus* clade has a K2P distance ≥ 0.088 from *H. univittatus* from localities 9 and 6 and a distance between 0.086-0.111 to other taxa of the genus (Table 3).

One solution to the paraphyly observed among population of *H. univittatus* would be to consider *univittatus*, *rufocanus*, *badius*, *basilii*, and *eisentrauti* as synonyms and recognize this taxon as *H. univittatus* (Peters, 1876). However, this would lump several populations that demonstrate considerable morphological variation and genetic differentiation (K2P > 8-9%). Musser & Carleton (2005) noted that the degree of morphological variation observed among populations of *H. univittatus* suggests that it consists of several morphologically similar species.

Pending further geographic sampling of *H. univittatus* we would suggest the recognition of samples previously recognized as *H. univittatus* from north of the River Sanaga, including *badius* and *eisentrauti*, as *H. rufocanus* as previously suggested by Missoup et al. (2018). Furthermore, we would suggest restricting the distribution of *H. univittatus* to the region between the Sanaga and Ogooue rivers and suggest that the specimens from south of the River Ogooue currently recognized as *H. univittatus* represent an undescribed species (Table 3). The eastern boundaries of either of these species are not known, nor are the areas of contact with populations of *H. lunaris* (Fig. 3B).

Biogeography and emergence of the *Hybomys* division

The middle to late Miocene was an eventful period that saw major faunal interchange between Africa and Eurasia, a movement of ancestral stocks facilitated by lower sea levels, a global trend toward cooler and drier climates, and the intermediacy of the Arabian Plate between southern Asia and north-eastern Africa (see summary in Morley & Kingdon 2013). Certainly, African landscapes were integral to the phylogenesis of murine rodents as the continent's Sub-Saharan region contains representatives of five of the ten tribes formally recognized to date (sensu Lecompte et al. 2008). Two of these tribes, Malacomyini and Otomyini, are endemic to Sub-Saharan Africa; the taxonomic diversity of two, Arvicanthini and Praomyini, is principally confined to this region; the tribal distribution of only one, Murini, extends across Africa and Eurasia. Arvicanthini numbers some 88 species representing 19 genera (including one genus and species in Asia – Hoffman et al. 2009, Happold 2013, Bryja et al. 2017) and is the largest of the five African tribes, compared with the Malacomyini (one genus, three species – Happold 2013), Otomyini (two genera, 31 species – Taylor et al. 2011, Happold 2013), Praomyini (nine genera, 55 species – Hoffman et al. 2009, Happold 2013, Carleton et al. 2015), and Murini (two genera, 20 species native to Africa – Happold 2013). The initial entry of murine rodents into Africa transpired around 9 to 12 mya, an interval bracketed by both fossil records (Jacobs et al. 1990, Jacobs & Flynn 2005) and molecular chronograms calibrated to key "palaeontological events" (Lecompte et al. 2008, Steppan & Schenk 2017). Like the rapid diversification of core Murinae into its tribal-level lineages (Fabre et al. 2013, Kimura et al. 2017, Steppan & Schenk 2017), the murine stem groups that entered Africa also underwent an explosive radiation commensurate with the continent's vastness and its geological, climatological, and ecological heterogeneity. Fossils assignable to living arvicanthine genera date from the late Miocene through early Pliocene, around 5 to 7 mya (e.g. *Aethomys* – Denys 1990, Manthi 2007; *Arvicanthis* – Denys 1999, Winkler 2002; *Lemniscomys* – Manthi 2007).

The basal radiation of Arvicanthini coincides with a prolonged period of cooler, drier climate, about 6 to 8 mya (Fig. S4), and the accompanying proliferation of grasslands and open woodlands (Maley 1996, Plana 2004, Morley & Kingdon 2013). The expansion of grasslands and concomitant retreat of high forests over this period are firmly documented, drawing upon palynological records (Morley & Richards 1993, Morley et al. 2003) and isotopic evidence that tracks the pronounced increase in C_4 grasses (Poaceae) that now dominate

tropical ecosystems (Cerling et al. 1997, Sage et al. 2012). Sub-Saharan biomes support by far the greatest biodiversity within Arvicanthini (see species accounts in Happold 2013), with only three species recorded outside this region – two in northern Africa and the single Asian extralimital, *Golunda ellioti*, in the Indian subcontinent. Many arvicanthine genera – such as *Aethomys*, *Arvicanthis*, *Grammomys*, *Lemniscomys*, *Rhabdomys*, and *Thallomys* – typically constitute the ecologically abundant, small mammal guild that populates Africa's grasslands and moorlands, bushlands and shrublands, savannahs and woodlands, and all ecological gradations between these habitats.

In contrast to such open environments, species of the *Hybomys* division are denizens of closed-canopied and deep forest, the Guineo-Congolian Region of White (1983). According to our fossil-calibrated phylogeny (Fig. S4), the origin of the *Hybomys* division dates from 7.4 (95% HPD = 6.9-9.4) mya, consistent with a late Miocene (Tortonian) appearance. The *Hybomys* division is among the earliest clades to separate within Arvicanthini, following the divergence of the *Golunda* and *Oenomys* lineages and preceding the many branches that evolved into the extant genera that inhabit Africa's expansive grasslands and savannahs. The same chronological order of basal divergences within Arvicanthini was captured in other molecular studies (Lecompte et al. 2008, Fabre et al. 2013). Nonetheless, the critical basal branch lengths are short and nodal support weak, statistically rendering early branches as a polytomy (e.g. as depicted by Missoup et al. 2016). Appeal to other genes, perhaps coupled with more precise determinations of common ancestry illuminated by palaeontological investigation (Kimura et al. 2015, 2017, 2021), may amplify statistical confidence in the early cladogenesis of Arvicanthini and its primal association with Guineo-Congolian rainforest.

Closed-canopied, tropical rainforest developed by the late Cretaceous, and as of the middle Miocene climatic optimum, it extended coast to coast across the equatorial zone of central Africa (Maley 1996, Morley & Kingdon 2013). The maximum extent of the African rainforests has been shrinking since the Eocene and Miocene (22 to 15 million km^2), Pliocene (10 million km^2) to current day (3.4 million km^2) (Hardy et al. 2013). The long-term contraction of rainforests was punctuated with shorter cycles of range expansion and contraction in the Late Miocene, Early Pliocene, and glacial-interglacial cycles of the Quaternary (Hardy et al. 2013). The antiquity of these lowland forests and their relatively stable climatic regime are thought to have provided optimal conditions for sustaining ancient lineages (palaeoendemics) and minimizing extinctions (Moritz et al. 2000); these expectations are generally supported by the concentration of genealogically older species within Guineo-Congolian rainforests, sometimes characterized as "museums" of biodiversity (Fjeldså & Bowie 2008, Murienne et al. 2012). Those sectors within the Guineo-Congolian Region that harbour exceptional species richness and high endemism (Fig. 3A), whether of plants or animals, decidedly support the notion of former rainforest refugia (Maley 1996, Plana 2004, Fjeldså & Bowie 2008, Hardy et al. 2013). While the hypothesized refugia (pictured in Fig. 3A) are from the Late Quaternary (Maley 1996), they may roughly represent the refugia in the Pleistocene, Pliocene and Miocene due to the congruent placement of the areas of endemism (Happold 1996). The Miocene emergence of the *Hybomys* division (Fig. S4) and the geographic complementarity of its generic and specific distributions apropos subdivisions of the Guineo-Congolian Region (Figs. 1B, 3B) intimate a similar biogeographic history.

Diversification within the *Hybomys* division in African rainforests

The following discussion entails three assumptions: 1) the common ancestor of the *Hybomys* division inhabited lowland rainforest, whether dwelling in forest proper or in environments dependent upon evergreen moist forest. This supposition seems reasonable in view of the association of all living species with rainforest environments, primary or secondary, and the tight distributional coalignment of the division with the Guineo-Congolian Region (Figs. 1B, 3B); 2) speciation has transpired as an allopatric process, with vicariant barriers such as dry savannahs or impassable rivers fragmenting ancestral populations and promoting genetic differentiation. Authoritative synopses of many tropical organisms encourage acceptance of this assumption (e.g. Moritz et al. 2000, Plana 2004, Fjeldså & Bowie 2008). We lack requisite sample sizes and fine-scaled geographic representation to adequately test whether our cladogram fits a parapatric speciation model consistent with differentiation along some environmental gradient; 3) descendant species within the *Hybomys* division have retained the essential ecological

characteristics and physiological tolerances of their distant Miocene ancestors. The question of niche conservatism must remain an inference in view of our fragmentary ecological knowledge of the forest species under study and the absence of any fossils of the four genera that might support paleoenvironmental interpretation.

According to our fossil-calibrated consensus tree (Fig. S4), the four descendant genera within the *Hybomys* division arose during the late Miocene (Messinian) and early Pliocene, sequentially delineated by three major lineage splits at approximately 7.4 (*Typomys*), 6.7 (*Hybomys*), and 4.8 mya (*Dephomys-Stochomys*). Only the youngest of these phyletic divisions gave rise to genera that are now wholly allopatric, the distributions of *Dephomys* and *Stochomys* being divided by the River Volta (Fig. 1B). Living descendants of the two older branching episodes are partially or fully overlapping in their areal distributions (Fig. 1B), indicating considerable range expansion and secondary contact following their divergence (again, assuming an allopatric speciation process). Thus, *Typomys* is broadly sympatric with *Dephomys* in Upper Guinea forest and with *Stochomys* in Lower Guinea west of the River Niger; whereas, the distribution of *Hybomys* overlaps that of *Stochomys* in Lower Guinea and Congolia (Fig. 1B). Post-isolation range expansion and secondary geographic overlap are similarly necessary to account for the specific distributions of *Typomys*, following their separation in the middle Pliocene (Fig. S4). The ranges of *T. planifrons* and *T. trivirgatus* intersect in the western reaches of the Upper Guinea forest block, in the area of the hypothesized Liberian refuge (Fig. 3).

Genera within the *Hybomys* division likely derive from common ancestors that spanned multiple forest blocks, if not the full range of Upper Guinea to Congolia. These early Pliocene ancestral taxa lived through wet cycles involving extensive forestation across Africa (chequered region in Fig. 3A). By the end of the early Pliocene, however, modern patterns of generic distribution may have emerged, with *Typomys* excluded from Congolia, *Dephomys* restricted to Upper Guinea, and *Hybomys* and *Stochomys* excluded from Upper Guinea.

The collection of *S. longicaudatus* from eastern Ghana (Decher et al. 2021) highlights the limited role that the Dahomey Gap appears to play in the evolutionary history of the *Hybomys* division. The Dahomey Gap is a wide swath of Sudan-like savannah that reaches the Atlantic coast and separates West African rainforest into the Upper Guinea and Lower Guinea sectors (Fig. 1A). Although earlier syntheses of mammalian distributions had minimized the significance of the Dahomey Gap as a vicariant barrier in West Africa (Booth 1954, Robbins 1978), recent floristic investigations have revitalized the biogeographic role of the Gap and underscored its recurrent formation, demonstrably in younger epochs (Salzmann & Hoelzmann 2005, Duminil et al. 2013) and inferentially in deeper time (Plana 2004, Couvreur et al. 2008). Pollen analyses document several Holocene fluctuations between rainforest and savannah vegetation in this region, the last encroachment of savannah occurring around 1,100 yr BP (Salzmann & Hoelzmann 2005). A surprisingly recent divergence time separates *S. longicaudatus* from eastern Ghana and a clade uniting samples from Gabon and western Cameroon (0.50 (95% HPD = 0.23 to 0.78) mya). Among remaining members of the *Hybomys* division, the isolation of populations of *T. trivirgatus* in western Nigeria, separated from the main species distribution to the west of the Dahomey Gap (Fig. 3B), is plausibly interpreted as a another very recent occurrence.

Riverine barriers have clearly played an important role in isolating and restricting the geographic spread of rodents in the *Hybomys* division, but most examples of isolation are accompanied by counter examples. *Typomys planifrons* does not extend east of the River Sassandra in Côte d'Ivoire, but both *T. trivirgatus* and *D. defua* are found on both sides. The River Volta separates *Dephomys* from *Stochomys*, but does not separate *T. trivirgatus* (though this needs testing). *Typomys trivirgatus* on either side of the Volta exhibit different striping pattern with forms east of the Volta displaying longer dorsal stripes compared to those from the west (Happold 2013). The Niger represents the easternmost edge of the distribution of *Typomys* and the westernmost edge for *Hybomys*, but the range of *S. longicaudatus* spans it. Finally, the Sanaga and Ogooue rivers appear to delineate potential species within *Hybomys*. Overall, these riverine barriers broadly align with intrageneric studies on other small mammals of African forests such as *Malacomys* (Bohoussou et al. 2015), *Hylomyscus* (Nicolas et al. 2020), *Grammomys* (Bryja et al. 2017), and *Crocidura* (Jacquet et al. 2014, 2015). The foundation for a comparative phylogeography model for the evolution of sylvan small mammals

has been laid. Such a model may involve allopatry via forest refugia (Fig. 3A) followed by subsequent maintenance of isolation due to large rivers (Haffer 1982, Maley 1996, Bohoussou et al. 2015, Nicolas et al. 2019). More extensive intraspecific sampling of species in the *Hybomys* division, particularly, *S. longicaudatus*, *D. defua*, and *T. trivirgatus* will better illuminate these patterns.

Our results fail to support the distinctiveness of montane forms of *Hybomys* (*badius* and *eisentrauti*) found along the Cameroon Volcanic Line (Mount Oku, Bamenda Highlands) as compared with neighbouring lowland *Hybomys*. In contrast, the Albertine Rift taxon, *H. lunaris*, is the earliest diverging species of *Hybomys*. This divergence dates to the late Pliocene, during a dry phase (3.0 to 3.5 mya) when forests would have retreated and conceivably isolated the *H. lunaris* progenitor in a montane refugium. The Albertine Rift region has long been recognized as a biodiversity hotspot (Kerbis Peterhans et al. 1998, Mazel et al. 2014). Biogeographic studies of Afrotropical resident birds have consistently identified the Albertine Rift as a region of rich endemism where phylogenetically distinct species are concentrated (Fjeldså et al. 2007, Fjeldså & Bowie 2008). Likewise, the montane forests of the Albertine Rift exhibit numerous mammalian endemics (Kityo et al. 2003, Plumptre et al. 2007) including many that have been described recently such as bats in the genus *Rhinolophus* (Kerbis Peterhans et al. 2013a), shrews in the genera *Crocidura* and *Myosorex* (Kerbis Peterhans et al. 2010, 2013b); rodents in the genus *Hylomyscus* (Demos et al. 2014a, Kerbis Peterhans et al. 2020) and *Lophuromys* (Verheyen et al. 2007); and a primate (Davenport et al. 2006). Additional potential Albertine Rift species have been identified based on unique evolutionary lineages in *Sylvisorex* (Demos et al. 2014b, 2015), *Miniopterus* (Demos et al. 2020), and *H. lunaris* (Huhndorf et al. 2007).

Located in the Gulf of Guinea near the Cameroon coast, Bioko Island is an amalgam of three stratovolcanoes. Bioko is part of the Cameroon Volcanic Line, a string of volcanoes that include the islands of Annobón, São Tomé, Príncipe, and Bioko along with several highlands on the African continent such as Mount Cameroon, Mount Oku, and the Ngaoundéré and Biu Plateaus (Jones 1994, Aka et al. 2004). Although our results do not support the distinctiveness of *Hybomys* from the Cameroon Line highlands on the African continent (*badius* on Mount Cameroon, *rufocanus* s.s. from the Bakossi Mountains, and *eisentrauti* from Mount Oku and Mount Lefo), the Bioko Island species, *H. basilii*, is quite distinctive, having diverged from mainland *Hybomys* 2.0 (95% HPD = 1.5 to 2.5) mya. Although our data allow for the arrival of *Hybomys* on Bioko any time between its divergence from mainland *Hybomys* until the most recent common ancestor of the two haplotypes of *H. basilii* sampled (~100 kya), our 1.2 (95% HPD = 0.83-1.66) mya estimate is surprisingly congruent with the formation of the stratovolcanoes that comprise the island, which took place 1.3 mya (K-Ar dating – Aka et al. 2004). Bioko was a peninsula during glacial cycles, was repeatedly connected to mainland Africa near Mount Cameroon, and the most recent connection was, ~10 kya, after the Last Glacial Maximum (Jones 1994). *Hybomys basilii* is not related to *H. rufocanus*, the mainland species found in the part of Africa to which Bioko has shared a past physical connection but is instead related to *Hybomys* from Congo and Gabon. This rare animal is probably an old endemic to Bioko and is one of only three endemic mammal species found on the island (Amori et al. 2008). The others are both shrews, *Sylvisorex isabella* and *Myosorex eisentrauti* (though see Groves & Grubb 2011, who consider the Bioko blue duiker, *Philantomba melanorheus*, to be its own species). Several Bioko endemic subspecies of primate, rodent, and hyrax have been recognized along with distinct intraspecific clades of small mammal (Missoup et al. 2012, Nicolas et al. 2019), but these taxa likely arrived much later in the Pleistocene compared to *H. basilii*. Our findings highlight the importance of conservation efforts to protect this endangered and evolutionary distinctive rodent (Kennerley 2016).

Future research needs

The molecular evidence presented above supports the monophyly of the *Hybomys* division (Fig. 2), evaluates relationships and divergence times among its members (Fig. S4), and recommends their taxonomic rank (Table S4). We also have formulated a preliminary interpretation of the historical biogeography of the *Hybomys* division, highlighting its intimate association with forests of the Guineo-Congolian Region since the late Miocene. Several research avenues would improve our biogeographical understanding of these forest-dwelling rodents.

Foremost is the need to markedly augment geographic sampling in order to compare patterns

of intraspecific genetic variation with interspecific relationships. In spite of having a similar range, *Stochomys* and *Hybomys* yield markedly different results. Based on only three localities, we found surprisingly little genetic variation in *S. longicaudatus*. Broader geographic sampling, especially from eastern Congolian forests and south of the River Congo are needed to confirm this result and to determine what patterns, even recent ones, are present in this species. Taxonomic problems within *H. univittatus* have been identified (Carleton & Robbins 1985, Musser & Carleton 2005, this study). Table S4 should be viewed as a temporary taxonomic solution for *H. univittatus*, as the species as delineated there remains paraphyletic. Additional sampling across more of Congolia is also needed in *H. univittatus*. Expansion of geographic representation within *Hybomys* must include additional samples of *H. lunaris* from the Albertine Rift. Morphological and genetic evidence casts doubt that only one *Hybomys* species inhabits montane forests of the Albertine Rift (Musser & Carleton 2005, Huhndorf et al. 2007). We also lack sampling from a single species, *D. eburneae*.

The genetic signature of *T. trivirgatus* in western Nigeria, Lower Guinea, invites attention in view of its isolation from the main distribution of the species in Upper Guinea forest, west of the Dahomey Gap (Fig. 3B). The Nigerian isolate had been named as a subspecies, *pearsei* Ingoldby, 1929, distinguished by its weaker definition of trilinear dorsal striping compared with animals from Upper Guinea forest, where *T. trivirgatus* overlaps *T. planifrons*. Does the Nigerian segment represent a recent expansion (Holocene) eastward across the Dahomey Gap or an older relict (Pliocene) that dates from the divergence of *T. trivirgatus* and *T. planifrons* in separate refugia?

Comparative phylogeographic analysis of multiple murine taxa indigenous to the Guineo-Congolian Region, with largely congruent distributions, may assist in delimiting contemporaneous episodes of speciation and in pinpointing older zones of vicariance. Along with members of the *Hybomys* division, potentially informative candidates include the genus *Malacomys* (Bohoussou et al. 2015), *Colomys* (Giarla et al. 2020), the *Thamnomys poensis* group (Bryja et al. 2017), the *Hylomyscus alleni* group (Nicolas et al. 2006, 2020), the *Hylomyscus anselli* group (Kerbis Peterhans et al. 2020), and the *Praomys tullbergi* complex (Nicolas et al. 2008, Missoup et al. 2012).

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Supplementary online material

Fig. S1. Maximum Likelihood Majority rule consensus tree of the *Hybomys* division, other Arvicanthini divisions and outgroup taxa based on concatenated sequences of two mitochondrial (Cyt*b*, 12S rRNA) and two nuclear (*Ghr*, *Rbp3*) genes (https://www.ivb.cz/wp-content/uploads/JVB-vol.-70-2-2021-Pradhan-et-al.-Fig.-S1.tif).

Fig. S2. Bayesian Majority rule consensus tree of the *Hybomys* division, other Arvicanthini divisions and outgroup taxa based on concatenated sequences of two mitochondrial (Cyt*b*, 12S rRNA) and two nuclear (*Ghr, Rbp3*) genes (https://www.ivb.cz/wp-content/uploads/JVB-vol.-70-2-2021-Pradhan-et-al.-Fig.-S2.tif).

Fig. S3. Fossil calibrated phylogeny of the *Hybomys* division with mean node ages ± 95% highest posterior density intervals based on concatenated sequences of mitochondrial (Cyt*b*, 12S rRNA) and nuclear (*Rbp3*, *Ghr*) genes. Calibrated using estimates from Aghová et al. (2018) for crown Murinae, *Arvicanthis*/*Mus*, Arvicanthini/Otomyini/Millardini, and stem *Arvicanthis*. Outgroups not shown (https://www.ivb.cz/wp-content/uploads/JVB-vol.-70-2-2021-Pradhan-et-al.-Fig.-S3-1.tif).

Fig. S4. Fossil calibrated phylogeny of the *Hybomys* division with mean node ages ± 95% highest posterior density intervals based on concatenated sequences of mitochondrial (Cyt*b*, 12S rRNA) and nuclear (*Rbp3*, *Ghr*) genes. Full tree presented in Fig. S5 with calibration points (*): Crown Murinae (Median: 14.2 mya; 95% HPD: 13.3-16.0 mya), *Arvicanthis*/*Mus* (Median: 11.6 mya; 95% HPD: 10.6-13.0 mya) and *Arvicanthini/Otomyini/Millardini* (Median: 9.2 mya; 95% HPD: 7.9-10.6 mya) (https://www.ivb.cz/wp-content/uploads/JVB-vol.-70-2-2021-Pradhan-et-al.-Fig.-S4-1.tif).

Fig. S5. Fossil calibrated phylogeny of the *Hybomys* division, select Arvicanthini and outgroups with mean node ages ± 95% highest posterior density intervals based on concatenated sequences of mitochondrial (Cyt*b*, 12S rRNA) and nuclear (*Rbp3*, *Ghr*) genes. Calibration points (*): *Arvicanthis*/*Mus*, *Arvicanthini/Otomyini/Millardini*, and crown Murinae (https://www.ivb.cz/wp-content/uploads/JVB-vol.-70-2-2021-Pradhan-et-al.-Fig.-S5.tif).

Table S1. Specimens of the *Hybomys* division from which sequence data were examined in this study.

Table S2. Accession numbers of select taxa of Arvicanthini other than members of the *Hybomys* division and murid outgroups accessed from GenBank for mitochondrial (Cyt*b*, 12 S) and nuclear (*Rbp3*, *Ghr*) genes used in this study.

Table S3. Primers and primer sequences used to amplify target genes in this study.

Table S4. Revised taxonomy of the *Hybomys* division (Muridae: Murinae: Arvicanthini[a]), with abridged generic synonymies (first usage of unique name combinations) and valid species (in boldface).

Table S5. Sources of funding and permits and list of field and laboratory assistants.

(https://www.ivb.cz/wp-content/uploads/JVB-vol.-70-2-2021-Pradhan-et-al.-Tables-S1-S5-1.pdf)