Dear Editors,

We wish to submit our manuscript "*Phylogenomics of African radiation of Praomyini (Muridae: Murinae) rodents: first fully resolved phylogeny, evolutionary history and delimitation of extant genera*" to the *Molecular Phylogenetics and Evolution*. The study is a logical continuation of our previous work (Mikula et al. 2021, Mol Phyl Evol), in which we are focussing on solving the phylogeny of most important (in terms of abundance, practical importance to human and the level of evolutionary diversification) groups of African rodents. Here we provide the first fully resolved phylogeny of all major lineages in the murid tribe Praomyini, which contains probably the most abundant taxa of extant mammals in Africa. We again used the genomic data (both nuclear and mitochondrial) and the complete taxon sampling (i.e. all but one currently recognized genera and representatives of major intrageneric clades across sub-Saharan Africa) to reconstruct the phylogenetic relationships. The resolved phylogeny is then analysed in temporal context by using the new set of well-selected fossils. The output of the divergence dating analysis (i.e. dated tree) is used to propose the evolutionary scenario of the (adaptive) radiation in Late Miocene. Important part of the manuscript is its taxonomic part. Our analyses clearly confirmed the presence of three polyphyletic genera and we review current knowledge of them and propose corresponding taxonomic solutions. To keep genera monophyletic, we suggest taxonomic re-arrangements and delimit four new genera. Furthermore, we discovered a new highly divergent genetic lineage of Praomyini in southwestern Ethiopia, which is described as a new mammalian species and genus.

We believe this manuscript is appropriate for publication in the *Molecular Phylogenetics and Evolution* as it provides large amount of new results, especially (1) fully resolved phylogenomic/mitogenomic trees of the very successful mammalian radiation in Africa; (2) evolutionary scenario of (adaptive) radiation in last 7 million years in Africa, i.e. the continent where our own species evolved during the same time period; (3) taxonomic solution for intensively studied and practically important African mammals. We believe the paper should be of interest not only to specialists using African rodents as a model group in historical biogeography research, but also to readers using phylogenomic approaches in answering wide spectrum of questions in systematic and evolutionary biology.

None of the material in this manuscript has been published or is under consideration for publication elsewhere. All data used in the paper are made available. The manuscript has been approved by all the co-authors who agreed to its submission.

Thank you for considering this manuscript, we will look forward to hearing from you.

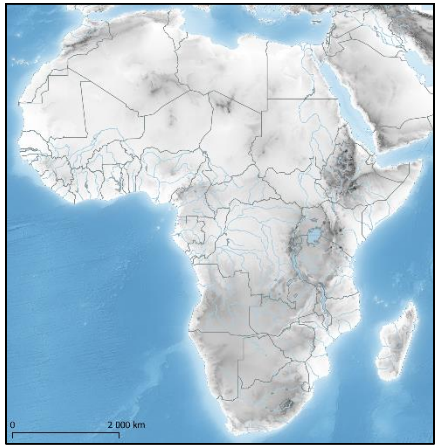
Yours Sincerely,

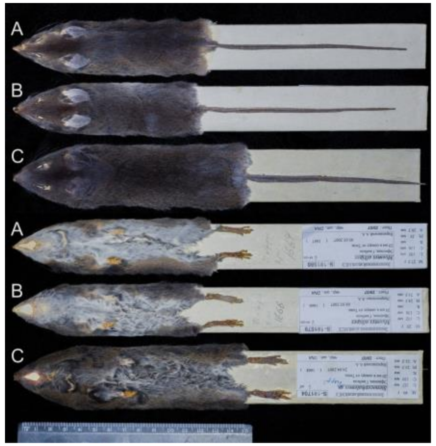
Josef Bryja (on behalf of all co-authors)

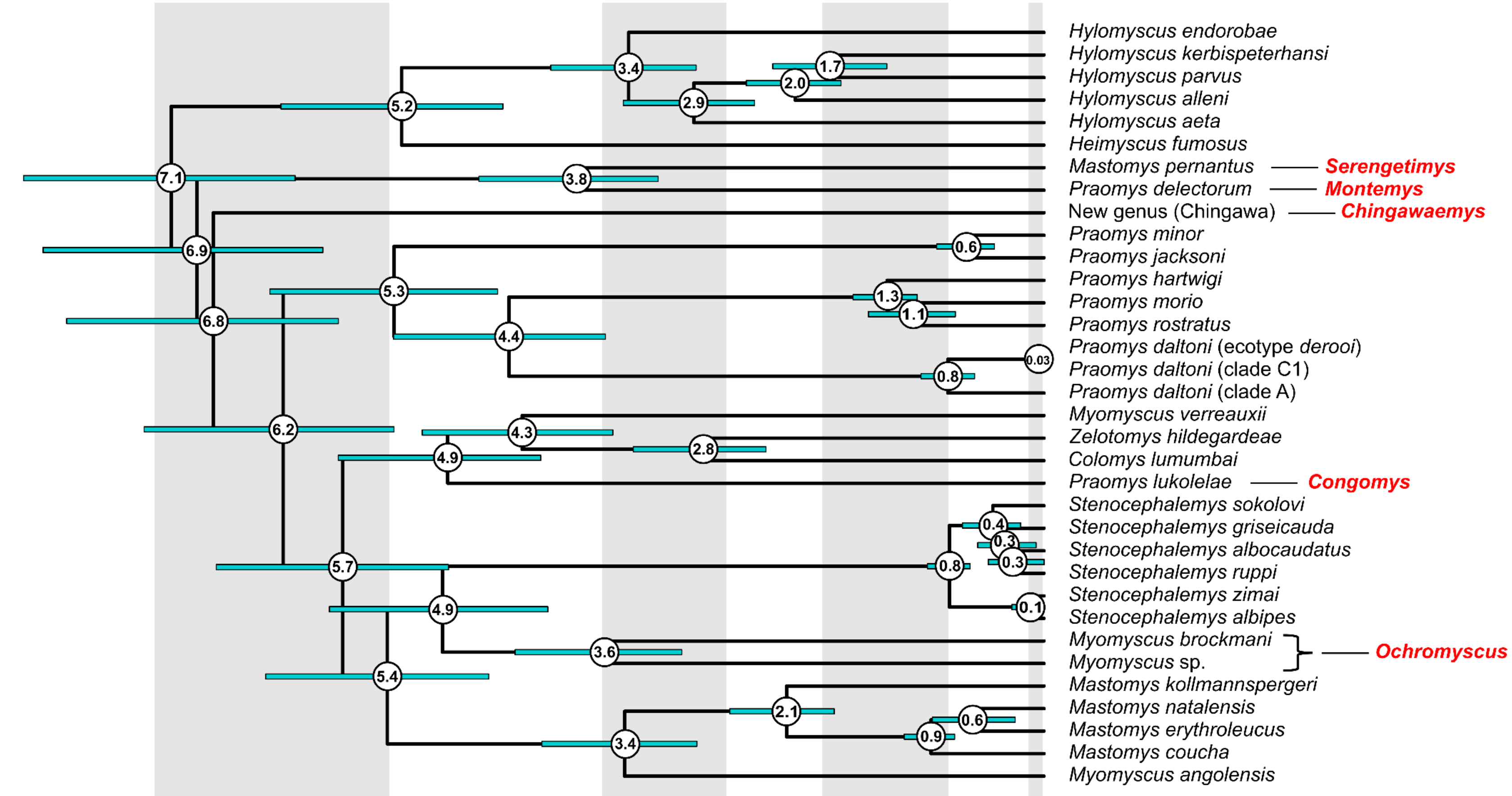
Highlights

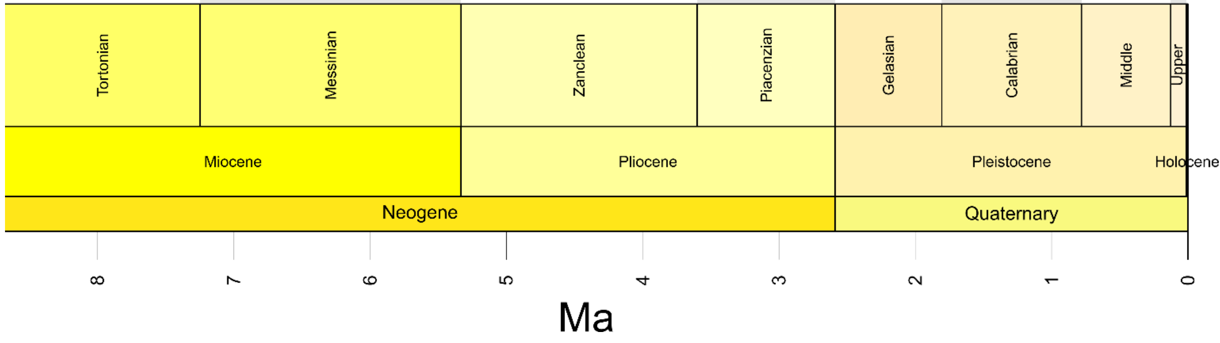
- fully resolved phylogeny of a highly diversified group of African mammals using genome-scale data
- mechanisms of adaptive radiation in Late Miocene/Early Pliocene
- delimitation of monophyletic genera in Praomyini rodents
- discovery of a new mammal genus in Ethiopian forests

Graphical Abstract









Phylogenomics of African radiation of Praomyini (Muridae: Murinae) rodents: first fully resolved phylogeny, evolutionary history and delimitation of extant genera

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Authors´ contributions: VN, OM, EV, LAL, RS, and JB conceived the study and provided funding, VN, EV, ADM, YM, LAL, RS, JB sampled analysed specimens and/or provided samples under their care, ARL and EML produced the anchored phylogenomics dataset, VB and AB did significant part of the lab work and assembled mitogenomes, OM analysed data (with help of VN, VB, JB), VN, OM, LAL and JB drafted the manuscript. All authors contributed to the editing of the manuscript, gave final approval for publication and agreed to be held accountable for the work performed therein.

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ABSTRACT

The tribe Praomyini is a diversified group including 64 species and eight extant rodent genera. They live in a broad spectrum of habitats across whole sub-Saharan Africa. Members of this tribe are often very abundant, they have a key ecological role in ecosystems, they are hosts of many potentially pathogenic microorganisms and comprise numerous agricultural pests. If this tribe is well supported by both molecular and morphological data, its intergeneric relationships and the species contents of several genera are not yet fully resolved. Recent molecular data suggest that at least three genera in current sense are paraphyletic. However, in these studies the species sampling was sparse and the resolution of relationships among genera was poor, probably due to a fast radiation of the tribe dated to the Miocene and insufficient amount of genetic data. Here we used genomic scale data (395 nuclear loci = 610,965 bp long alignment and mitogenomes = 14,745 bp) and produced the first fully resolved species tree containing most major lineages of the Praomyini tribe (i.e. all but one currently delimited genera and major intrageneric clades). Results of a fossil-based divergence dating analysis suggest that the radiation started during the Messinian stage (ca. 7 Ma) and was likely linked to a fragmentation of the pan-African Miocene forest. Some lineages remained in the rain forests, while many others adapted to a broad spectrum of new open lowland and montane habitats that appeared at the beginning of Pliocene. Our analyses clearly confirmed the presence of three polyphyletic genera (*Praomys*, *Myomyscus* and *Mastomys*). We review current knowledge of these three genera and suggest corresponding taxonomic changes. To keep genera monophyletic, we propose taxonomic re-arrangements and delimit four new genera. Furthermore, we discovered a new highly divergent genetic lineage of Praomyini in southwestern Ethiopia, which is described as a new species and genus.

Keywords: Late Miocene, radiation, anchored phylogenomics, Rodentia, tropical Africa, complete mitochondrial DNA, taxonomy

1. Introduction

The phylogeny and evolutionary history of the most successful group of mammals worldwide, i.e. murid rodents (Rodentia: Muridae), is relatively well known thanks to recent analyses of large multi-locus genetic datasets and calibration of molecular clock based on multiple paleontological records (Aghová et al., 2018; Steppan and Schenk, 2017; Upham et al., 2019). This family is divided in five subfamilies, among which the Murinae is the most species-rich (ca. 656 species) (Wilson et al., 2017). Within this subfamily 15 tribes were delimited (Wilson et al., 2017), and five of them (Otomyini, Arvicanthini, Malacomyini, Murini, Praomyini) are indigenous in sub-Saharan Africa (Denys et al., 2017; Lecompte et al., 2008).

The tribe Praomyini is monophyletic, it is the sister clade of the Murini tribe (Aghová et al., 2018; Lecompte et al., 2008; Steppan and Schenk, 2017; Upham et al., 2019), and it is characterized by several autapomorphic characters (Lecompte et al., 2005). According to Denys et al. (2017) it includes eight modern genera (*Colomys*, *Heimyscus*, *Hylomyscus*, *Mastomys*, *Myomyscus*, *Praomys*, *Stenocephalemys* and *Zelotomys*), all endemic to sub-Saharan Africa, except the genus *Myomyscus* with one species (*M. yemeni*) found in Yemen and Saudi Arabia, and the genus *Mastomys*, which includes one species (*M. erythroleucus*) distributed also in North Africa (Morocco). The most recent Handbook of the Mammals of the World (Wilson et al., 2017) lists 54 species of Praomyini. The very rare or even extinct genus *Nilopegamys* shares some morphological characters with this tribe and has been suggested as a possible member of this group (Wilson et al., 2017). The recent genetic analysis of the only known individual captured at the type locality in Ethiopia confirmed its sister relationship with *Colomys*, i.e. its membership in Praomyini (Giarla et al., 2020). Additionally, four new species of *Hylomyscus* were recently described by Kerbis Peterhans et al. (2020), two *Stenocephalemys* by Mizerovská et al. (2020), and three additional *Colomys* were delimited by Giarla et al. (2020), making the number of species of Praomyini equal to 64 (see https://mammaldiversity.org/). It is not a final number, as numerous species are awaiting their formal descriptions (Kennis et al., 2011; Missoup et al., 2012; Mizerovská et al., 2019; Nicolas et al., 2020a; Nicolas et al., 2012b). Several genera are species rich and widely distributed (e.g. 22 recognized species of *Hylomyscus*, 16 species of *Praomys*), while others have low diversity (e.g. the monospecific genus *Heimyscus* or *Zelotomys* with two species) or restricted ranges (e.g. the genera *Stenocephalemys* and *Nilopegamys* restricted to Ethiopian Highlands). Praomyine rodents colonized whole sub-Saharan Africa, where they live in a broad spectrum of habitats, from lowland and montane rainforests through various types of open habitats (marshlands, savannas, woodlands and alpine moorlands), agricultural fields and human habitations. Based on molecular data the fast radiation leading to major lineages of Praomyini occurred at the

Messinian age of Miocene and most extant genera appeared almost simultaneously (Aghová et al., 2018).

The tribe Praomyini is a very important group of African rodents for several reasons. They are hosts of many potentially pathogenic microorganisms, like mycobacteria (Durnez et al., 2010) and viruses (Borremans et al., 2011; Briese et al., 2009; Coulibaly-N'Golo et al., 2011; Durnez et al., 2008; Fichet-Calvet et al., 2007; Gryseels et al., 2017; Gryseels et al., 2015; Klempa et al., 2006; Konstantinov et al., 2006; Lecompte et al., 2006; Meheretu et al., 2012; Olayemi et al., 2016; Olayemi and Fichet-Calvet, 2020; Tesikova et al., 2017), and some of them are important for human health, e.g. the Lassa virus which causes several thousand people dead in West Africa annually. They were also shown to be potential mammalian reservoirs of bubonic plague (Isaacson et al., 1983; Makundi et al., 2008). Moreover, this tribe comprises numerous agricultural pests; the most important among them, widespread *Mastomys natalensis*, can cause extensive damage to crop and stored grain. It was estimated that it can cause yield losses up to 48% during populations outbreaks and even in non-outbreak years average annual crops loss is in the range of 5-15% (Leirs, 2002; Mwanjabe et al., 2002). They have also a key ecological role in ecosystems, representing the most abundant members of rodent communities (Happold, 2013; Nicolas and Colyn, 2003; Nicolas et al., 2020b), serving as seed dispersers and relevant part of diet in carnivores. While some species are among the most common, widespread and abundant African rodents (e.g. *M. natalensis* or *Praomys jacksoni*), others are rare and classified as near threatened (*Praomys mutoni*), vulnerable (*Praomys hartwigi*, *P. degraaffi*), endangered (*Hylomyscus baeri*, *Praomys morio*, *P. obscurus*) or even critically endangered (*Hylomyscus grandis*, *Nilopegamys plumbeus*) on the IUCN Red list (Wilson et al., 2017). Members of the Praomyini tribe are becoming important models in biogeographic and evolutionary studies, and were recently used as model taxa to assess the relative role of topographical structure and climatic changes as drivers of diversification of African biota (Brouat et al., 2009; Bryja et al., 2010; Bryja et al., 2018; Bryja et al., 2014; Colangelo et al., 2013; Kennis et al., 2011; Missoup et al., 2012; Mizerovská et al., 2019; Mouline et al., 2008; Nicolas et al., 2008; Nicolas et al., 2020a; Nicolas et al., 2012a; Nicolas et al., 2011).

If this tribe is well supported by both molecular and morphological data, the intergeneric relationships, and the species contents of several genera are still a matter of debate. Musser and Carleton (2005) placed the members of Praomyini in two divisions: the *Stenocephalemys* division (including *Heimyscus*, *Hylomyscus*, *Mastomys*, *Myomyscus*, *Praomys* and *Stenocephalemys*) and the *Colomys* division (comprising *Colomys* and *Zelotomys*), based primarily upon morphological characters. However, more recent molecular multi-locus data (Aghová et al., 2018; Lecompte et al., 2008; Steppan and Schenk, 2017; Upham et al., 2019) suggest a different arrangement of taxa within this group. Specifically, three current genera appear as paraphyletic: 1) *Myomyscus* (*M. verreauxii* does not cluster with other *Myomyscus* species, but rather with *Colomys* and *Zelotomys*), 2) *Praomys* (*P. delectorum* can be the sister clade of *Mastomys pernanus*, and this clade can be the sister clade of *Hylomyscus*+*Heimyscus*; *P. lukoleale* and *P. vershureni* form the lukolelae species group, which can be the sister clade of *Myomyscus verreauxi*+*Colomys*+*Zelotomys*), 3) *Mastomys* (*M. pernanus* can be the sister clade of *P. delectorum*). Furthermore, *Heimyscus* is in all recent molecular analyses, including the last revision of the genus (Nicolas et al., 2020a), the sister clade of *Hylomyscus*, except the study of Upham et al. (2019), where it is part of *Hylomyscus*. However, in all these molecular phylogenetic studies the resolution of deeper nodes of the trees was poor, suggesting fast radiation and/or insufficient amount of used molecular markers. Moreover, the species sampling was sparse, except the work of Upham et al. (2019) that included most species present in the GenBank database. This approach, on the other hand, might introduce an error caused by misidentifications (see Krásová et al., 2021 for an outstanding example).

A well-resolved phylogeny of the Praomyini tribe is crucial to understand the diversity, evolution and biogeographical patterns of sub-Saharan African mammals. Here we used the samples from all but one (*Nilopegamys*) major phylogenetic lineages of the tribe Praomyini defined by a combination of previous studies and employed the so-called anchored phylogenomic approach that uses high throughput sequencing of targeted enriched genomic libraries (Lemmon et al., 2012). This method enables rapid construction of phylogenomic datasets that incorporate hundreds to thousands of nuclear loci, and can resolve difficult nodes at varied taxonomical and time scales, including taxa that diverged since the Miocene (e.g. Chen et al., 2017; Garcia-R et al., 2020; Li et al., 2019; Mikula et al., 2021; Wu et al., 2020). As a complementary approach we assembled complete mitogenomes (parts of them correspond to the most frequently used markers in mammalian phylogeny) and reconstructed their phylogenetic relationships. Based on the results of molecular phylogenomic analyses and other available data, we propose taxonomic changes and delimit monophyletic genera of the tribe Praomyini.

2. Methods

2.1 Taxon sampling

This study includes 34 specimens of Praomyini, representing all currently recognized genera of the tribe, except *Nilopegamys* (known only from the holotype, recently analysed by Giarla et al., 2020), and all taxa whose systematics position and taxonomy was recently subject to debate (e.g. *Myomyscus verreauxii*, *M. brockmani*, *M. angolensis*, *Praomys delectorum*, *Praomys lukolelae*, *Mastomys pernanus*). For the species-rich genera (*Hylomyscus* and *Praomys*) we selected representatives of all recognized species groups (Mikula et al., 2020; Missoup et al., 2012; Mizerovská et al., 2019; Nicolas et al., 2020a). Additionally, we also included one genetically very divergent specimen from an unknown genus, recently discovered in the Chingawa forest in south-western Ethiopia, called "New genus (Chingawa)". As outgroups in all phylogenetic analyses we used two species from the tribe Arvicanthini (*Aethomys chrysophilus* and *Arvicanthis somalicus*), one from Otomyini (*Otomys typus*) and one from Millardini (*Millardia meltada*). All details about the used specimens, including localities and museum numbers, are shown in Table 1. The tissue samples originate from the tissue collections of authors and their collaborators and the sampling was carried out in accordance with local legislation in particular African countries.

Table 1. List of material of Praomyini (+ four outgroups) used in phylogenomic analyses, their current/proposed generic classification, and the GenBank accession numbers of mitogenomes.

2.2 Anchored hybrid enrichment (AHE) data collection and assembly of nuclear dataset

Probe design and data collection were performed by the Center for Anchored Phylogenomics (www.anchoredphylogeny.com). The details about the improved vertebrate AHE target loci of Lemmon et al. (2012) for optimal use in mammals are provided in Mikula et al. (2021). Briefly, genomic DNA was extracted using the Invisorb® Spin Tissue Mini Kit (Stratec, Germany). After extraction, indexed libraries were prepared on a Beckman Coulter FXP liquid-handling robot following Lemmon et al. (2012) and Prum et al. (2015). Libraries were then pooled at equal concentrations in three groups of ~14 samples and enriched using an Agilent SureSelect XT kit containing the probes described above. Enriched library pools were then sequenced on one paired-end 150 bp lane of an Illumina HiSeq 2500 sequencer at the Translational lab in the Florida State University. Paired reads were merged prior to assembly following Rokyta et al. (2012), which also removes adapter sequences. A quasi-de novo assembly approach was taken using *Homo sapiens* as the reference. Assembly clusters derived from fewer than 175 reads were removed from further analysis in order to reduce the possible effects of low level contamination and mis-indexing. Orthology was established among the consensus sequences recovered at each of the target loci using the pairwise sequence distances among the consensus sequences (see Hamilton et al., 2016 for details). More details about the alignment and trimming procedures are provided in Mikula et al. (2021).

2.3 Assembly and alignment of mitogenomes

Mitochondrial DNA is usually highly prevalent in genomic DNA extractions and it still persists even in genomic libraries enriched for particular conserved loci. We used the raw data of Illumina reads to assembly the complete mitogenomes of 38 analysed taxa (34 ingroups, 4 outgroups) as a by-product of the AHE approach. Heavy-strand protein-coding genes (12 genes) and genes for non-coding RNA (two ribosomal RNAs and 22 transfer RNAs) were extracted from the complete mitochondrial sequences in the Geneious software (Biomatters Ltd.) according to the annotated reference of complete mtDNA of *Mastomys coucha* (GenBank accession number MF062946). We excluded the control region (CR) sequences because of alignment difficulties due to highly variable non-coding sequences (Pozzi et al., 2014), and ND6 gene because it is encoded on the mitochondrial L-strand which has a different nucleotide composition from the H-strand, and has been shown to have poor phylogenetic signal (Gissi et al., 2000). The protein-coding genes were individually aligned based on their corresponding amino acid translations in Geneious. Two genes for ribosomal RNA (12S-rDNA and 16S-rDNA) and 22 genes for transfer RNA were aligned following Mikula et al. (2021).

2.4 Phylogenetic analysis of nuclear loci

First, we concatenated all 395 nuclear loci and subjected them to the same ML and Bayesian tree inference procedures as described below for complete mtDNA. Second, the species tree was inferred in ASTRAL III v. 5.7.5 (Zhang et al., 2018) – a summary method using topologies of pre-estimated gene trees as its input. In ASTRAL each gene tree is represented by a set of its compatible quartet subtrees and the algorithm searches for the species tree whose topology is compatible with the most frequently observed quartet subtrees (Mirarab and Warnow, 2015). In addition to the unrooted species tree topology, the frequencies of quartet tree topologies are used to approximate PPs of species tree bipartitions and inner branch lengths in coalescent units (Sayyari and Mirarab, 2016). ASTRAL tree was rooted post hoc, using four outgroups specified above.

The input gene trees were inferred in separate Bayesian analyses performed in MrBayes 3.2.6 (Ronquist et al., 2012). They were inferred as unrooted (uniform prior probability over tree topologies) with unconstrained branch lengths. The analysis sampled over GTR nucleotide substitution models (option nst=mixed in MrBayes; Huelsenbeck et al., 2004) with discrete gamma rate variation among sites. Markov Chain Monte Carlo (MCMC) was run for 5 million generations per run, sampling every 2000 generations. For each run, 25% of trees were discarded as burn-in. We conducted two independent runs and checked their convergence in R packages '*rwty*' (Warren et al., 2017) and '*coda*' (Plummer et al., 2006). The convergence diagnostics were average standard deviation of split frequencies (Lakner et al., 2008) and potential scale reduction factor (Gelman and Rubin, 1992), which should be close to zero for tree topologies and model parameters, respectively. We also checked if the effective sample size of all sampled parameters was large enough (>200). In ASTRAL, every gene was represented by its maximum bipartition credibility (MBC) tree calculated in '*phangorn*'. Bipartitions with PP < 0.90 were collapsed and thus the lack of resolution in MBC trees introduced uncertainty but not bias into ASTRAL.

2.5 Phylogenetic reconstruction of complete mtDNA

We used maximum likelihood (ML) and Bayesian approaches to infer phylogenetic relationships within Praomyini tribe using complete concatenated mitogenomes (without CR and ND6; see above). For ML inference we used IQ-TREE v. 2.1.2 (Nguyen et al., 2015), for Bayesian inference MrBayes v. 3.2.7 (Ronquist et al., 2012). In both cases the trees were calculated as unrooted with branch lengths unconstrained by clock assumptions. ModelFinder tool of IQ-TREE (Kalyaanamoorthy et al., 2017) was used to find the optimal partition scheme and the best nucleotide substitution model for each of the partitions. The candidate models included combinations of all general time reversible (GTR) substitution schemes with equal or unequal base frequencies and different models of rate heterogeneity among sites: a proportion of invariant sites, discrete gamma (Yang, 1994) and FreeRate model (Soubrier et al., 2012). Bayesian inference used the same partition scheme, but with models selected in a separate ModelFinder run, constrained to models available in MrBayes. After using outgroups for post-hoc rooting and their subsequent discarding, Bayesian posterior sample was summarized by the maximum clade credibility (MCC) tree estimated in R (R Core Team 2021) by findMCCT function (https://github.com/onmikula/mcctree_mrbayes) relying on packages '*ape*' (Paradis and Schliep, 2019) and '*phangorn*' (Schliep, 2011). Branch support was evaluated by ultra-fast bootstrap (UFBoot) (Hoang et al., 2018) in ML tree and by posterior probabilities (PP) in Bayesian MCC tree.

2.6 Sub-sampling of nuclear loci and time-calibrated phylogeny

Divergence dating analysis was performed on 57 nuclear loci that passed the following three criteria: (1) they were successfully sequenced in all ingroup taxa, (2) praomyines were monophyletic on MBC gene tree, and (3) Bayes Factor analysis supported strict over relaxed (lognormal uncorrelated) clock model. Bayes Factors (BFs) were calculated in RevBayes v. 1.1.0 (Höhna et al., 2016) using stepping-stone algorithm (Xie et al. 2012) for estimation of model marginal likelihoods (50 steps, α parameter of beta distribution = 0.2). In these calculations, we used GTR+G substitution model with parameters fixed to the means of posterior sample from inference of MBC gene tree. Outgroups were used for initial rooting of the trees but then discarded.

The time-calibrated phylogeny was inferred in StarBEAST 2 (Ogilvie et al., 2017) as a species tree, accounting for incomplete lineage sorting predicted by multispecies coalescent model (Yang and Rannala 2003). The species tree was assumed to originate from homogenous birth-death process, but its topology was fixed to the ASTRAL solution. Topologies of gene trees were fixed to those of MBC trees (without collapsing of poorly resolved branches) and nucleotide substitution model parameters to their mean values as in BF analysis. Only branch lengths, clock rates and species tree parameters were therefore sampled by MCMC under uninformative priors.

For time calibration we used two node constraints: the root of the tree was constrained to 6.1–8.5 million years (Ma) and the most recent common ancestor (MRCA) of *Colomys* and *Zelotomys* to 1.9–5.3 Ma before present (with uniform calibration densities). The minimum ages were constrained by the fossils from Lemudong-o' (Kenya, 6.1 Ma) reported as belonging to *Mastomys* (Manthi, 2007) and by *Zelotomys leakeyi* described by Jaeger (1976) from Olduvai Bed I (Tanzania, 1.9 Ma). Age estimates of the sites are due to Deino and Ambrose (2007) and Deino (2012), respectively. Manthi (2007) provided no determination clues for the fossils, but given their presumed similarity to extant *Mastomys* we assumed them to belong to crown Praomyini.

Paucity of African fossil sites from the upper Miocene precludes reasonable choice of the maximum ages. At this point we turned, therefore, to secondary calibration. A supplemental analysis was conducted (described in detail in SM1), dating the phylogeny of Praomyini and six related tribes under fossilized birth-death model (Heath et al., 2014) as implemented in BEAST 2 (Bouckaert et al., 2014). The analysis revealed *Colomys-Zelotomys* clade to be definitely of Plio-Pleistocene age and the earliest praomyine fossil from Chorora (Ethiopia, 8.5 Ma) as pre-dating the origin of extant Praomyini. This fossil was described by Geraads (2001) and reviewed by Denys and Winkler (2015) who report it to possess the same arrangement of t1 and t3 tubercles on the upper M1 as in other praomyines. Suwa et al. (2015) revised the age of the site and give the estimate of 8.5 Ma for it. Together with one tentative arvicanthine, the Chorora fossil is the only murine in the sample otherwise dominated by nesomyids and deomyines (Denys and Winkler, 2015). Similar community (presumably of comparable age) is known from Harasib (Namibia), and also contains just a single murine species (Mein et al. 2004). The Chorora fossil was therefore used as evidence the praomyine stem lineage already existed 8.5 Ma ago, but the other observations justify the assumption that it predates radiation that gave rise to the extant species.

2.7 Reconstruction of ancestral habitats

The ancestral habitats of Praomyini were inferred based on the habitats occupied by extant taxa.
We assigned species to one of the three habitat states: (i) forest (lowland, submontane and montane forest), (ii) open lowland vegetation (miombo woodland, savanna, grassland, agricultural fields, swampy marshes, rocky outcrops with sparse vegetation) and (iii) open montane habitat (alpine

moorlands, upland grasslands and scrub vegetation at elevation of ca. 3000-4500 m). This assignation was based on Wilson et al. (2017) and personal observations made by the authors. Because individual species can sometimes occupy multiple habitats, we used each species most prominent habitat.
Traits were mapped onto our time-calibrated phylogeny inferred in StarBEAST 2. We applied two methods, parsimony and maximum likelihood (ML), using Mesquite v. 3.61 (Maddison and Maddison, 2019). ML reconstructions were performed using the Markov k-state 1-parameter model of evolution (mk1) for discrete unordered characters (Lewis, 2001), which gives equal probability for changes between any two character states. Similarly, parsimony analysis used Fitch (unordered or non-additive) optimisation, which gives equal cost to all character-state changes.

3. Results

3.1 Nuclear phylogenomics

Both ML (in IQ-TREE) and Bayesian (in MrBayes) analyses of the concatenated dataset of 395 loci (610,965 bp long alignment) produced identical and well supported topology (Fig. 1A). The trees were almost fully resolved and most nodes had a maximum support, except the relationships between recently evolved species of the genus *Stenocephalemys*, where two pairs of sister species were supported with UFBoot = 79 in ML analysis. The species tree inferred from 395 gene trees in ASTRAL (see topology in Fig. 2) was almost completely resolved (with PP = 1.00), except two nodes (*Hylomyscus kerbispeterhansi/H. parvus* and *Praomys rostratus/P. morio*) with PPs = 0.99, and *Stenocephalemys sokolovi/S. ruppi* relationship with PP = 0.96. One intrageneric node (*Stenocephalemys ruppi/S. albocaudatus*) had a weak support (PP = 0.43). Relationships among species within the latter genus were the only differences in topologies between concatenated and species trees (compare Fig. 1A and Fig. 2). The nuclear phylogenomic analysis confirmed clear polyphyletic character of currently recognized genera *Mastomys*, *Myomyscus* and *Praomys*.

Fig. 1: Bayesian trees (MrBayes) reconstructed from: (A) concatenated alignment of 395 nuclear loci (in total 610,965 bp) and (B) complete mitogenomes (14,745 bp). The topologies produced by ML analyses (IQtree) were identical to those of Bayesian trees. Black circles on particular nodes indicate full support in both BI and ML analyses (i.e. PP=1.00/UFBoot=100). In remaining nodes the support is shown by numbers. The trees were rooted and outgroups removed. Red frames indicate the differences in topologies of nuclear and mitochondrial tree.

3.2 Complete mitogenomes

The total length of concatenated alignment of mitochondrial sequences was 14,745bp (after excluding CR and ND6 gene; see above). The topologies of both ML and Bayesian mitogenomic trees were congruent and the support from both analyses is shown in Fig. 1B. The topology of mtDNA tree is similar to nDNA tree with following exceptions (see red frames in Figs. 1A and 1B): (1) the relationships within *Stenocephalemys* genus differ according to used markers (incongruence caused by past mtDNA introgression, see more details in Bryja et al. 2018, Mizerovská et al. 2020); (2) the "New genus (Chingawa)" is placed as sister to *Mastomys pernanus/Praomys delectorum* clade in the mitogenomic tree, but as long basal branch in the nuclear trees; (3) the group of two *Myomyscus* taxa from eastern Africa is sister to the clade grouping *Mastomys* (excluding *M. pernanus*) and *Myomyscus angolensis* in mitochondrial phylogeny, but it is a sister to *Stenocephalemys* in nuclear trees.

3.3 Divergence dating

The time to the most recent common ancestor (TMRCA) of Praomyini was estimated to 7.11 Ma, when the clade of *Heimyscus*/*Hylomyscus* split from the rest of the tribe. The successive offshoots, still in Messinian period of Miocene, were East African clade *Praomys delectorum*/*Mastomys pernanus* (6.90 Ma) and the Ethiopian endemic "New genus (Chingawa)" (6.77 Ma). Intensive radiation leading to current genera (and major splits within them) occurred at Miocene/Pliocene border. The youngest intergeneric splits are between *Mastomys pernanus* and *Praomys delectorum* (3.81 Ma) and between *Colomys* and *Zelotomys* (2.78 Ma). These estimates overlap with oldest divergences within genera *Praomys* (5.30 Ma; even after excluding *P. delectorum* and *P. lukolelae*), *Hylomyscus* (3.39 Ma), and eastern African *Myomyscus* (3.58 Ma).

Fig. 2: Divergence dating of the species tree inferred using a multi-species coalescent approach in StarBEAST2, based on 57 selected loci and two fossil constraints (the root and the MRCA of *Colomys* and *Zelotomys*; see text and SM1 for more details). The topology was fixed to the ASTRAL solution of the species tree based on all 395 loci (the support of particular nodes is described in the text). The numbers in circles are TMRCAs of particular clades in million years ago (Ma). The names of newly delimited genera are shown in red on the right side of the figure. We also suggest to move *Myomyscus angolensis* in the genus *Mastomys* based on its phylogenetic position and evolutionary distances (see text for more details).

3.4 Reconstruction of ancestral habitat types

Results of ancestral habitat reconstruction by parsimony and ML analyses are congruent and reveal an ancestor of Praomyini living in a forest (Fig. 3). Multiple transitions between habitat types occurred in the evolution of the tribe. Based on likelihood scores there have likely been three independent shifts into open lowland savannah-like habitats from a forest ancestor in Miocene/Pliocene boundary (one in *M. pernanus*, one in the ancestor of the *P. daltoni* species complex, and one in the ancestor of the large clade grouping *Colomys* + *Zelotomys* + *M. verreauxi* + *P. lukolelae* + *Mastomys* + East African *Myomyscus + Stenocephalemys*). In this group, the analysis revealed a single colonization of open montane habitats in the ancestor of *Stenocephalemys*, two recolonizations of the forest habitat from an open lowland savannah-dwelling ancestor (*C. goslingi*, *P. lukolelae*) and two from open montane habitat ancestor (*S. albipes*, *S. ruppi*).

Fig. 3: Parsimony (branch coloration) and likelihood (pie charts) reconstruction of ancestral habitats across Praomyini mapped on the chronogram resulting from our divergence dating of the species tree in StarBEAST 2. White = forest, grey = open lowland savannah-like vegetation, black = open montane habitats. Pictures on the right side of the figure illustrate these habitats.

4. Discussion

4.1 First fully resolved phylogeny of the tribe Praomyini

Our approach combining samples from all major phylogenetic lineages of the tribe Praomyini and a phylogenomic approach allowed us for the first time to successfully reconstruct phylogenetic relationships within this tribe. We obtained a fully resolved tree with the nuclear dataset (395 loci; 610,965 bp long alignment). The mitogenomic tree (14,745bp) was also nearly fully resolved, and the topology of the mtDNA tree was similar to nDNA tree with three exceptions. The relationships inferred by anchored phylogenomics have higher credit here because mtDNA tree represents just a single-locus tree (due to the lack of recombination), which may differ from the species tree due to incomplete lineage sorting and, especially on shallow scales, also due to mitochondrial introgression. Past mtDNA introgression explains the incongruence observed between the two datasets in the genus *Stenocephalemys* (see more details in Bryja et al., 2018; Mizerovská et al., 2020). The two other incongruent nodes (placement of the “New genus (Chingawa)” and placement of the two *Myomyscus* taxa from eastern Africa) are not fully supported by the ML analysis of mitogenomic data (bootstrap support of 98 and 78, respectively).

Relationships among Praomyini genera recovered in previous molecular studies (Aghová et al., 2018; Lecompte et al., 2008; Steppan and Schenk, 2017) are characterized by low support values and/or small branch-lengths, indicative of either the occurrence of ‘soft polytomy’ (i.e. insufficient molecular data) or a ‘hard polytomy’ (i.e. a burst of diversification). Previous studies were based on a low number of molecular markers (between 2 and 6 nDNA gene fragments and between 1 and 9 mtDNA fragments), resulting in a total alignment length varying between 3,070 pb and 10,482 bp (with up to 42% of missing data), and these data were analysed through concatenation analyses. It is well known that this kind of data can provides insufficient synapomorphies for resolving species relationships, and that with a small number of loci it is difficult to deal with inconsistencies related to incomplete lineage sorting and ancestral polymorphisms (Martin-Hernanz et al., 2019; Nesi et al., 2021). Moreover, over long periods of time, historical signal in sequence data may be overwritten by multiple substitutions, contributing to "nonhistorical signal" (Ho and Jermiin, 2004). Our divergence time analysis shows that the diversification between major lineages (recognized usually as separate genera) within the tribe was relatively rapid, with most splits occurring in the Miocene-Pliocene boundary (roughly between 7 and 5 Ma). Unresolved polytomies within the Praomyini tribe in previous studies thus represented 'soft' polytomies that are now resolved into sequential bifurcations with genome-scale data and proper methods of phylogenetic analysis.

4.2 Taxonomic implications - delimitation of monophyletic genera

All our analyses clearly confirmed the presence of three (previously suggested) polyphyletic genera: *Praomys*, *Myomyscus* and *Mastomys*. Even if there are almost no general rules for the definition of taxonomic category of a genus in mammals (e.g. the level of genetic or morphological distinctiveness), it should be at least monophyletic. Below we review current knowledge of these three genera and propose taxonomic solutions (i.e. definition of monophyletic genera) in agreement with our phylogenomic analyses. Furthermore, we discovered a new highly divergent genetic lineage of Praomyini in southwestern Ethiopia, which is described below as a new genus.

4.2.1 Polyphyletic Praomys

In agreement with previous genetic works (Aghová et al., 2018; Kennis et al., 2011; Steppan and Schenk, 2017; Upham et al., 2019), we recognised three very divergent lineages within *Praomys* in current sense (e.g. Musser and Carleton, 2005; Wilson et al., 2017) that do not cluster into a monophyletic group. We therefore propose to recognise them as three distinct genera: *Praomys*, *Montemys* gen. nov., and *Congomys* gen. nov. This change in classification is supported by: (1) the polyphyletic nature of the genus *Praomys* in current sense, the delectorum complex (sensu Missoup et al., 2012) being the sister clade of *Mastomys* (= *Serengetimys* gen. nov.; see below) *pernanus*, and the lukolelae complex (sensu Missoup et al., 2012) being the sister clade of the *Myomyscus verreauxi-Zelotomys-Colomys* clade; (2) the level of genetic divergence observed between these lineages and sister lineages, (3) the presence of a unique combination of morphological traits allowing the integrative delimitation of the two new genera.

Montemys Nicolas & Bryja, gen. nov.

Zoobank: urn:lsid:zoobank.org:act:DE668ECF-7AEC-4693-B803-4F9E4850E5ED

Type species: *Epimys delectorum* Thomas, 1910. Ann. Mag. Nat. Hist., ser. 8, 6: 430.

The name *Epimys* Trouessart, 1881 is no longer available, as it was placed in synonymy with *Rattus* Fischer, 1803 (Musser and Carleton, 2005). Many murid rodent species were described as belonging to the genus *Epimys* and then elevated to generic rank such as *Aethomys* (type species: *Epimys hindei*), *Praomys* (*Epimys tullbergi*), *Hylomyscus* (*Epimys aeta*) or *Berylmys* (*Epimys manipulus*).

Etymology: The new generic name is a masculine noun composed of Latin "montem" (mountain) and greek "mys" (mouse). Oldfield Thomas described the type species of this genus in 1910 from S Malawi, Mulanje (=Mlanji) Plateau, 5500 ft., and all known populations of the genus are known to live in montane forests of Eastern Africa (Bryja et al., 2014; Carleton and Stanley, 2012).

Generic diagnosis: This genus is morphologically strongly circumscribed, unique in its combination of traits compared with *Praomys* and *Congomys* gen. nov. (Carleton and Stanley, 2012; Happold, 2013): palatal ridges is 2 + 5 = 7; plantar pads 6; anterior palatal foramina reach to front edge of first root of M^1; t3 of M^1 well developed; t3 in M^2 larger than in other species of *Praomys* and *Congomys* gen. nov.; weak supraorbital ridges not raised; chromosome number 2n = 48; four pairs of nipples (2 + 2 = 8).

Species included: *Montemys delectorum* (Thomas, 1910).

Note: Carleton & Stanley (2012) recognized three allopatric species in this group, slightly differing by the skull morphology. Later analysis by Bryja et al. (2014) showed negligible genetic structure among particular populations, only partly corresponding to the three morphological species proposed by Carleton & Stanley (2012). This view is followed in all recent lists of African rodents (Happold, 2013; Monadjem et al., 2015; Wilson et al., 2017) and the genus should be considered monotypic.

English name: Several names were previously proposed for this species: Delicate Soft-furred Mice, Delectable Soft-furred Mouse, Delicate *Praomys* and East African *Praomys* (Wilson et al., 2017). Given that it is no longer included in the genus *Praomys* and that the term “soft-furred” is usually used for *Praomys* species, we propose to retain the name Delicate Montane Mouse for *Montemys delectorum*.

Congomys Nicolas & Bryja, gen. nov.

Zoobank: urn:lsid:zoobank.org:act:91607156-03B2-47DC-B016-056C8755796D

Type species: *Praomys tullbergi lukolelae* Hatt, 1934. Am. Mus. Novit., 708: 13.

Etymology: The new generic name is a masculine noun composed of "Congo" (geographical name) and "*mys*" (= mouse). The name acknowledges the Congo Basin, where the two currently known species of this genus are endemic.

Generic diagnosis: This genus is unique in its combination of traits compared with *Montemys* gen. nov. and *Praomys* (Happold, 2013; Van der Straeten and Dudu, 1990): anterior palatal foramina short, not reaching to M^1; t3 on M^1 obsolete; weak supraorbital ridges not raised; the long hindfoot (range 28-32 mm), long ears and the form of the skull are more similar to *Malacomys* than to *Praomys*. However, *Malacomys* belongs to the genetically distinct tribe Malacomyini and they have only 5 plantar tubercles instead of 6 as usual in *Praomys, Congomys* gen. nov. and *Montemys* gen. nov.

Species included: *Congomys lukolelae* (Hatt, 1934); *Congomys verschureni* (Verheyen & Van der Straeten, 1977).

English names: Several names were previously proposed for *C. lukolelae* (Lukolela soft-furred mouse, Lukolela Praomys and Lukolela Swamp rat) and *C. verschureni* (Verschuren's Praomys or Verschuren Swamp rat) (Wilson et al., 2017). Given that these species are no longer included into the genus *Praomys* and that the term "soft-furred" is usually used for *Praomys* species, we propose using the names Lukolela Swamp rat for *C. lukolelae* and Verschuren´s Swamp rat for *C. verschureni.*

Praomys

After exclusion of *Montemys* gen. nov., and *Congomys* gen. nov., the genus *Praomys* is now monophyletic and contains three major clades corresponding to three well-known species groups highlighted by previous morphological and molecular studies (Happold, 2013; Kennis et al., 2011; Lecompte et al., 2005; Lecompte et al., 2002a; Lecompte et al., 2002b; Missoup et al., 2012; Monadjem et al., 2015; Musser and Carleton, 2005; Nicolas et al., 2005; Van der Straeten, 2008; Van der Straeten and Dieterlen, 1987; Van der Straeten and Dudu, 1990; Van der Straeten and Kerbis Peterhans, 1999): (i) the *jacksoni* species-group (including *P. jacksoni*, *P. mutoni*, *P. minor* and *P. degraffi*; represented in our study by *P. jacksoni* and *P. minor*), (ii) the *tullbergi* species-group (including *P. tullbergi*, *P. hartwigi*, *P. misonnei*, *P. morio*, *P. rostratus*, *P. obscurus, P. petteri* and *P. coetzeei;* represented in our study by *P. hartwigi, P. morio* and *P. rostratus*) and (iii) the *daltoni* species-group (including *P. daltoni*; represented in our study by three specimens belonging to three different clades). The evolutionary history and phylogenetic relationships in these species groups were recently investigated in molecular studies including more specimens and species but fewer genetic markers than in the present study: see Missoup et al. (2012) for the *tullbergi* species-group, Mizerovská et al. (2019) for the *jacksoni* species-group and Bryja et al. (2010) and Mikula et al. (2020) for the *daltoni* species-group. These studies highlighted that at least one new species should be described within the *tullbergi* species-group, and the same is true for the *jacksoni* species-group. The situation of the *daltoni* species-group is complex since two species differing in external appearance and lifestyle were described within it (*P. daltoni* and *P. derooi*), but recent integrative study of Mikula et al. (2020) strongly suggests that *P. derooi* is an ingroup of *P. daltoni* and could represent an ecotype rather than a distinct species. Here we used genomic data and estimated the age of TMRCA of the *daltoni* species-group to 0.8 Ma, which is significantly younger than previous estimates largely affected by mtDNA (e.g. 3 Ma in Bryja et al., 2010). Also, the split of the *derooi* ecotype is very recent (30 kya; Fig. 2), which agrees with a hypothesis on the role of commensalism on phenotypic changes. All these results support the view of *P. daltoni* as a single species, with a phylogeographic structure similar to those observed in other species in Sudanian savanna (e.g. *M. erythroleucus* or *A. niloticus* C2-C4), with recently evolved changes due to commensalism, mainly in the Dahomey Gap (see Mikula et al., 2020, and references therein).

These three species-groups can be distinguished on morphological ground (Happold, 2013):

- *tullbergi* species-group: palatal ridges 2 + 7 = 9; plantar pads 6; anterior palatal foramina reach to front edge of first root of M^1; t3 of M^1 obsolete or difficult to detect; weak supraorbital ridges not raised. Habitat is usually a primary rainforest, and most species are found in lowland forests (see Missoup et al. 2012).
- *jacksoni* species-group: palatal ridges 2 + 5 = 7; plantar pads 6; anterior palatal foramina reach to middle of first root of M^1; t3 of M^1 well developed; supraorbital ridges raised. They live in various forest habitats, and there are narrow specialists for both montane and lowland forests as well as habitats generalist (Mizerovská et al. 2019).
- *daltoni* species-group: palatal ridges 2 + 5 = 7; plantar pads 6; anterior palatal foramina reach the front edge of first root of M^1; t3 of M^1 well developed; supraorbital ridges not raised. This species is distributed in the mosaic of the Guinean forest and Sudanian savanna, and can be partially commensal (Mikula et al. 2020).

The TMRCA of the three species-groups is dated to 5.3 Ma, which is comparable to the time of divergence between some genera of Praomyini (e.g. *Hylomyscus*-*Heimyscus*: 5.2 Ma, *Ochromyscus* gen. nov.-*Stenocephalemys:* 4.9 Ma) and even older than those observed between *Serengetimys* gen. nov. and *Montemys* gen. nov. (3.8 Ma), or *Zelotomys* and *Colomys* (2.8 Ma). Such comparison suggests that three complexes of *Praomys* could be considered as three distinct genera. However, given that they are monophyletic in our phylogenetic tree and that this genus can be discriminated from other Praomyini genera based on a combination of morphological traits, we prefer to keep the three species groups in a single genus.

Generic diagnosis: this genus can be distinguished from *Montemys* gen. nov. and *Congomys* gen. nov. by the following combination of traits: anterior palatal foramina reach to front edge or the middle of the first root of M^1; t3 in M^2 smaller than in *Montemys* gen. nov.

4.2.2 Polyphyletic Myomyscus

The genus *Myomyscus,* as reconstituted by Musser and Carleton (2005), contains four species: *yemeni*, *brockmani*, *angolensis*, and *verreauxii*. In our phylogenomic analyses, we included four species bearing this name. Unfortunately, we failed to sequence *M. yemeni*, clearly sister to *M. brockmani* (Lecompte et al. (2008), Steppan & Schenk (2017), our unpubl. mtDNA data), but we included two genetically very distinct species from eastern Africa (*M. brockmani* and one new undescribed species). The four used taxa of *Myomyscus* clustered into three different clades that split already at Miocene/Pliocene boundary and should be considered as three different genera. (1) The type species of the genus *Myomyscus*, *M. verreauxii* from the Cape region in South Africa, is the sister lineage of *Colomys* and *Zelotomys*; (2) *M. angolensis* is sequenced here at many loci for the first time (see also Krásová et al., under review) and it forms a sister lineage to all *Mastomys* species (except *M. pernanus*, which is transferred to *Serengetimys* gen. nov., see below); (3) two East African taxa form a monophyletic clade, sister to *Stenocephalemys* at nuclear markers (diverged from them at 4.9 Ma), and to *Mastomys* at mitogenomes. Based on the results of phylogenomic analyses, we propose (1) to retain the genus name *Myomyscus* only for the type species *M. verreauxii* from South Africa; (2) to transfer *angolensis* to *Mastomys* (see also Krásová et al., under review); and (3) to describe a new genus grouping the two East African taxa (*brockmani* and one undescribed species) and *yemeni* from the Arabian Peninsula.

Myomyscus

Generic diagnosis: This genus is readily diagnosable by its restricted distribution: it is endemic to the Fynbos biome of South Africa. Small brown mouse similar in general appearance to *Mastomys* spp., from which it can be distinguished by its longer tail (ca 130-140% of head and body length [HB]) and five pairs of nipples.

Species included: *M. verreauxii* (Smith, 1834)

English name: The names Verreaux's Meadow Mouse, Verreaux's Myomyscus, Verreaux's White-footed Rat and White-footed Mouse are commonly used for this species (Wilson et al. 2017). We propose to retain the name Verreaux's Meadow Mouse for this species.

Note: It is possible that another species of this genus occurs in Angola. As pointed out by Crawford-Cabral (1989), the species *angolensis* described from Capangombe by Bocage (1890) as *Mus angolensis* might be different from the species considered here as *Mastomys angolensis* (see below). The type material of Bocage´s (1890) description was lost during the fire in the Lisbon Museum in 1978, but Crawford-Cabral (1989) claimed that this taxon is distinct from a more widespread and abundant species that was given the same name by Thomas in 1904 (Bocage´s species is characterized by a tail much longer than head and body, white feet, soft and thick fur, all characters typical for the genus *Myomyscus* as considered here). However, Musser & Carleton (2005) did not accept this view ("In our view he [Crawford-Cabral 1989] simply renamed Bocage's angolensis") and consequently only one taxon with this name (i.e. *Myomyscus angolensis*) is reported from Angola in most recent compendia (Monadjem et al., 2015; Wilson et al., 2017).

Mastomys angolensis (Bocage, 1890), comb. nov.

Note: In a report devoted to the identity of Bocage's *Mus angolensis*, Crawford-Cabral (1989) noted that the type series was destroyed by fire in the Lisbon Museum in 1978. According to the original description the specimens represented a species with a tail much longer than head and body, white feet, soft and thick fur, and five pairs of teats (3 + 2), all characters very typical for *Myomyscus*, as defined here (see above). Crawford-Cabral considered Angolan specimens collected after 1890 outside of the Capangombe region and identified as *angolensis* to be another species. He proposed *Praomys angolae* for this rat and considered it a *Mastomys* (this was not accepted by Musser & Carleton 2005, and the taxonomic situation of Angolan taxa remained unresolved; see above). Here we propose to include the widespread Angolan species (living also in southern DRC; see Krásová et al., under review) into *Mastomys*. Despite the fact that the type material of *angolensis* cannot be compared with recent material, we prefer to keep the name *angolensis* (and not *angolae*), in agreement with Musser & Carleton (2005). The new combination is also supported by morphological data: according to Monadjem et al. (2015) this species is very similar to *Mastomys shortridgei*, with which it shares many cranio-dental features and lower number of nipples compared to other *Mastomys*, but the tail is distinctly shorter in the latter species (ca. 87% of HB in *M. shortridgei* versus ca. 100% of HB in *M. angolensis)* (Monadjem et al., 2015). The only other species of *Mastomys* co-occuring with *M. angolensis* is *M. natalensis* (Krásová et al., under review), which differs in number of nipples (usually 12 pairs in *M. natalensis*). Here, we confirmed these findings, as the individuals of *M. angolensis* at locality Namba (used for anchored phylogenomic analysis) had 5 pairs of nipples and the tail was roughly equal in length to head+body (ranging from 91 to 117%; N=17).

English name: Following English names were proposed for this species: Angolan Meadow Mouse, Angolan Multimammate Mouse and Angolan Myomyscus (Wilson et al., 2017). We propose to retain the name Angolan Multimammate Mouse, since this species now belongs to the genus *Mastomys*. Most *Mastomys* species have 8 to 12 pairs of mammae, much more than any other rodent, which explain the frequently used English name (Multimammate mice) of the genus (Monadjem et al., 2015). However there are two exceptions: *M. angolensis* and *M. shortridgei* which have only 5 pairs of teats (or maximum 8, respectively; see discussion about *M. shortridgei* in Eiseb et al., 2021).

Ochromyscus Nicolas, Mikula & Bryja, gen. nov.

Zoobank: urn:lsid:zoobank.org:act:A4B2BA6B-1C1F-49DF-BB58-FE73ADE0AD44

Type species: *Mus brockmani* Thomas, 1906. Ann. Mag. Nat. Hist., ser. 7, 18: 298.

Etymology: The new generic name is a masculine noun composed of "ωχρος" [ochros] (which means “pale” in Greek) and "myscus" (derived from *myskos* = small mouse, diminutive of *mys* = mouse). The name acknowledges the typical color of these rodents, which has no bright hue.

Generic diagnosis: This genus is characterized by its long tail (135-160% of HB), pale yellow-brown dorsal pelage, pure white ventral pelage, and four or five pairs of nipples.

Species included: *Ochromyscus brockmani* (Thomas, 1906); *Ochromyscus yemeni* (Sanborn & Hoogstraal, 1953).

English name: We propose the name “white-bellied rocky mouse”, because the purely white belly is typical of all species within this genus and they are most abundant in rocky outcrops.

Note: *Ochromyscus* sp. (see Figs. 1-2) represents very likely a new species belonging to this genus and will be described in a separate integrative taxonomic revision of this genus. Preliminary genetic data show that the two *Ochromyscus* species have parapatric distribution in Eastern Africa. One taxon was found in a part of Afar Triangle and in eastern Ethiopia and we call it *brockmani* here, because the type locality of this species lies in relatively nearby Somaliland. Based on mtDNA phylogeny, *O. yemeni* from Yemen and southwestern Saudi Arabia is its sister species (not shown). The second African species has relatively wide distribution from southern Ethiopia, through Kenya and Uganda to northern Tanzania (not shown) and a new name should be defined for this taxon after performing profound taxonomic revision and analysis of the type material.

4.2.3 Polyphyletic Mastomys

The current genus *Mastomys* (sensu Musser and Carleton, 2005; Wilson et al., 2017) contains a monophyletic group of multimammate mice and a taxon *pernanus* that has been considered as a member of this genus on the basis of external and cranio-dental morphology (Kershaw, 1921; Van der Straeten, 1999). However, our phylogenomic analyses, in agreement with previous molecular works (Lecompte et al., 2008; Steppan and Schenk, 2017; Upham et al., 2019), show that *pernanus* do not cluster with other *Mastomys* species, but is the sister clade of *Montemys* gen. nov. Given the high level of genetic differentiation between *pernanus* and *Montemys* gen. nov., and their morphological and ecological distinctiveness we propose a new generic name for *pernanus*.

Serengetimys Nicolas & Bryja, gen. nov.

Zoobank: urn:lsid:zoobank.org:act:D659BBCB-A36E-4CD6-8DA3-93523D2C8304

Type species: *Rattus pernanus* Kershaw, 1921. Ann. Mag. Nat. Hist., ser. 9, 8: 568.

Etymology: The new generic name is a masculine noun composed of "Serengenti" (geographical name) and "*mys*" (= mouse). P. S. Kershaw described the type species of this genus in 1921 from Amala (= upper course of Mara) River in southern Kenya. All known records (except an aberrant specimen from

Eastern Tanzania and an unconfirmed record from Rwanda) of this monotypic genus are from the so-called Serengeti ecosystem with prevailing grasslands in northern Tanzania and southern Kenya (Van der Straeten, 1999).

Generic diagnosis: The skull bears the general characteristics of the *Mastomys* genus: the anterior palatal foramina reach from just between the molars up to the beginning of the middle root of M^1 and the palatine bone from the junction of M1 and M2 to the middle of M2; the t3 is present and somewhat smaller than t1 on M^1; the interorbital region has the typical *Mastomys* structure. The mesopterygoid fossa is very narrow on the posterior margin of the palatine becoming relatively wide towards the end; as a result, this fossa has a very peculiar triangular aspect. Smaller size (head and body mean = 78 mm; range 73-88 mm) than other *Mastomys* species and *Montemys* gen. nov (Monadjem et al., 2015). Tail length shorter than head and body length (85% of head and body), i.e. similar to most other *Mastomys* species and significantly shorter than *Montemys* gen. nov., which has a tail significantly longer than the head and body. Prominent spot of white hairs behind each ear (Fig. 4). Five pairs of nipples (3 + 2 = 10). This monotypic genus mainly inhabits *Acacia-Comniphora* wooded grasslands and edaphic grasslands (based on Lillesø et al., 2011 vegetation map) (Fig. S2 in SM2).

Species included: *Serengetimys pernanus* (Kershaw, 1921).

English name: Dwarf Serengeti mouse. Happold (2013) proposed the English name "Dwarf Multimammate Mouse", because it was thought that the species belong to the genus *Mastomys* ("multimammate mice"). However, our first observation of a lactating female from southern Kenya revealed that they have only five pairs of nipples.

Fig. 4: (A) Ventral, dorsal and lateral view of *Serengetimys pernanus* from northern Tanzania (specimen TZ27869, adult male, locality Ikona). (B) All known localities of this species (based on Van der Straeten 1999, Stanley et al. 2007, and our unpublished data). Note that the specimen from the southernmost locality (Dakawa) has an aberrant morphology (Van der Straeten 1999), but another genotyped individual from the same locality differentiated from remaining sympatric *Mastomys* (Lecompte et al. 2005) and clustered with our new samples from northern Tanzania and southern Kenya (not shown). An inset shows the map of Africa and the red frame indicates its zoomed part.

Mastomys

Generic diagnosis: Medium-sized rodents (mean HB ca. 100-136 mm) with a tail sparsely haired with small concentric scales and typically shorter or equal to the head and body length (85-103% of HB). The dorsal pelage is soft-furred with sparse guard hairs and variable colour, typically dark greyish to grey-brown. The ventral colour is grey. Females of most species are immediately recognisable by having 8 to 12 pairs of mammae, with two exceptions, *M. angolensis* and *M. shortridgei*, which have only 5 or 8 pairs of teats, respectively (see discussion above and Eiseb et al. 2020). Based on body measurements *Mastomys* is similar to *Zelotomys* and *Stenocephalemys.* However *Zelotomys* can be distinguished by its entirely white tail and stephanodont molars (Monadjem et al., 2015; Wilson et al., 2017), and *Stenocephalemys* by its narrower interorbital constriction and macrodont molars (Monadjem et al., 2015).

Species included: *M. angolensis* (Bocage, 1890), *M. awashensis* Lavrenchenko, Likhnova & Baskevich (in Lavrenchenko et al., 1998a), *M. coucha* (Smith, 1834), *M. erythroleucus* (Temminck, 1853), *M. huberti* (Wroughton, 1909), *M. kollmannspergeri* (Petter, 1957), *M. natalensis* (Smith, 1834), *M. shortridgei* (St. Leger, 1933)

4.2.4 Discovery of a new genus in south-western Ethiopia

Chingawaemys Lavrenchenko, Mikula & Bryja, gen. nov.

Zoobank: urn:lsid:zoobank.org:act:74ACB5B5-422C-4E61-B7F1-640693E937C6

Type species: *Chingawaemys rarus*, the new species described below.

Etymology: The new generic name is a masculine noun composed of "Chingawa" (geographical name) and the Greek "mys", referring to mouse, or rat in this case. The name acknowledges the Chingawa Forest, where the single known species of this genus is endemic.

Generic diagnosis: Medium-sized rodent similar in general appearance to sympatric *Stenocephalemys albipes* and *S. ruppi* (Fig. 5), and similar in general cranial shape to *Ochromyscus* gen. nov., from which it can be distinguished by considerably narrower zygomatic plate with a straight anterior margin.

Fig. 5. Dorsal (above) and ventral (below) views of *Chingawaemys* gen. nov. and *Stenocephalemys* skins. (A) *Chingawaemys rarus* sp. nov. ZMMU S-181580 (holotype), (B) *Stenocephalemys albipes* ZMMU S-181579, (C) *Stenocephalemys ruppi* ZMMU S-181704. All specimens collected in the Chingawa Forest in April-May 2007.

Chingawaemys rarus Lavrenchenko, Mikula & Bryja, sp. nov.

Zoobank: urn:lsid:zoobank.org:act:8CECFAF7-6FA3-46CA-8893-306E596B6457

Holotype: ZMMU S-181580; subadult female; skull and dry skin; collected by L.A. Lavrenchenko and A.A. Warshavsky (05 May 2007); collecting number 1667.

Type locality: Chingawa Forest, 25 km north of Tepi (07°25′ N 35°24′ E, 2340 m a.s.l.), southwestern Ethiopia.

Etymology: The species name is derived from the Latin word “rarus” – rare (see Ecology).

Diagnosis: Because *rarus* is the only known species of *Chingawaemys*, generic and specific diagnoses are the same.

Description: *Chingawaemys rarus* sp. nov. is a medium-sized representative of the tribe Praomyini. The dorsal pelage is brownish-greyish. The bristles are grey in basal two thirds and black in distal one third. The guard hairs are grey at the base with pale rufous subterminal bands and blackish-grey tips. Ventral pelage is whitish-grey without a yellowish shade, the individual hairs grey at the base and tipped with white. The transition between dorsal and ventral coloration is conspicuous. Dorsal surface of the forefeet is greyish with sparse and short pale fur; digits are covered by longer whitish hairs; claws are whitish. Dorsal surface of the relatively short hindfeet (21 mm) is greyish with sparse and short grey hairs with white tips; digits with ungual tufts of white hairs; claws are greyish at the base and white in distal one third. The ears are blackish-grey (including inner surface). The tail is appreciably longer than the length of head and body (133% of HB) and does not appear distinctly bicoloured. Relatively short hairs are black on the upper tail surface and greyish on the lower surface. The tail tip covered by longer hairs. The skull is similar in size and shape to *Ochromyscus* gen. nov., but with considerably larger tympanic bullae, and considerably narrower zygomatic plate with a straight anterior margin not protruding forward (rostrally). Relatively short incisive foramens end in front of the first cusp row of the first upper molars. The toothrows are relatively short and narrow (Fig. 6).

Fig. 6. Dorsal (above), ventral (middle) and lateral (below) views of *Chingawaemys* gen. nov. and *Stenocephalemys* skulls. (A) *Chingawaemys rarus* sp. nov. ZMMU S-181580 (holotype), (B) *Stenocephalemys albipes* ZMMU S-181579, (C) *Stenocephalemys ruppi* ZMMU S-181704. All specimens collected in the Chingawa Forest in April-May 2007.

Comparisons: *Chingawaemys rarus* sp. nov. differs from sympatric and syntopic *Stenocephalemys albipes* and *S. ruppi* in smaller body size (head and body length of the holotype is 102 mm, while it ranges 109-148 mm in *S. albipes* and 124-156 mm in *S. ruppi*), shorter hindfeet (length of hind foot without claw is 21.0 mm in the holotype, while 23.4-30.0 in *S. albipes* and 26.0-30.0 mm in *S. ruppi*; see Mizerovská et al. 2020 for more details), longer hairs on the end of tail, greyish (not white) colouration of dorsal surface of forefeet and hindfeet (Fig. 5), and considerably narrower zygomatic plate with a straight anterior margin (Fig. 6).

Distribution: The new species has been found only in the Chingawa Forest (07°25′ N 35°24′ E, 2340 m a.s.l.) (Fig. 7). We failed to trap *Chingawaemys rarus* sp. nov. in other humid Afromontane forest blocks of SW Ethiopia: the Sheko Forest (07°04'N, 35°30'E, 1930 m a.s.l.), the Dushi Area of the Godare Forest (07°21'N, 35°13'E, 1200 m a.s.l.), the Meti Area of the Godare Forest (07°17'N, 35°16'E, 1370 m a.s.l.)

and the Beletta Forest (07º34'N, 36º31'E, 1900 m a.s.l.) which are, however, situated at a lower altitude. Therefore, the currently known distribution range of the new species and genus is extremely limited.

Fig. 7. Panoramic view of the type locality of *Chingawaemys rarus* sp. nov., the Chingawa Forest (southwestern Ethiopia).

Ecology: The single known specimen of *Chingawaemys rarus* sp. nov. was captured in a very moist Afromontane forest with notable abundance of tree ferns (Fig. 7). The following small mammal species were also collected at the same trapping site: *Lophuromys chrysopus* Osgood 1936, *L. brunneus* Thomas 1906, *Otomys fortior* Thomas 1906, *Stenocephalemys albipes* (Ruppell 1842), *S. ruppi* (Van der Straeten, Dieterlen 1983), new undescribed species of the genus *Mus* (Krásová et al., in prep.), and a shrew *Crocidura yaldeni* Lavrenchenko, Voyta, Hutterer, 2016. It seems likely that *Chingawaemys rarus* sp. nov. is a very rare species, since no additional specimens were collected despite intensive sampling efforts at the type locality in 2007 and 2017. Those collections yielded numerous specimens of two externally similar rodent species, *Stenocephalemys albipes* and *S. ruppi*. For example, during two-nights trapping in November 2017 we captured 42 *S. albipes* and 22 *S. ruppi* (all of them confirmed by genotyping). Very restricted range of *Chingawaemys rarus* sp. nov. and its rarity (at least in collections) can be associated with yet unknown habitat requirements and mode of life. However, no morphological adaptations to some specific life style (e.g. semi-aquatic or arboreal adaptations) were observed, even if shorter hindfeet and long tail suggest that they can be partly arboreal. No data on reproduction and diet are available.

English name: We propose the vernacular name “Chingawa Forest Rat” for *Chingawaemys rarus* sp. nov. The name reflects that this rare rodent appears to be endemic to the unique Chingawa Forest.

4.3 Evolutionary scenario of the Praomyini radiation in Late Miocene/Early Pliocene

The origin of the tribe Praomyini is associated with the cessation of the Late Miocene faunal exchange between Asia and Africa. The analysis of rodent fossils in Africa suggests that the modern rodent fauna, with taxa assignable to extant tribes or even genera, appears in the interval 7-5 Ma (reviewed in Lecompte et al., 2008; see also Table S2 in SM1). In the same period, the dominance of fossil gerbils increased in the Middle East, indicating very arid conditions (Tchernov, 1992), presenting a barrier for dispersal of murine ancestors between Asia and Africa. Palaeontological studies therefore imply that two most divergent and speciose tribes of recent African rodents, Arvicanthini and Praomyini, started their African radiation in the same geological period in terminal Miocene. This fits very well recent molecular studies. Using genomic-scale data and multiple fossils, the first diversification in African Arvicanthini was dated to 7.6 Ma (Mikula et al., 2021), while the first split in Praomyini is estimated at 7.1 Ma (Fig. 2).

Reconstruction of ancestral habitats revealed that ancestors of Praomyini lived in tropical forests (Fig. 3) and similar habitat preference was expected for the first African Arvicanthini (Mikula et al., 2021). Forests were predominating ecosystems in equatorial Africa during humid and warm climate in most of Miocene, albeit not always continuously distributed from coast to coast (Couvreur et al., 2021 and references therein). Representatives of long basal branches on the Praomyini tree still live in rain forests, but the successful radiation of the tribe was likely facilitated by their ability to adapt to changing environment. Late Miocene Cooling (LMC) was a period of steeper decrease in temperature between ca. 7 and 5.4 Ma, that was very likely driven by a decrease in atmospheric $p\mathrm{CO}_2$ (Herbert et al., 2016). Even if cooling is expected to be less marked in tropics, LMC is thought to have triggered a progressive aridification, supported by palaeovegetation records (reviewed by Couvreur et al., 2021). In general, there was a strong trend towards more open habitats and the rise of grasslands. These climatic changes had two major consequences for diversification processes: (i) fragmentation of more or less continuous Miocene forests supported allopatric speciation; (ii) spreading of open habitats provided new ecological niches and allowed evolutionary shifts in habitat preferences.

Fragmentation of Late Miocene pan-African forests into western, central and eastern forests (Lovett, 1993; Plana, 2004) is being increasingly supported by the dated phylogenetic studies in animal and plant taxa. For example, the splits between Congolese and eastern African species of the plant genera *Uvariodendron* and *Monodora* are dated to ca. 8.4 Ma (Couvreur et al., 2008). Similarly, the contraction and fragmentation of the forest in Late Miocene/Early Pliocene played a key role in the diversification of some groups of African chameleons (Tolley et al., 2013) and murid rodents from the Arvicanthini tribe (Bryja et al., 2017; Mikula et al., 2021). In Praomyini, we can see very similar patterns. It is generally difficult to reconstruct the area of origin of widely distributed forest clades of *Praomys* and *Hylomyscus*/*Heimyscus*. However, the oldest splits in Miocene/Pliocene boundary have obvious geographical component (i.e. fragmentation of forests), because they separated taxa with the highest diversity in Upper and Lower Guinean forests (the *tullbergi*+*daltoni* complexes of *Praomys* and *Heimyscus*, respectively) from those with highest evolutionary diversity, i.e. the presence of most divergent lineages, in Albertine Rift montane forests (i.e. the *jacksoni* complex of *Praomys* and *Hylomyscus*, respectively) (Mizerovská et al., 2020; Nicolas et al., 2020a). This pattern is even more obvious in two other clades of forest Praomyini, because they have restricted distribution in montane forests of eastern Africa, which are geographically marginal to the more continuous central African forests. *Montemys* gen. nov. diverged from remaining Praomyini at 6.9 Ma, almost at the same time as *Chingawaemys* gen. nov. (6.8 Ma). The first one is currently known from isolated East African montane forests from southern Kenya to central Mozambique (Sabuni et al., 2018), while the second is known only from the holotype collected in a very humid montane forest in southwestern Ethiopia (this study). The biogeographical importance of East African Mountains (e.g. Eastern Arc Mts., Southern Rift Mts. etc.) as museums of forest evolutionary diversity is well recognized (e.g. Burgess et al., 2007). On the other hand, forests in southwestern Ethiopia are not currently officially protected, but they should be considered as a very important refugium of unique palaeoendemic biota, separated from other tropical forests in Africa for almost 7 million years.

Another important change in Late Miocene in Africa (besides LMC) was the formation of the Rift Valley resulting in greater rainfall seasonality, and the spread of grassy vegetation (Bobe, 2006). This trend was reversed in the Early Pliocene, the warmest period over the last 5 Myr, associated with forests re-expansion (Feakins and deMenocal, 2010). The aridification events are observable again in Plio-Pleistocene, after 3.5 Ma, when the decrease of temperatures led to significant expansion of grass-dominated ecosystems. In the evolutionary history of Praomyini, these environmental changes are documented by independent expansion of multiple lineages into newly appearing open habitats. The first aridification period (in Late Miocene) is concordant with the origin of the clade grouping *Mastomys*, *Ochromyscus* gen. nov. and *Stenocephalemys*, all of them living predominantly in non-forested habitats. *Mastomys* are probably the most successful rodents in various types of African savannahs, *Ochromyscus* gen. nov. live in rocky shrubland habitats in Somali-Masai region (Monadjem et al., 2015), and the original habitats of *Stenocephalemys* are mid-elevational marshlands in Ethiopian Highlands, from where they expanded to both Afroalpine ecosystems and montane forests (Bryja et al., 2018). Later Plio-Pleistocene aridification period (intensifying at 4-3 Ma) can be similarly associated with ecological shifts leading to the emergence of the grassland genus *Serengetimys* gen. nov. (morphologically very distinct from genetically closely related forest-dwelling *Montemys* gen. nov.), but also to colonization of western Sudanian savanna by the *daltoni* complex of *Praomys* (Mikula et al., 2020).

The ancestral habitat preference was not well resolved in the clade grouping *Colomys-Zelotomys-Myomyscus-Congomys* gen. nov. (Fig. 3). Either there were two shifts from forests to open habitats or vice versa. However, when looking at habitat preferences of extant taxa, it seems that this clade can be characterized by the affinity to wetland habitats. This is best expressed in semi-aquatic forest taxa *Colomys* (+ their sister clade *Nilopegamys,* not included in the present study; Giarla et al., 2020) and swamp-dwelling *Congomys* gen. nov. (see above). Two remaining genera live in non-forested habitats, mostly in southern and eastern Africa, but they have very specific micro-habitat requirements. *Myomyscus verreauxi* occurs in damp grasslands and vleis, *Zelotomys hildegardeae* is often found on the edge of swamps and in tall wet grasslands in moist grassy savanna (e.g. Monadjem et al. 2015). The third species, *Z. wosnami* (not included in the present study), is found in dry savanna on Kalahari sands, but it occurs along river beds and around pans frequently associated with Acacias and lime-clay silty soils (Cassola, 2016). It is therefore possible that the shift in habitat preferences allowed the colonization of newly appearing wetland habitats in both forests and savannas. This ecological shift has again a parallel in Arvicanthini rodents, where the wetland-specialized genus *Dasymys* split from other genera very soon in the radiation of the tribe (at the border of Miocene/Pliocene, ca. 6 Ma; Mikula et al., 2021), which is comparable with the split of the clade of "wetland" Praomyini, i.e. *Colomys-Zelotomys-Myomyscus*-Congomys gen. nov., from the clade *Mastomys-Stenocephalemys-Ochromyscus* gen. nov.

5. Conclusion

In this study we used genomic-scale data to reconstruct the phylogeny of a very successful group of African murine rodents. The results of divergence dating and ancestral habitat reconstructions are in good agreement with paleoenvironmental research and suggest that rodents can be used as very suitable models for testing the role of environmental changes on the evolutionary processes in sub-Saharan Africa since Late Miocene. Large amount of genetic data ("anchored phylogenomics") allowed to resolve even notoriously difficult nodes in rodent phylogeny and to delimit monophyletic genera, including the discovery of a new genus in moist forest of southwestern Ethiopia. This study shows that even important groups of African animals (i.e. mammals, some of them responsible for transmission of zoonotic pathogens) are still insufficiently known and further research can bring numerous surprises, even in their alpha-taxonomy.

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Data availability statement

Complete mitochondrial genomes are available in in GenBank, accession numbers are provided in Table 1. Alignments of nuclear loci obtained by anchored phylogenomic approach (as partitioned nexus file) and the Bayesian gene trees used as input for ASTRAL analysis (in newick format) will be available in the public repository of the Czech Academy of Sciences (http://hdl.handle.net/XXXXX) and in Mendeley Data repository (DOI:XXXX).

Figure legends

Fig. 1. Bayesian trees (MrBayes) reconstructed from: (A) concatenated alignment of 395 nuclear loci (in total 610,965 bp) and (B) complete mitogenomes (14,745 bp). The topologies produced by ML analyses (IQtree) were identical to those of Bayesian trees. Black circles on particular nodes indicate full support in both BI and ML analyses (i.e. PP=1.00/UFBoot=100). In remaining nodes the support is shown by numbers. The trees were rooted and outgroups removed. Red frames indicate the differences in topologies of nuclear and mitochondrial tree.

Fig. 2. Divergence dating of the species tree inferred using a multi-species coalescent approach in StarBEAST2, based on 57 selected loci and two fossil constraints (the root and the MRCA of *Colomys* and *Zelotomys*; see text and SM1 for more details). The topology was fixed to the ASTRAL solution of the species tree based on all 395 loci (the support of particular nodes is described in the text). The numbers in circles are TMRCAs of particular clades in million years ago (Ma). The names of newly delimited genera are shown in red on the right side of the figure. We also suggest to move *Myomyscus angolensis* in the genus *Mastomys* based on its phylogenetic position and evolutionary distances (see text for more details).

Fig. 3. Parsimony (branch coloration) and likelihood (pie charts) reconstruction of ancestral habitats across Praomyini mapped on the chronogram resulting from our divergence dating of the species tree in StarBEAST 2. White = forest, grey = open lowland savannah-like vegetation, black = open montane habitats. Pictures on the right side of the figure illustrate these habitats.

Fig. 4. (A) Ventral, dorsal and lateral view of *Serengetimys pernanus* from northern Tanzania (specimen TZ27869, adult male, locality Ikona). (B) All known localities of this species (based on Van der Straeten 1999, Stanley et al. 2007, and our unpublished data). Note that the specimen from the southernmost locality (Dakawa) has an aberrant morphology (Van der Straeten 1999), but another genotyped individual from the same locality differentiated from remaining sympatric *Mastomys* (Lecompte et al. 2005) and clustered with our new samples from northern Tanzania and southern Kenya (not shown). An inset shows the map of Africa and the red frame indicates its zoomed part.

Fig. 5. Dorsal (above) and ventral (below) views of *Chingawaemys* gen. nov. and *Stenocephalemys* skins. (A) *Chingawaemys rarus* sp. nov. ZMMU S-181580 (holotype), (B) *Stenocephalemys albipes* ZMMU S-181579, (C) *Stenocephalemys ruppi* ZMMU S-181704. All specimens collected in the Chingawa Forest in April-May 2007.

Fig. 6. Dorsal (above), ventral (middle) and lateral (below) views of *Chingawaemys* gen. nov. and *Stenocephalemys* skulls. (A) *Chingawaemys rarus* sp. nov. ZMMU S-181580 (holotype), (B) *Stenocephalemys albipes* ZMMU S-181579, (C) *Stenocephalemys ruppi* ZMMU S-181704. All specimens collected in the Chingawa Forest in April-May 2007.

Fig. 7. Panoramic view of the type locality of *Chingawaemys rarus* sp. nov., the Chingawa Forest (southwestern Ethiopia).

Table 1. List of material of Praomyini (+ four outgroups) used in phylogenomic analyses, their current/proposed generic classification, and the GenBank accession numbers of mitogenomes.

ID	Species (according Wilson et al. 2017 and recent publications)	Descriptor(s)	Museum number	Locality	% of mitogenome	Genbank accession number	Proposed generic name
Tribe Praomyini							
LEG2329	*Colomys lumumbai*	Kerbis Peterhans, Giarla & Demos, 2020	RUCA_LEG2329	Tshopo, DRC	99.9%	MZ131545	*Colomys*
R16900	*Heimyscus fumosus*	(Brosset, Dubost & Heim de Balsac, 1965)	MNHN-ZM-2016-2632	Mbomo, Republic of Congo	100%	MN964123	*Heimyscus*
MSP144	*Hylomyscus aeta*	(Thomas, 1911)	MNHN_2017-1619	Mt Cameroon, Cameroon	100%	MZ131546	*Hylomyscus*
R17191	*Hylomyscus alleni*	(Waterhouse, 1838)	MNHN-ZM-2007-503	Illego, Republic of Congo	100%	MZ131547	*Hylomyscus*
KE215	*Hylomyscus endorobae*	(Heller, 1910)	USB_KE215	Mt Kenya National Park, Kenya	100%	MZ131548	*Hylomyscus*
KE429	*Hylomyscus kerbispeterhansi*	Demos, Agwanda & Hickerson, 2014	USB_KE429	Mt Elgon National Park, Kenya	100%	MZ131549	*Hylomyscus*
GA0262	*Hylomyscus parvus*	Brosset, Dubost & Heim de Balsac, 1965	MNHN-ZM-2016-1257	Kili, Gabon	100%	MZ131550	*Hylomyscus*
ANG0202	*Myomyscus angolensis*	(Bocage, 1890)	USB_ANG0202	Namba, Angola	100%	MZ131556	*Mastomys*
RVF1547	*Mastomys coucha*	(A. Smith, 1834)	no voucher	Ndengeza, Limpopo, South Africa	100%	MZ131551	*Mastomys*
ETH0374	*Mastomys erythroleucus*	(Temminck, 1853)	USB_ETH0374	Yabello Wildlife Sanctuary, Ethiopia	100%	MZ131552	*Mastomys*
ETH0541	*Mastomys kollmannspergeri*	(Petter, 1957)	USB_ETH0541	Mai-Temen, Ethiopia	100%	MZ131553	*Mastomys*
TZ27600	*Mastomys natalensis*	(A. Smith, 1834)	USB_TZ27600	Monduli, Tanzania	98.9%	MZ131554	*Mastomys*
TZ27869	*Mastomys pernanus*	(Kershaw, 1921)	USB_TZ27869	Ikona WMA, Tanzania	100%	MZ131555	*Serengetimys* gen. nov.
ETH0898	*Myomyscus* sp.	-	USB_ETH0898	Yabello town, Ethiopia	100%	MZ131558	*Ochromyscus* gen. nov.
ETH1019	*Myomyscus brockmani*	(Thomas, 1906)	USB_ETH1019	Sof Omar caves, Ethiopia	100%	MZ131557	*Ochromyscus* gen. nov.
MNHN-VV1999-102	*Myomyscus verreauxii*		no voucher	Paarl Mountains, RSA	100%	MZ131559	*Myomyscus*
LAV1667	New genus (Chingawa)	Lavrenchenko, Mikula & Bryja, this study	ZMMU_S-181580	Chingawa forest, Ethiopia	100%	MZ131560	*Chingawaemys*gen. nov.
MNHN-VV1999-391	*Praomys daltoni* (clade C1)	(Thomas, 1892)	no voucher	Emnal'here, Mali	100%	MZ131562	*Praomys*

BE0974	*Praomys daltoni* (clade A)	(Thomas, 1892)	MNHN-ZM-2016-348	Gotcha, Benin	99.8%	MZ131561	*Praomys*
VN0251	*Praomys daltoni* (ecotype *derooi*)	(Thomas, 1892)	MNHN-ZM-2010-994	Koto, Benin	96.2%	MZ131563	*Praomys*
CAM13	*Praomys hartwigi*	Eisentraut, 1968	no voucher	Mt Oku, Cameroon	100%	MZ131564	*Praomys*
KE291	*Praomys jacksoni*	(de Winton, 1897)	USB_KE291	Mt Kenya NP, Kenya	100%	MZ131565	*Praomys*
RS0765	*Praomys minor*	Hatt, 1934	USB_RS0765	Nchila Wildlife Reserve, Zambia	100%	MZ131567	*Praomys*
MSP5	*Praomys morio*	(Trouessart, 1881)	MNHN-ZM-2011-27	Mt Cameroon, Cameroon	100%	MZ131568	*Praomys*
VN1252	*Praomys rostratus*	(G. S. Miller, 1900)	MNHN-ZM-2013-391	Zogota, Guinea	100%	MZ131569	*Praomys*
KE542	*Praomys delectorum*	(Thomas, 1910)	USB_KE542	Taita Hills, Kenya	100%	MN807618	*Montemys* gen. nov.
LEG1788	*Praomys lukolelae*	Hatt, 1934	RUCA LEG1788	Yoko, Democratic Republic of Congo	97%	MZ131566	*Congomys* gen. nov.
ETH1333	*Stenocephalemys albipes*	(Rüppell, 1842)	USB_ETH1333	Borena Saynt National Park, Ethiopia	100%	MT408172	*Stenocephalemys*
ETH0157	*Stenocephalemys albocaudatus*	(Frick, 1914)	USB_ETH0157	Bale Mts, Ethiopia	100%	MN807617	*Stenocephalemys*
ETH0182	*Stenocephalemys griseicauda*	Petter, 1972	USB_ETH0182	Bale Mts, Ethiopia	100%	MT408176	*Stenocephalemys*
ETH1533	*Stenocephalemys ruppi*	(Van der Straeten & Dieterlen, 1983)	USB_ETH1533	Chingawa forest, Ethiopia	98.8%	MT408167	*Stenocephalemys*
LAV1947	*Stenocephalemys sokolovi*	Lavrenchenko & Bryja, 2020	ZMMU_S-189428	Debre Sina, Ethiopia	100%	MT408179	*Stenocephalemys*
LAV1413	*Stenocephalemys zimai*	Lavrenchenko & Bryja, 2020	ZMMU_S-178783	Semien Mts., Ethiopia	100%	MT408184	*Stenocephalemys*
TA233	*Zelotomys hildegardeae*	(Thomas, 1902)	USB_TA233	Kelebe, Biharamulo FR, Tanzania	100%	MZ131570	*Zelotomys*
Outgroup: Tribe Arvicanthini							
TA066	*Aethomys chrysophilus*	(de Winton, 1897)	USB_TA066	Singida, Tanzania	94.1%	MN807612	
ETH1068	*Arvicanthis somalicus*	Thomas, 1903	USB_ETH1068	Geralle National Park, Ethiopia	100%	MN807588	
Outgroup: Tribe Otomyini							
ETH1342	*Otomys typus*	(Heuglin, 1877)	USB_ETH1342	Borena Saynt Natioanl Park, Ethiopia	100%	MN807603	
Outgroup: Tribe Millardini							
T1054	*Millardia meltada*	(Grey, 1837)	MVZ-182982 (Berkeley)	Avallanchi, India	100%	MN807616	

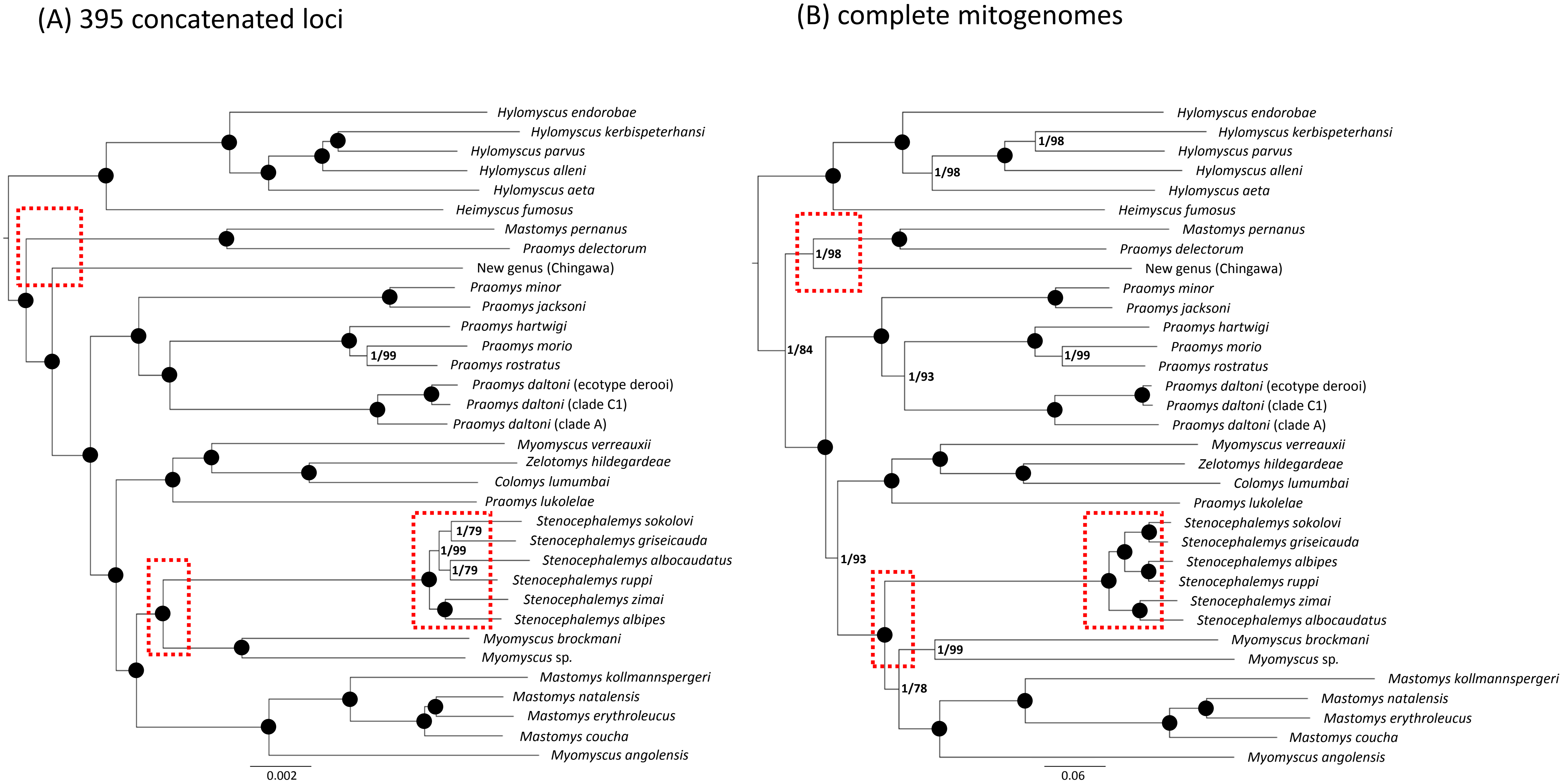
(A) 395 concatenated loci
Hylomyscus endorobae
Hylomyscus kerbispeterhansi
Hylomyscus parvus
Hylomyscus alleni
Hylomyscus aeta
Heimyscus fumosus
Mastomys pernanus
Praomys delectorum
New genus (Chingawa)
Praomys minor
Praomys jacksoni
Praomys hartwigi
Praomys morio
1/99
Praomys rostratus
Praomys daltoni (ecotype derooi)
Praomys daltoni (clade C1)
Praomys daltoni (clade A)
Myomyscus verreauxii
Zelotomys hildegardeae
Colomys lumumbai
Praomys lukolelae
Stenocephalemys sokolovi
1/79
Stenocephalemys griseicauda
1/99
Stenocephalemys albocaudatus
1/79
Stenocephalemys ruppi
Stenocephalemys zimai
Stenocephalemys albipes
Myomyscus brockmani
Myomyscus sp.
Mastomys kollmannspergeri
Mastomys natalensis
Mastomys erythroleucus
Mastomys coucha
Myomyscus angolensis
0.002
(B) complete mitogenomes
Hylomyscus endorobae
Hylomyscus kerbispeterhansi
1/98
Hylomyscus parvus
1/98
Hylomyscus alleni
Hylomyscus aeta
Heimyscus fumosus
Mastomys pernanus
1/98
Praomys delectorum
New genus (Chingawa)
Praomys minor
Praomys jacksoni
1/84
Praomys hartwigi
Praomys morio
1/99
Praomys rostratus
1/93
Praomys daltoni (ecotype derooi)
Praomys daltoni (clade C1)
Praomys daltoni (clade A)
Myomyscus verreauxii
Zelotomys hildegardeae
Colomys lumumbai
Praomys lukolelae
Stenocephalemys sokolovi
Stenocephalemys griseicauda
1/93
Stenocephalemys albipes
Stenocephalemys ruppi
Stenocephalemys zimai
Stenocephalemys albocaudatus
Myomyscus brockmani
1/99
Myomyscus sp.
1/78
Mastomys kollmannspergeri
Mastomys natalensis
Mastomys erythroleucus
Mastomys coucha
Myomyscus angolensis
0.06

Figure 1

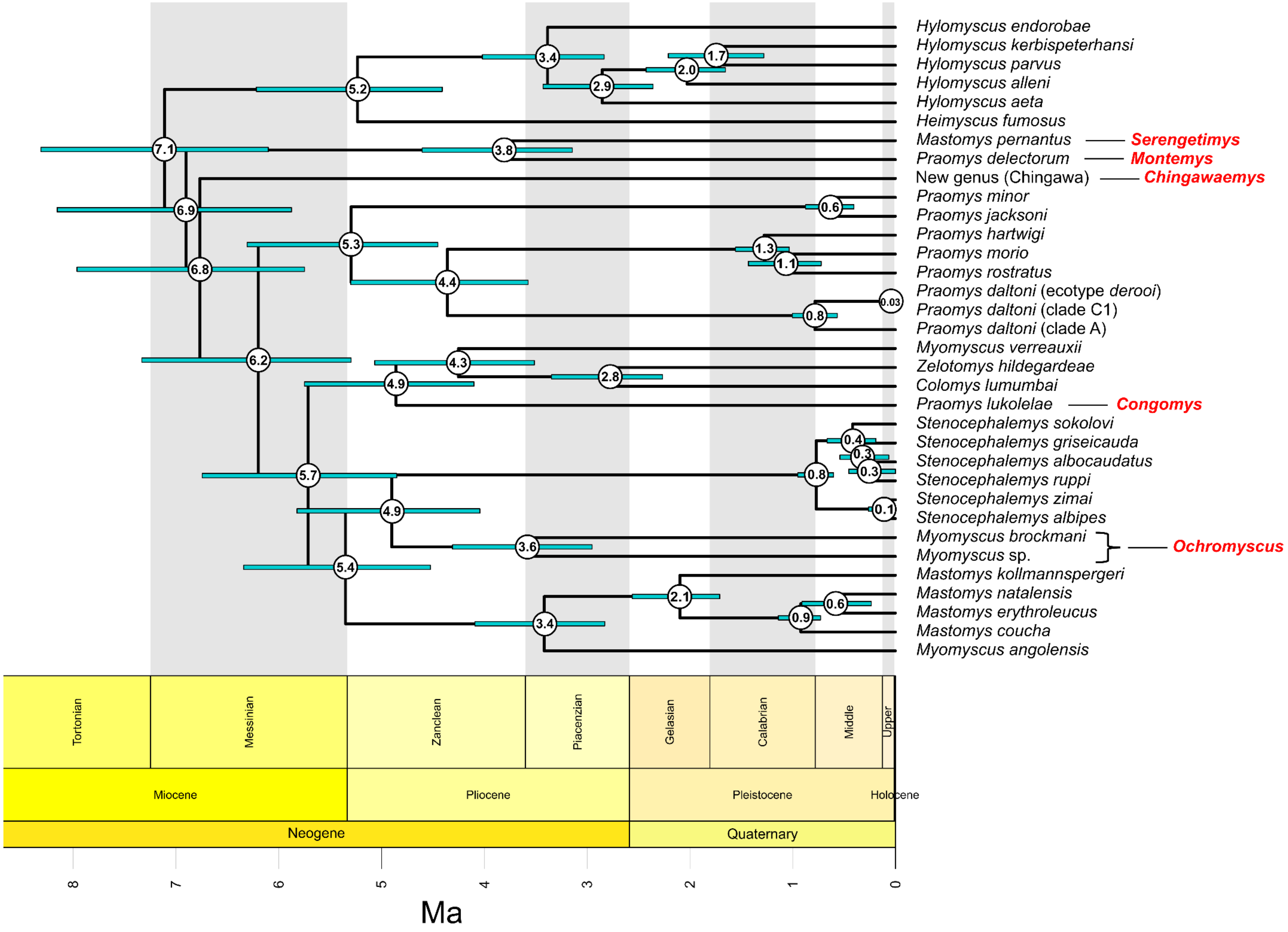
Hylomyscus endorobae
Hylomyscus kerbispeterhansi
Hylomyscus parvus
Hylomyscus alleni
Hylomyscus aeta
Heimyscus fumosus
Mastomys pernantus
Serengetimys
Praomys delectorum
Montemys
New genus (Chingawa)
Chingawaemys
Praomys minor
Praomys jacksoni
Praomys hartwigi
Praomys morio
Praomys rostratus
Praomys daltoni (ecotype derooi)
Praomys daltoni (clade C1)
Praomys daltoni (clade A)
Myomyscus verreauxii
Zelotomys hildegardeae
Colomys lumumbai
Praomys lukolelae
Congomys
Stenocephalemys sokolovi
Stenocephalemys griseicauda
Stenocephalemys albocaudatus
Stenocephalemys ruppi
Stenocephalemys zimai
Stenocephalemys albipes
Myomyscus brockmani
Myomyscus sp.
Ochromyscus
Mastomys kollmannspergeri
Mastomys natalensis
Mastomys erythroleucus
Mastomys coucha
Myomyscus angolensis
7.1
6.9
6.8
6.2
5.7
5.4
5.2
5.3
4.9
4.9
4.4
4.3
3.4
3.8
3.6
3.4
2.9
2.8
2.1
2.0
1.7
1.3
1.1
0.9
0.8
0.8
0.8
0.6
0.6
0.4
0.3
0.3
0.1
0.03
Tortonian
Messinian
Zanclean
Piacenzian
Gelasian
Calabrian
Middle
Upper
Miocene
Pliocene
Pleistocene
Holocene
Neogene
Quaternary
8
7
6
5
4
3
2
1
0
Ma

Figure 2

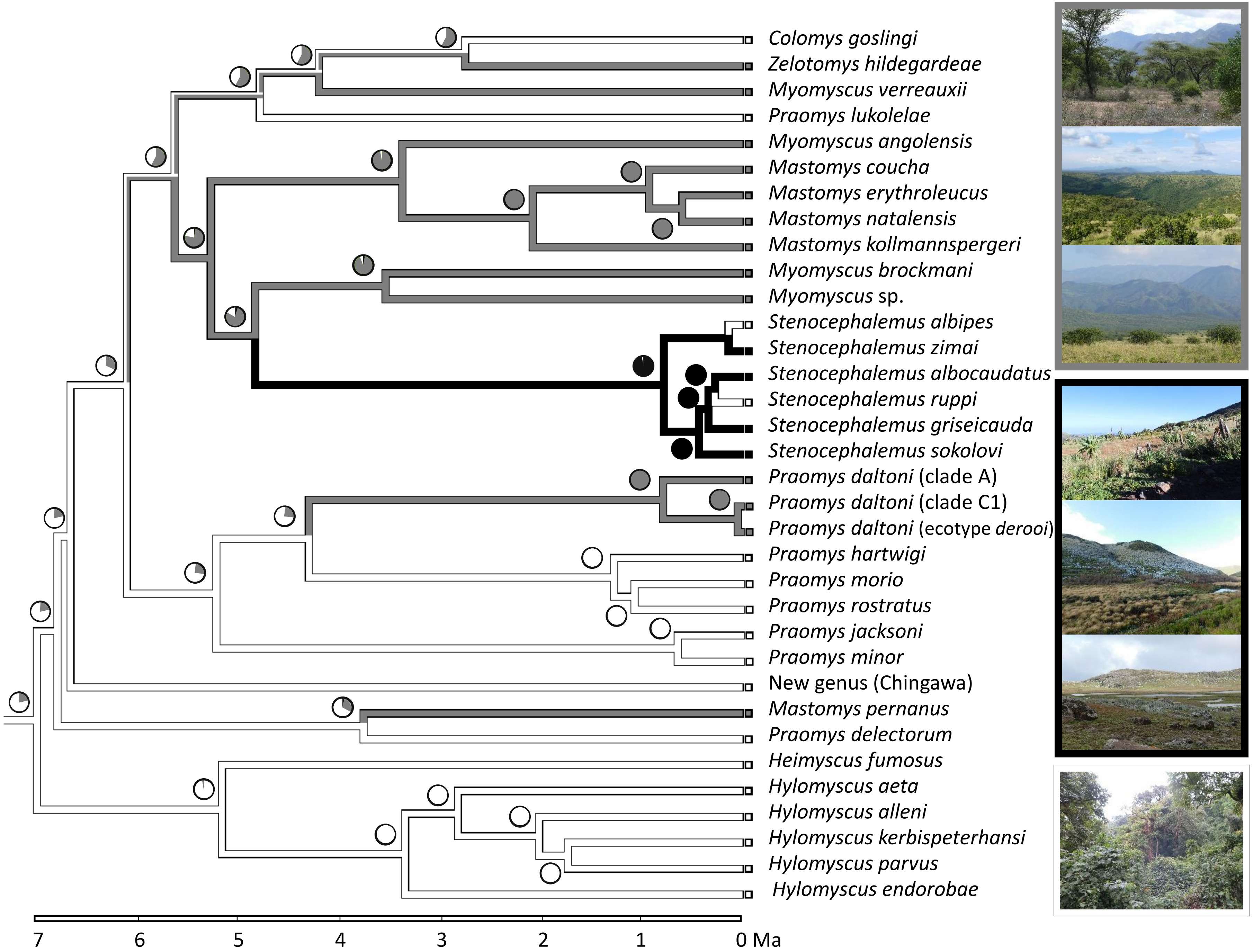
Colomys goslingi
Zelotomys hildegardeae
Myomyscus verreauxii
Praomys lukolelae
Myomyscus angolensis
Mastomys coucha
Mastomys erythroleucus
Mastomys natalensis
Mastomys kollmannspergeri
Myomyscus brockmani
Myomyscus sp.
Stenocephalemus albipes
Stenocephalemus zimai
Stenocephalemus albocaudatus
Stenocephalemus ruppi
Stenocephalemus griseicauda
Stenocephalemus sokolovi
Praomys daltoni (clade A)
Praomys daltoni (clade C1)
Praomys daltoni (ecotype derooi)
Praomys hartwigi
Praomys morio
Praomys rostratus
Praomys jacksoni
Praomys minor
New genus (Chingawa)
Mastomys pernanus
Praomys delectorum
Heimyscus fumosus
Hylomyscus aeta
Hylomyscus alleni
Hylomyscus kerbispeterhansi
Hylomyscus parvus
Hylomyscus endorobae
7
6
5
4
3
2
1
0 Ma

Figure 3

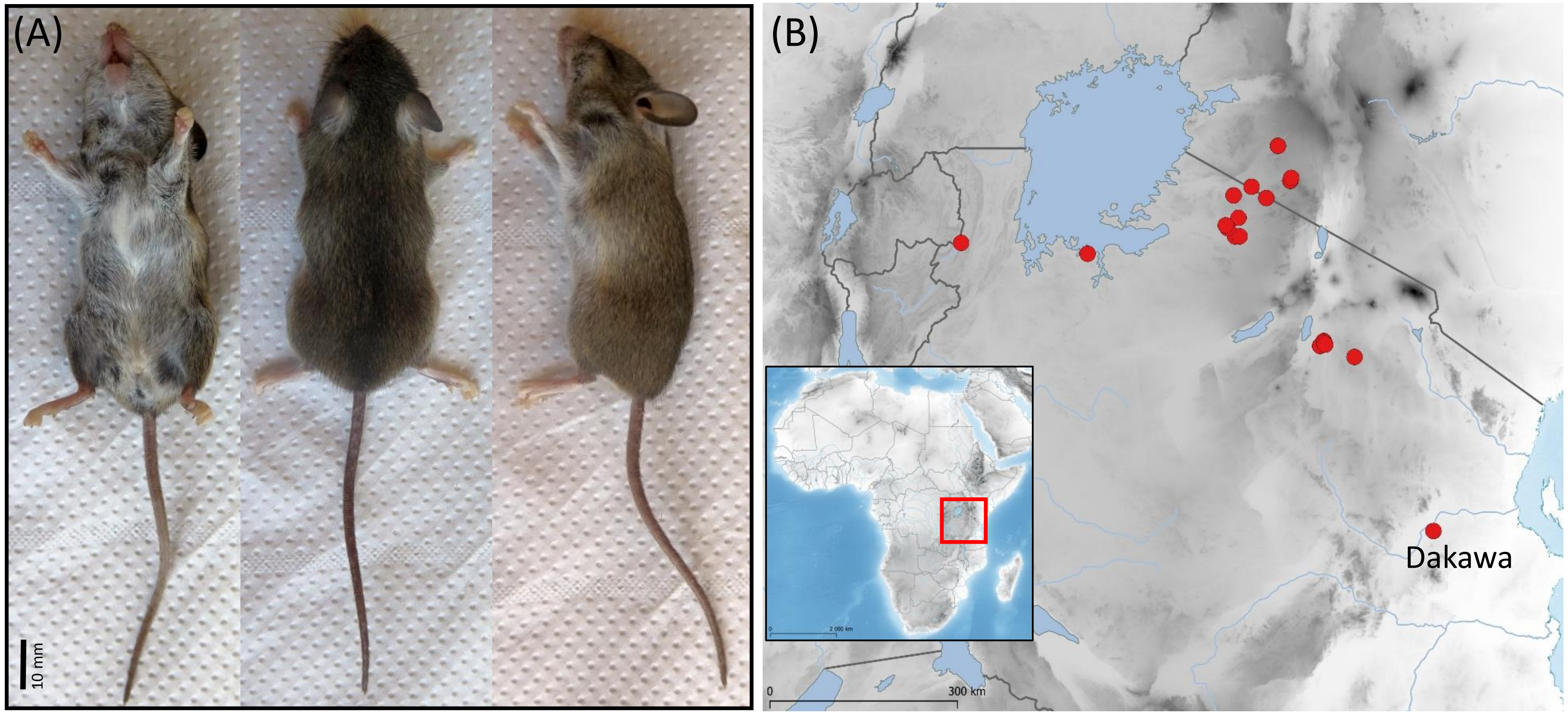

Figure 4

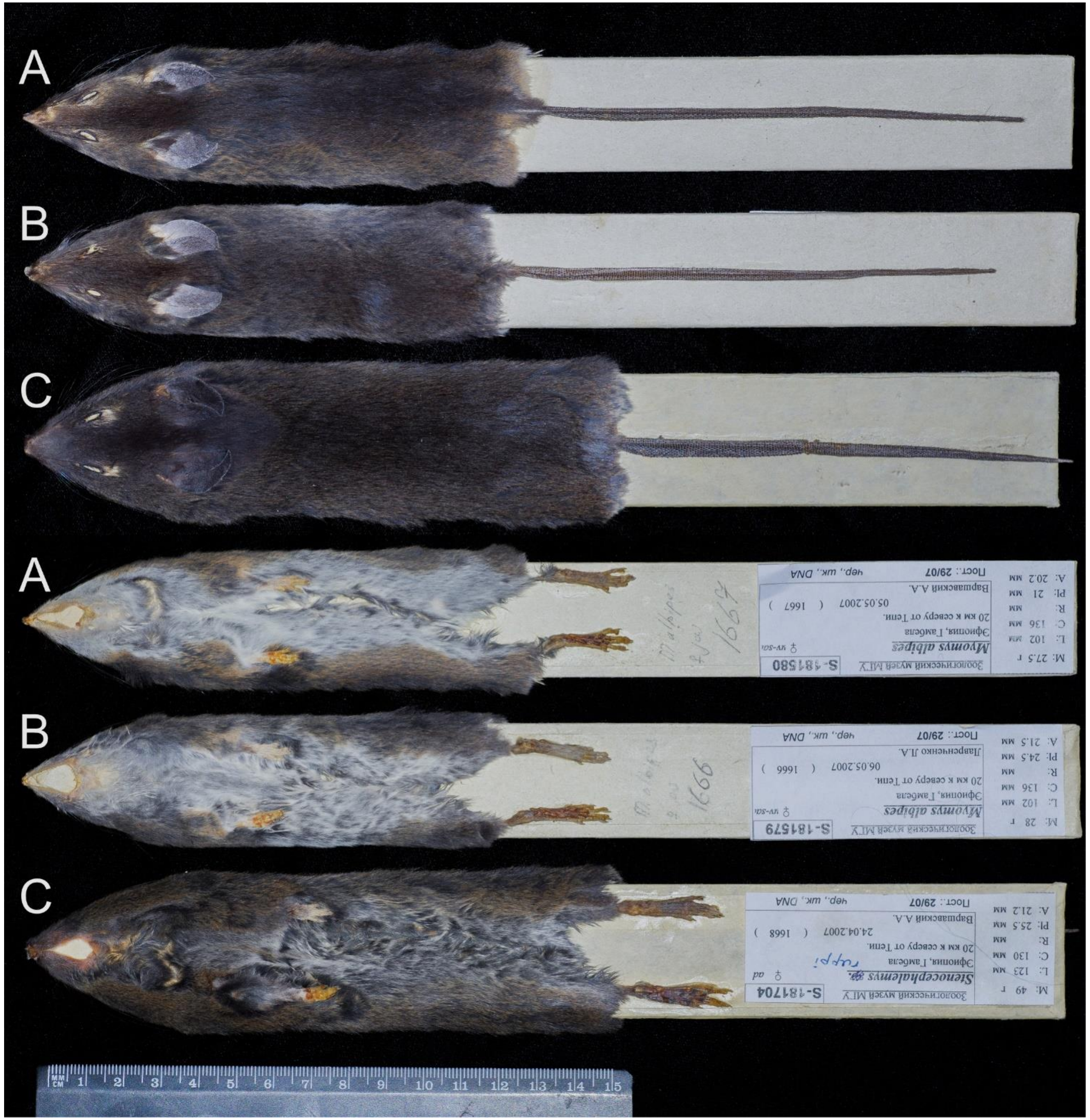
A
B
C
A
B
C
Зоологический музей МГУ
S-181580
Myomys albipes
♀ uv-sa
M: 27.5 г
L: 102 мм
C: 136 мм
R: мм
Pl: 21 мм
A: 20.2 мм
Эфиопия, Гамбела
20 км к северу от Тепи.
05.05.2007 (1667)
Варшавский А.А.
Пост.: 29/07
чер., шк., DNA
1667
Зоологический музей МГУ
S-181579
Myomys albipes
♀ uv-sa
M: 28 г
L: 102 мм
C: 136 мм
R: мм
Pl: 24.5 мм
A: 21.5 мм
Эфиопия, Гамбела
20 км к северу от Тепи.
06.05.2007 (1666)
Лавренченко Л.А.
Пост.: 29/07
чер., шк., DNA
1666
Зоологический музей МГУ
S-181704
Stenocephalemys ~~sp.~~
ruppi
♀ ad
M: 49 г
L: 123 мм
C: 130 мм
R: мм
Pl: 25.5 мм
A: 21.2 мм
Эфиопия, Гамбела
20 км к северу от Тепи.
24.04.2007 (1668)
Варшавский А.А.
Пост.: 29/07
чер., шк., DNA
MM
CM
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15

Figure 5

Figure 6

Figure 7

Supplementary Material