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

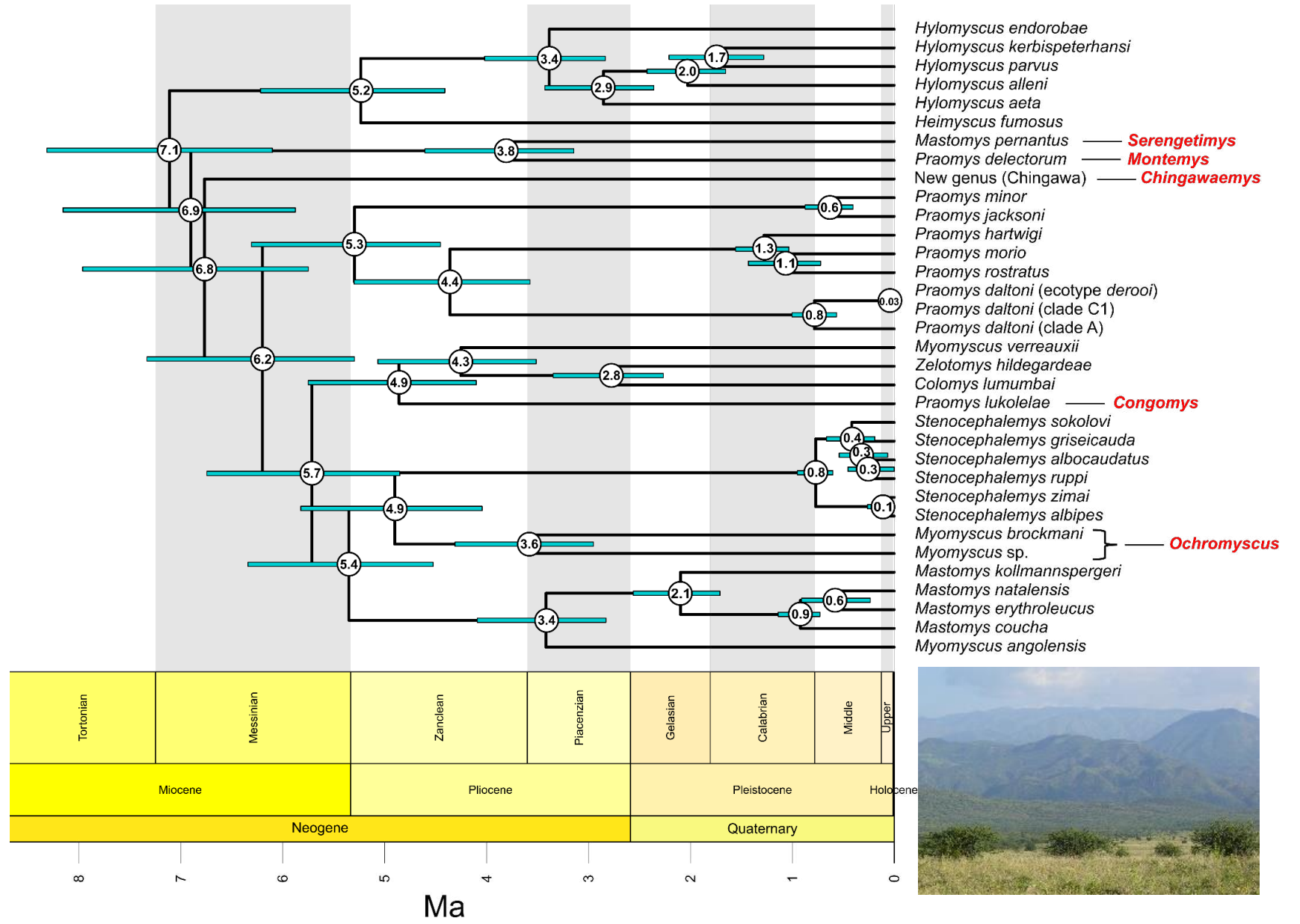
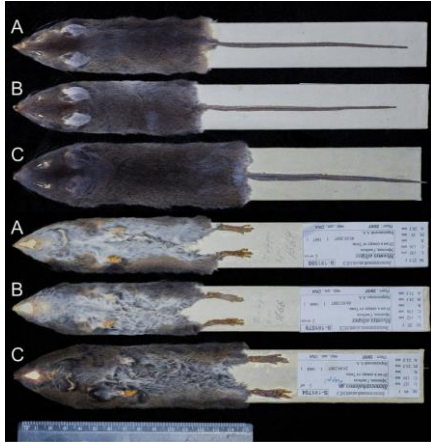
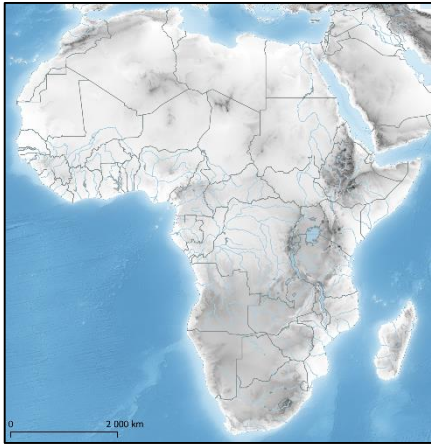
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1 **Phylogenomics of African radiation of Praomyini (Muridae: Murinae) rodents: first fully resolved**
2 **phylogeny, evolutionary history and delimitation of extant genera**

3
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31

32 **Running head:** Phylogenomics of African Praomyini rodents

33

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

40

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43

44 **ABSTRACT**

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

65

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

68 1. Introduction

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

77

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

102 Messinian age of Miocene and most extant genera appeared almost simultaneously (Aghová et al.,
103 2018).

104

105 The tribe Praomyini is a very important group of African rodents for several reasons. They are hosts of
106 many potentially pathogenic microorganisms, like mycobacteria (Durnez et al., 2010) and viruses
107 (Borremans et al., 2011; Briese et al., 2009; Coulibaly-N'Golo et al., 2011; Durnez et al., 2008; Fichet-
108 Calvet et al., 2007; Gryseels et al., 2017; Gryseels et al., 2015; Klempa et al., 2006; Konstantinov et al.,
109 2006; Lecompte et al., 2006; Meheretu et al., 2012; Olayemi et al., 2016; Olayemi and Fichet-Calvet,
110 2020; Tesikova et al., 2017), and some of them are important for human health, e.g. the Lassa virus
111 which causes several thousand people dead in West Africa annually. They were also shown to be
112 potential mammalian reservoirs of bubonic plague (Isaacson et al., 1983; Makundi et al., 2008).
113 Moreover, this tribe comprises numerous agricultural pests; the most important among them,
114 widespread *Mastomys natalensis*, can cause extensive damage to crop and stored grain. It was
115 estimated that it can cause yield losses up to 48% during populations outbreaks and even in non-
116 outbreak years average annual crops loss is in the range of 5-15% (Leirs, 2002; Mwanjabe et al., 2002).
117 They have also a key ecological role in ecosystems, representing the most abundant members of
118 rodent communities (Happold, 2013; Nicolas and Colyn, 2003; Nicolas et al., 2020b), serving as seed
119 dispersers and relevant part of diet in carnivores. While some species are among the most common,
120 widespread and abundant African rodents (e.g. *M. natalensis* or *Praomys jacksoni*), others are rare and
121 classified as near threatened (*Praomys mutoni*), vulnerable (*Praomys hartwigi*, *P. degraaffi*),
122 endangered (*Hylomyscus baeri*, *Praomys morio*, *P. obscurus*) or even critically endangered (*Hylomyscus*
123 *grandis*, *Nilopegamys plumbeus*) on the IUCN Red list (Wilson et al., 2017). Members of the Praomyini
124 tribe are becoming important models in biogeographic and evolutionary studies, and were recently
125 used as model taxa to assess the relative role of topographical structure and climatic changes as drivers
126 of diversification of African biota (Brouat et al., 2009; Bryja et al., 2010; Bryja et al., 2018; Bryja et al.,
127 2014; Colangelo et al., 2013; Kennis et al., 2011; Missoup et al., 2012; Mizerovská et al., 2019; Mouline
128 et al., 2008; Nicolas et al., 2008; Nicolas et al., 2020a; Nicolas et al., 2012a; Nicolas et al., 2011).

129

130 If this tribe is well supported by both molecular and morphological data, the intergeneric relationships,
131 and the species contents of several genera are still a matter of debate. Musser and Carleton (2005)
132 placed the members of Praomyini in two divisions: the *Stenocephalemys* division (including *Heimyscus*,
133 *Hylomyscus*, *Mastomys*, *Myomyscus*, *Praomys* and *Stenocephalemys*) and the *Colomys* division
134 (comprising *Colomys* and *Zelotomys*), based primarily upon morphological characters. However, more
135 recent molecular multi-locus data (Aghová et al., 2018; Lecompte et al., 2008; Stepan and Schenk,
136 2017; Upham et al., 2019) suggest a different arrangement of taxa within this group. Specifically, three

137 current genera appear as paraphyletic: 1) *Myomyscus* (*M. verreauxii* does not cluster with other
138 *Myomyscus* species, but rather with *Colomys* and *Zelotomys*), 2) *Praomys* (*P. delectorum* can be the
139 sister clade of *Mastomys pernanus*, and this clade can be the sister clade of *Hylomyscus*+*Heimyscus*; *P.*
140 *lukoleale* and *P. vershureni* form the *lukoleale* species group, which can be the sister clade of
141 *Myomyscus verreauxii*+*Colomys*+*Zelotomys*), 3) *Mastomys* (*M. pernanus* can be the sister clade of *P.*
142 *delectorum*). Furthermore, *Heimyscus* is in all recent molecular analyses, including the last revision of
143 the genus (Nicolas et al., 2020a), the sister clade of *Hylomyscus*, except the study of Upham et al.
144 (2019), where it is part of *Hylomyscus*. However, in all these molecular phylogenetic studies the
145 resolution of deeper nodes of the trees was poor, suggesting fast radiation and/or insufficient amount
146 of used molecular markers. Moreover, the species sampling was sparse, except the work of Upham et
147 al. (2019) that included most species present in the GenBank database. This approach, on the other
148 hand, might introduce an error caused by misidentifications (see Krásová et al., 2021 for an
149 outstanding example).

150

151 A well-resolved phylogeny of the Praomyini tribe is crucial to understand the diversity, evolution and
152 biogeographical patterns of sub-Saharan African mammals. Here we used the samples from all but one
153 (*Nilopegamys*) major phylogenetic lineages of the tribe Praomyini defined by a combination of
154 previous studies and employed the so-called anchored phylogenomic approach that uses high
155 throughput sequencing of targeted enriched genomic libraries (Lemmon et al., 2012). This method
156 enables rapid construction of phylogenomic datasets that incorporate hundreds to thousands of
157 nuclear loci, and can resolve difficult nodes at varied taxonomical and time scales, including taxa that
158 diverged since the Miocene (e.g. Chen et al., 2017; Garcia-R et al., 2020; Li et al., 2019; Mikula et al.,
159 2021; Wu et al., 2020). As a complementary approach we assembled complete mitogenomes (parts of
160 them correspond to the most frequently used markers in mammalian phylogeny) and reconstructed
161 their phylogenetic relationships. Based on the results of molecular phylogenomic analyses and other
162 available data, we propose taxonomic changes and delimit monophyletic genera of the tribe
163 Praomyini.

164

165 **2. Methods**

166 *2.1 Taxon sampling*

167 This study includes 34 specimens of Praomyini, representing all currently recognized genera of the
168 tribe, except *Nilopegamys* (known only from the holotype, recently analysed by Giarla et al., 2020),
169 and all taxa whose systematics position and taxonomy was recently subject to debate (e.g. *Myomyscus*
170 *verreauxii*, *M. brockmani*, *M. angolensis*, *Praomys delectorum*, *Praomys lukoleale*, *Mastomys*
171 *pernanus*). For the species-rich genera (*Hylomyscus* and *Praomys*) we selected representatives of all

172 recognized species groups (Mikula et al., 2020; Missoup et al., 2012; Mizerovská et al., 2019; Nicolas
173 et al., 2020a). Additionally, we also included one genetically very divergent specimen from an unknown
174 genus, recently discovered in the Chingawa forest in south-western Ethiopia, called "New genus
175 (Chingawa)". As outgroups in all phylogenetic analyses we used two species from the tribe Arvicanthini
176 (*Aethomys chrysophilus* and *Arvicanthis somalicus*), one from Otomyini (*Otomys typus*) and one from
177 Millardini (*Millardia meltada*). All details about the used specimens, including localities and museum
178 numbers, are shown in Table 1. The tissue samples originate from the tissue collections of authors and
179 their collaborators and the sampling was carried out in accordance with local legislation in particular
180 African countries.

181

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

184

185 2.2 Anchored hybrid enrichment (AHE) data collection and assembly of nuclear dataset

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

202

203 2.3 Assembly and alignment of mitogenomes

204 Mitochondrial DNA is usually highly prevalent in genomic DNA extractions and it still persists even in
205 genomic libraries enriched for particular conserved loci. We used the raw data of Illumina reads to

206 assembly the complete mitogenomes of 38 analysed taxa (34 ingroups, 4 outgroups) as a by-product
207 of the AHE approach. Heavy-strand protein-coding genes (12 genes) and genes for non-coding RNA
208 (two ribosomal RNAs and 22 transfer RNAs) were extracted from the complete mitochondrial
209 sequences in the Geneious software (Biomatters Ltd.) according to the annotated reference of
210 complete mtDNA of *Mastomys coucha* (GenBank accession number MF062946). We excluded the
211 control region (CR) sequences because of alignment difficulties due to highly variable non-coding
212 sequences (Pozzi et al., 2014), and ND6 gene because it is encoded on the mitochondrial L-strand which
213 has a different nucleotide composition from the H-strand, and has been shown to have poor
214 phylogenetic signal (Gissi et al., 2000). The protein-coding genes were individually aligned based on
215 their corresponding amino acid translations in Geneious. Two genes for ribosomal RNA (12S-rDNA and
216 16S-rDNA) and 22 genes for transfer RNA were aligned following Mikula et al. (2021).

217

218 *2.4 Phylogenetic analysis of nuclear loci*

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

228

229 The input gene trees were inferred in separate Bayesian analyses performed in MrBayes 3.2.6
230 (Ronquist et al., 2012). They were inferred as unrooted (uniform prior probability over tree topologies)
231 with unconstrained branch lengths. The analysis sampled over GTR nucleotide substitution models
232 (option nst=mixed in MrBayes; Huelsenbeck et al., 2004) with discrete gamma rate variation among
233 sites. Markov Chain Monte Carlo (MCMC) was run for 5 million generations per run, sampling every
234 2000 generations. For each run, 25% of trees were discarded as burn-in. We conducted two
235 independent runs and checked their convergence in R packages '*rwtv*' (Warren et al., 2017) and '*coda*'
236 (Plummer et al., 2006). The convergence diagnostics were average standard deviation of split
237 frequencies (Lakner et al., 2008) and potential scale reduction factor (Gelman and Rubin, 1992), which
238 should be close to zero for tree topologies and model parameters, respectively. We also checked if the
239 effective sample size of all sampled parameters was large enough (>200). In ASTRAL, every gene was
240 represented by its maximum bipartition credibility (MBC) tree calculated in '*phangorn*'. Bipartitions

241 with PP < 0.90 were collapsed and thus the lack of resolution in MBC trees introduced uncertainty but
242 not bias into ASTRAL.

243

244 *2.5 Phylogenetic reconstruction of complete mtDNA*

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

262

263 *2.6 Sub-sampling of nuclear loci and time-calibrated phylogeny*

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

272

273 The time-calibrated phylogeny was inferred in StarBEAST 2 (Ogilvie et al., 2017) as a species tree,
274 accounting for incomplete lineage sorting predicted by multispecies coalescent model (Yang and
275 Rannala 2003). The species tree was assumed to originate from homogenous birth-death process, but

276 its topology was fixed to the ASTRAL solution. Topologies of gene trees were fixed to those of MBC
277 trees (without collapsing of poorly resolved branches) and nucleotide substitution model parameters
278 to their mean values as in BF analysis. Only branch lengths, clock rates and species tree parameters
279 were therefore sampled by MCMC under uninformative priors.

280

281 For time calibration we used two node constraints: the root of the tree was constrained to 6.1–8.5
282 million years (Ma) and the most recent common ancestor (MRCA) of *Colomys* and *Zelotomys* to 1.9–
283 5.3 Ma before present (with uniform calibration densities). The minimum ages were constrained by
284 the fossils from Lemudong-o' (Kenya, 6.1 Ma) reported as belonging to *Mastomys* (Manthi, 2007) and
285 by *Zelotomys leakeyi* described by Jaeger (1976) from Olduvai Bed I (Tanzania, 1.9 Ma). Age estimates
286 of the sites are due to Deino and Ambrose (2007) and Deino (2012), respectively. Manthi (2007)
287 provided no determination clues for the fossils, but given their presumed similarity to extant
288 *Mastomys* we assumed them to belong to crown Praomyini.

289

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

305

306 *2.7 Reconstruction of ancestral habitats*

307 The ancestral habitats of Praomyini were inferred based on the habitats occupied by extant taxa.

308 We assigned species to one of the three habitat states: (i) forest (lowland, submontane and montane
309 forest), (ii) open lowland vegetation (miombo woodland, savanna, grassland, agricultural fields,
310 swampy marshes, rocky outcrops with sparse vegetation) and (iii) open montane habitat (alpine

311 moorlands, upland grasslands and scrub vegetation at elevation of ca. 3000-4500 m). This assignment
312 was based on Wilson et al. (2017) and personal observations made by the authors. Because individual
313 species can sometimes occupy multiple habitats, we used each species most prominent habitat.
314 Traits were mapped onto our time-calibrated phylogeny inferred in StarBEAST 2. We applied two
315 methods, parsimony and maximum likelihood (ML), using Mesquite v. 3.61 (Maddison and Maddison,
316 2019). ML reconstructions were performed using the Markov k-state 1-parameter model of evolution
317 (mk1) for discrete unordered characters (Lewis, 2001), which gives equal probability for changes
318 between any two character states. Similarly, parsimony analysis used Fitch (unordered or non-additive)
319 optimisation, which gives equal cost to all character-state changes.

320

321 **3. Results**

322 *3.1 Nuclear phylogenomics*

323 Both ML (in IQ-TREE) and Bayesian (in MrBayes) analyses of the concatenated dataset of 395 loci
324 (610,965 bp long alignment) produced identical and well supported topology (Fig. 1A). The trees were
325 almost fully resolved and most nodes had a maximum support, except the relationships between
326 recently evolved species of the genus *Stenocephalemys*, where two pairs of sister species were
327 supported with UFBoot = 79 in ML analysis. The species tree inferred from 395 gene trees in ASTRAL
328 (see topology in Fig. 2) was almost completely resolved (with PP = 1.00), except two nodes (*Hylomyscus*
329 *kerbispeterhansi*/*H. parvus* and *Praomys rostratus*/*P. morio*) with PPs = 0.99, and *Stenocephalemys*
330 *sokolovi*/*S. ruppi* relationship with PP = 0.96. One intrageneric node (*Stenocephalemys ruppi*/*S.*
331 *albocaudatus*) had a weak support (PP = 0.43). Relationships among species within the latter genus
332 were the only differences in topologies between concatenated and species trees (compare Fig. 1A and
333 Fig. 2). The nuclear phylogenomic analysis confirmed clear polyphyletic character of currently
334 recognized genera *Mastomys*, *Myomyscus* and *Praomys*.

335

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

342

343 *3.2 Complete mitogenomes*

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

354

355 3.3 Divergence dating

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

365

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

374

375 3.4 Reconstruction of ancestral habitat types

376 Results of ancestral habitat reconstruction by parsimony and ML analyses are congruent and reveal an
377 ancestor of Praomyini living in a forest (Fig. 3). Multiple transitions between habitat types occurred in

378 the evolution of the tribe. Based on likelihood scores there have likely been three independent shifts
379 into open lowland savannah-like habitats from a forest ancestor in Miocene/Pliocene boundary (one
380 in *M. pernanus*, one in the ancestor of the *P. daltoni* species complex, and one in the ancestor of the
381 large clade grouping *Colomys* + *Zelotomys* + *M. verreauxi* + *P. lukolelae* + *Mastomys* + East African
382 *Myomyscus* + *Stenocephalemys*). In this group, the analysis revealed a single colonization of open
383 montane habitats in the ancestor of *Stenocephalemys*, two recolonizations of the forest habitat from
384 an open lowland savannah-dwelling ancestor (*C. goslingi*, *P. lukolelae*) and two from open montane
385 habitat ancestor (*S. albipes*, *S. ruppi*).

386

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

391

392 4. Discussion

393 4.1 First fully resolved phylogeny of the tribe Praomyini

394 Our approach combining samples from all major phylogenetic lineages of the tribe Praomyini and a
395 phylogenomic approach allowed us for the first time to successfully reconstruct phylogenetic
396 relationships within this tribe. We obtained a fully resolved tree with the nuclear dataset (395 loci;
397 610,965 bp long alignment). The mitogenomic tree (14,745bp) was also nearly fully resolved, and the
398 topology of the mtDNA tree was similar to nDNA tree with three exceptions. The relationships inferred
399 by anchored phylogenomics have higher credit here because mtDNA tree represents just a single-locus
400 tree (due to the lack of recombination), which may differ from the species tree due to incomplete
401 lineage sorting and, especially on shallow scales, also due to mitochondrial introgression. Past mtDNA
402 introgression explains the incongruence observed between the two datasets in the genus
403 *Stenocephalemys* (see more details in Bryja et al., 2018; Mizerovská et al., 2020). The two other
404 incongruent nodes (placement of the “New genus (Chingawa)” and placement of the two *Myomyscus*
405 taxa from eastern Africa) are not fully supported by the ML analysis of mitogenomic data (bootstrap
406 support of 98 and 78, respectively).

407

408 Relationships among Praomyini genera recovered in previous molecular studies (Aghová et al., 2018;
409 Lecompte et al., 2008; Steppan and Schenk, 2017) are characterized by low support values and/or small
410 branch-lengths, indicative of either the occurrence of ‘soft polytomy’ (i.e. insufficient molecular data)
411 or a ‘hard polytomy’ (i.e. a burst of diversification). Previous studies were based on a low number of

412 molecular markers (between 2 and 6 nDNA gene fragments and between 1 and 9 mtDNA fragments),
413 resulting in a total alignment length varying between 3,070 pb and 10,482 bp (with up to 42% of
414 missing data), and these data were analysed through concatenation analyses. It is well known that this
415 kind of data can provides insufficient synapomorphies for resolving species relationships, and that with
416 a small number of loci it is difficult to deal with inconsistencies related to incomplete lineage sorting
417 and ancestral polymorphisms (Martin-Hernanz et al., 2019; Nesi et al., 2021). Moreover, over long
418 periods of time, historical signal in sequence data may be overwritten by multiple substitutions,
419 contributing to “nonhistorical signal” (Ho and Jermiin, 2004). Our divergence time analysis shows that
420 the diversification between major lineages (recognized usually as separate genera) within the tribe
421 was relatively rapid, with most splits occurring in the Miocene-Pliocene boundary (roughly between 7
422 and 5 Ma). Unresolved polytomies within the Praomyini tribe in previous studies thus represented
423 ‘soft’ polytomies that are now resolved into sequential bifurcations with genome-scale data and
424 proper methods of phylogenetic analysis.

425

426 4.2 Taxonomic implications - delimitation of monophyletic genera

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

434

435 4.2.1 Polyphyletic *Praomys*

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

447

448 *Montemys* Nicolas & Bryja, gen. nov.

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

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

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

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

459 *Generic diagnosis*: This genus is morphologically strongly circumscribed, unique in its combination of
460 traits compared with *Praomys* and *Congomys* gen. nov. (Carleton and Stanley, 2012; Happold, 2013):
461 palatal ridges is 2 + 5 = 7; plantar pads 6; anterior palatal foramina reach to front edge of first root of
462 M¹; t3 of M¹ well developed; t3 in M² larger than in other species of *Praomys* and *Congomys* gen. nov.;
463 weak supraorbital ridges not raised; chromosome number 2n = 48; four pairs of nipples (2 + 2 = 8).

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

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

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

474

475 *Congomys* Nicolas & Bryja, gen. nov.

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

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

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

481 *Generic diagnosis:* This genus is unique in its combination of traits compared with *Montemys* gen. nov.
482 and *Praomys* (Happold, 2013; Van der Straeten and Dudu, 1990): anterior palatal foramina short, not
483 reaching to M¹; t3 on M¹ obsolete; weak supraorbital ridges not raised; the long hindfoot (range 28-32
484 mm), long ears and the form of the skull are more similar to *Malacomys* than to *Praomys*. However,
485 *Malacomys* belongs to the genetically distinct tribe Malacomyini and they have only 5 plantar tubercles
486 instead of 6 as usual in *Praomys*, *Congomys* gen. nov. and *Montemys* gen. nov.
487 *Species included:* *Congomys lukolelae* (Hatt, 1934); *Congomys verschureni* (Verheyen & Van der
488 Straeten, 1977).
489 *English names:* Several names were previously proposed for *C. lukolelae* (Lukolela soft-furred mouse,
490 Lukolela *Praomys* and Lukolela Swamp rat) and *C. verschureni* (Verschuren's *Praomys* or Verschuren
491 Swamp rat) (Wilson et al., 2017). Given that these species are no longer included into the genus
492 *Praomys* and that the term "soft-furred" is usually used for *Praomys* species, we propose using the
493 names Lukolela Swamp rat for *C. lukolelae* and Verschuren's Swamp rat for *C. verschureni*.

494

495 *Praomys*

496 After exclusion of *Montemys* gen. nov., and *Congomys* gen. nov., the genus *Praomys* is now
497 monophyletic and contains three major clades corresponding to three well-known species groups
498 highlighted by previous morphological and molecular studies (Happold, 2013; Kennis et al., 2011;
499 Lecompte et al., 2005; Lecompte et al., 2002a; Lecompte et al., 2002b; Missoup et al., 2012; Monadjem
500 et al., 2015; Musser and Carleton, 2005; Nicolas et al., 2005; Van der Straeten, 2008; Van der Straeten
501 and Dieterlen, 1987; Van der Straeten and Dudu, 1990; Van der Straeten and Kerbis Peterhans, 1999):
502 (i) the *jacksoni* species-group (including *P. jacksoni*, *P. mutoni*, *P. minor* and *P. degraffi*; represented
503 in our study by *P. jacksoni* and *P. minor*), (ii) the *tullbergi* species-group (including *P. tullbergi*, *P.*
504 *hartwigi*, *P. misonnei*, *P. morio*, *P. rostratus*, *P. obscurus*, *P. petteri* and *P. coetzeei*; represented in our
505 study by *P. hartwigi*, *P. morio* and *P. rostratus*) and (iii) the *daltoni* species-group (including *P. daltoni*;
506 represented in our study by three specimens belonging to three different clades). The evolutionary
507 history and phylogenetic relationships in these species groups were recently investigated in molecular
508 studies including more specimens and species but fewer genetic markers than in the present study:
509 see Missoup et al. (2012) for the *tullbergi* species-group, Mizerovská et al. (2019) for the *jacksoni*
510 species-group and Bryja et al. (2010) and Mikula et al. (2020) for the *daltoni* species-group. These
511 studies highlighted that at least one new species should be described within the *tullbergi* species-
512 group, and the same is true for the *jacksoni* species-group. The situation of the *daltoni* species-group
513 is complex since two species differing in external appearance and lifestyle were described within it (*P.*
514 *daltoni* and *P. derooi*), but recent integrative study of Mikula et al. (2020) strongly suggests that *P.*
515 *derooi* is an ingroup of *P. daltoni* and could represent an ecotype rather than a distinct species. Here

516 we used genomic data and estimated the age of TMRCA of the *daltoni* species-group to 0.8 Ma, which
517 is significantly younger than previous estimates largely affected by mtDNA (e.g. 3 Ma in Bryja et al.,
518 2010). Also, the split of the *derooi* ecotype is very recent (30 kya; Fig. 2), which agrees with a hypothesis
519 on the role of commensalism on phenotypic changes. All these results support the view of *P. daltoni*
520 as a single species, with a phylogeographic structure similar to those observed in other species in
521 Sudanian savanna (e.g. *M. erythroleucus* or *A. niloticus* C2-C4), with recently evolved changes due to
522 commensalism, mainly in the Dahomey Gap (see Mikula et al., 2020, and references therein).

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

- 524 - *tullbergi* species-group: palatal ridges 2 + 7 = 9; plantar pads 6; anterior palatal foramina reach
525 to front edge of first root of M¹; t3 of M¹ obsolete or difficult to detect; weak supraorbital
526 ridges not raised. Habitat is usually a primary rainforest, and most species are found in lowland
527 forests (see Missoupe et al. 2012).
- 528 - *jacksoni* species-group: palatal ridges 2 + 5 = 7; plantar pads 6; anterior palatal foramina reach
529 to middle of first root of M¹; t3 of M¹ well developed; supraorbital ridges raised. They live in
530 various forest habitats, and there are narrow specialists for both montane and lowland forests
531 as well as habitats generalist (Mizerovská et al. 2019).
- 532 - *daltoni* species-group: palatal ridges 2 + 5 = 7; plantar pads 6; anterior palatal foramina reach
533 the front edge of first root of M¹; t3 of M¹ well developed; supraorbital ridges not raised. This
534 species is distributed in the mosaic of the Guinean forest and Sudanian savanna, and can be
535 partially commensal (Mikula et al. 2020).

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

544 *Generic diagnosis*: this genus can be distinguished from *Montemys* gen. nov. and *Congomys* gen. nov.
545 by the following combination of traits: anterior palatal foramina reach to front edge or the middle of
546 the first root of M¹; t3 in M² smaller than in *Montemys* gen. nov.

547

548 4.2.2 Polyphyletic *Myomyscus*

549 The genus *Myomyscus*, as reconstituted by Musser and Carleton (2005), contains four species: *yemeni*,
550 *brockmani*, *angolensis*, and *verreauxii*. In our phylogenomic analyses, we included four species bearing

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

565

566 *Myomyscus*

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

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

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

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

586

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

588 *Note:* In a report devoted to the identity of Bocage's *Mus angolensis*, Crawford-Cabral (1989) noted
589 that the type series was destroyed by fire in the Lisbon Museum in 1978. According to the original
590 description the specimens represented a species with a tail much longer than head and body, white
591 feet, soft and thick fur, and five pairs of teats (3 + 2), all characters very typical for *Myomyscus*, as
592 defined here (see above). Crawford-Cabral considered Angolan specimens collected after 1890 outside
593 of the Capangombe region and identified as *angolensis* to be another species. He proposed *Praomys*
594 *angolae* for this rat and considered it a *Mastomys* (this was not accepted by Musser & Carleton 2005,
595 and the taxonomic situation of Angolan taxa remained unresolved; see above). Here we propose to
596 include the widespread Angolan species (living also in southern DRC; see Krásová et al., under review)
597 into *Mastomys*. Despite the fact that the type material of *angolensis* cannot be compared with recent
598 material, we prefer to keep the name *angolensis* (and not *angolae*), in agreement with Musser &
599 Carleton (2005). The new combination is also supported by morphological data: according to
600 Monadjem et al. (2015) this species is very similar to *Mastomys shortridgei*, with which it shares many
601 cranio-dental features and lower number of nipples compared to other *Mastomys*, but the tail is
602 distinctly shorter in the latter species (ca. 87% of HB in *M. shortridgei* versus ca. 100% of HB in *M.*
603 *angolensis*) (Monadjem et al., 2015). The only other species of *Mastomys* co-occurring with *M.*
604 *angolensis* is *M. natalensis* (Krásová et al., under review), which differs in number of nipples (usually
605 12 pairs in *M. natalensis*). Here, we confirmed these findings, as the individuals of *M. angolensis* at
606 locality Namba (used for anchored phylogenomic analysis) had 5 pairs of nipples and the tail was
607 roughly equal in length to head+body (ranging from 91 to 117%; N=17).

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

615

616 *Ochromyscus* Nicolas, Mikula & Bryja, gen. nov.

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

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

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

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

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

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

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

637

638 4.2.3 Polyphyletic *Mastomys*

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

647

648 *Serengetimys* Nicolas & Bryja, gen. nov.

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

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

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

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

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

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

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

674

675 Fig. 4: (A) Ventral, dorsal and lateral view of *Serengetimys pernanus* from northern Tanzania (specimen
676 T227869, adult male, locality Ikona). (B) All known localities of this species (based on Van der Straeten
677 1999, Stanley et al. 2007, and our unpublished data). Note that the specimen from the southernmost
678 locality (Dakawa) has an aberrant morphology (Van der Straeten 1999), but another genotyped
679 individual from the same locality differentiated from remaining sympatric *Mastomys* (Lecompte et al.
680 2005) and clustered with our new samples from northern Tanzania and southern Kenya (not shown).
681 An inset shows the map of Africa and the red frame indicates its zoomed part.

682

683 *Mastomys*

684 *Generic diagnosis:* Medium-sized rodents (mean HB ca. 100-136 mm) with a tail sparsely haired with
685 small concentric scales and typically shorter or equal to the head and body length (85-103% of HB).
686 The dorsal pelage is soft-furred with sparse guard hairs and variable colour, typically dark greyish to
687 grey-brown. The ventral colour is grey. Females of most species are immediately recognisable by

688 having 8 to 12 pairs of mammae, with two exceptions, *M. angolensis* and *M. shortridgei*, which have
689 only 5 or 8 pairs of teats, respectively (see discussion above and Eiseb et al. 2020). Based on body
690 measurements *Mastomys* is similar to *Zelotomys* and *Stenocephalemys*. However *Zelotomys* can be
691 distinguished by its entirely white tail and stephanodont molars (Monadjem et al., 2015; Wilson et al.,
692 2017), and *Stenocephalemys* by its narrower interorbital constriction and macrodont molars
693 (Monadjem et al., 2015).

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

698

699 4.2.4 Discovery of a new genus in south-western Ethiopia

700 *Chingawaemys* Lavrenchenko, Mikula & Bryja, gen. nov.

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

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

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

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

709

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

714

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

716 *Zoobank:* urn:lsid:zoobank.org:act:8CECF7-6FA3-46CA-8893-306E596B6457

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

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

721 *Etymology:* The species name is derived from the Latin word "rarus" – rare (see Ecology).

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

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

739

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

744

745 *Comparisons:* *Chingawaemys rarus* sp. nov. differs from sympatric and syntopic *Stenocephalemys*
746 *albipes* and *S. ruppi* in smaller body size (head and body length of the holotype is 102 mm, while it
747 ranges 109-148 mm in *S. albipes* and 124-156 mm in *S. ruppi*), shorter hindfeet (length of hind foot
748 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*;
749 see Mizerovská et al. 2020 for more details), longer hairs on the end of tail, greyish (not white)
750 colouration of dorsal surface of forefeet and hindfeet (Fig. 5), and considerably narrower zygomatic
751 plate with a straight anterior margin (Fig. 6).

752 *Distribution:* The new species has been found only in the Chingawa Forest (07°25' N 35°24' E, 2340 m
753 a.s.l.) (Fig. 7). We failed to trap *Chingawaemys rarus* sp. nov. in other humid Afrotropical forest blocks
754 of SW Ethiopia: the Sheko Forest (07°04'N, 35°30'E, 1930 m a.s.l.), the Dushi Area of the Godare Forest
755 (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.)

756 and the Beletta Forest (07°34'N, 36°31'E, 1900 m a.s.l.) which are, however, situated at a lower
757 altitude. Therefore, the currently known distribution range of the new species and genus is extremely
758 limited.

759

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

762

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

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

780

781 4.3 Evolutionary scenario of the *Praomyini* radiation in Late Miocene/Early Pliocene

782 The origin of the tribe *Praomyini* is associated with the cessation of the Late Miocene faunal exchange
783 between Asia and Africa. The analysis of rodent fossils in Africa suggests that the modern rodent fauna,
784 with taxa assignable to extant tribes or even genera, appears in the interval 7-5 Ma (reviewed in
785 Lecompte et al., 2008; see also Table S2 in SM1). In the same period, the dominance of fossil gerbils
786 increased in the Middle East, indicating very arid conditions (Tchernov, 1992), presenting a barrier for
787 dispersal of murine ancestors between Asia and Africa. Palaeontological studies therefore imply that
788 two most divergent and speciose tribes of recent African rodents, *Arvicanthini* and *Praomyini*, started
789 their African radiation in the same geological period in terminal Miocene. This fits very well recent

790 molecular studies. Using genomic-scale data and multiple fossils, the first diversification in African
791 Arvicanthini was dated to 7.6 Ma (Mikula et al., 2021), while the first split in Praomyini is estimated at
792 7.1 Ma (Fig. 2).

793

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

808

809 Fragmentation of Late Miocene pan-African forests into western, central and eastern forests (Lovett,
810 1993; Plana, 2004) is being increasingly supported by the dated phylogenetic studies in animal and
811 plant taxa. For example, the splits between Congolese and eastern African species of the plant genera
812 *Uvariadendron* and *Monodora* are dated to ca. 8.4 Ma (Couvreur et al., 2008). Similarly, the contraction
813 and fragmentation of the forest in Late Miocene/Early Pliocene played a key role in the diversification
814 of some groups of African chameleons (Tolley et al., 2013) and murid rodents from the Arvicanthini
815 tribe (Bryja et al., 2017; Mikula et al., 2021). In Praomyini, we can see very similar patterns. It is
816 generally difficult to reconstruct the area of origin of widely distributed forest clades of *Praomys* and
817 *Hylomyscus/Heimyscus*. However, the oldest splits in Miocene/Pliocene boundary have obvious
818 geographical component (i.e. fragmentation of forests), because they separated taxa with the highest
819 diversity in Upper and Lower Guinean forests (the *tullbergi+daltoni* complexes of *Praomys* and
820 *Heimyscus*, respectively) from those with highest evolutionary diversity, i.e. the presence of most
821 divergent lineages, in Albertine Rift montane forests (i.e. the *jacksoni* complex of *Praomys* and
822 *Hylomyscus*, respectively) (Mizerovská et al., 2020; Nicolas et al., 2020a). This pattern is even more
823 obvious in two other clades of forest Praomyini, because they have restricted distribution in montane
824 forests of eastern Africa, which are geographically marginal to the more continuous central African

825 forests. *Montemys* gen. nov. diverged from remaining *Praomyini* at 6.9 Ma, almost at the same time
826 as *Chingawaemys* gen. nov. (6.8 Ma). The first one is currently known from isolated East African
827 montane forests from southern Kenya to central Mozambique (Sabuni et al., 2018), while the second
828 is known only from the holotype collected in a very humid montane forest in southwestern Ethiopia
829 (this study). The biogeographical importance of East African Mountains (e.g. Eastern Arc Mts.,
830 Southern Rift Mts. etc.) as museums of forest evolutionary diversity is well recognized (e.g. Burgess et
831 al., 2007). On the other hand, forests in southwestern Ethiopia are not currently officially protected,
832 but they should be considered as a very important refugium of unique palaeoendemic biota, separated
833 from other tropical forests in Africa for almost 7 million years.

834

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

853

854 The ancestral habitat preference was not well resolved in the clade grouping *Colomys-Zelotomys-*
855 *Myomyscus-Congomys* gen. nov. (Fig. 3). Either there were two shifts from forests to open habitats or
856 vice versa. However, when looking at habitat preferences of extant taxa, it seems that this clade can
857 be characterized by the affinity to wetland habitats. This is best expressed in semi-aquatic forest taxa
858 *Colomys* (+ their sister clade *Nilopegamys*, not included in the present study; Giarla et al., 2020) and
859 swamp-dwelling *Congomys* gen. nov. (see above). Two remaining genera live in non-forested habitats,

860 mostly in southern and eastern Africa, but they have very specific micro-habitat requirements.
861 *Myomyscus verreauxi* occurs in damp grasslands and vleis, *Zelotomys hildegardeae* is often found on
862 the edge of swamps and in tall wet grasslands in moist grassy savanna (e.g. Monadjem et al. 2015).
863 The third species, *Z. wosnami* (not included in the present study), is found in dry savanna on Kalahari
864 sands, but it occurs along river beds and around pans frequently associated with Acacias and lime-clay
865 silty soils (Cassola, 2016). It is therefore possible that the shift in habitat preferences allowed the
866 colonization of newly appearing wetland habitats in both forests and savannas. This ecological shift
867 has again a parallel in Arvicanthini rodents, where the wetland-specialized genus *Dasymys* split from
868 other genera very soon in the radiation of the tribe (at the border of Miocene/Pliocene, ca. 6 Ma;
869 Mikula et al., 2021), which is comparable with the split of the clade of "wetland" Praomyini, i.e.
870 *Colomys-Zelotomys-Myomyscus-Congomys* gen. nov., from the clade *Mastomys-Stenocephalemys-*
871 *Ochromyscus* gen. nov.

872

873 **5. Conclusion**

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

884

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907

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1244
1245
1246

1247 **Data availability statement**

1248 Complete mitochondrial genomes are available in in GenBank, accession numbers are provided in
1249 Table 1. Alignments of nuclear loci obtained by anchored phylogenomic approach (as partitioned nexus
1250 file) and the Bayesian gene trees used as input for ASTRAL analysis (in newick format) will be available
1251 in the public repository of the Czech Academy of Sciences (<http://hdl.handle.net/XXXXX>) and in
1252 Mendeley Data repository (DOI:XXXX).

1253

1254

1255 **Figure legends**

1256 **Fig. 1.** Bayesian trees (MrBayes) reconstructed from: (A) concatenated alignment of 395 nuclear loci
1257 (in total 610,965 bp) and (B) complete mitogenomes (14,745 bp). The topologies produced by ML
1258 analyses (IQtree) were identical to those of Bayesian trees. Black circles on particular nodes indicate
1259 full support in both BI and ML analyses (i.e. PP=1.00/UFBboot=100). In remaining nodes the support is
1260 shown by numbers. The trees were rooted and outgroups removed. Red frames indicate the
1261 differences in topologies of nuclear and mitochondrial tree.

1262
1263 **Fig. 2.** Divergence dating of the species tree inferred using a multi-species coalescent approach in
1264 StarBEAST2, based on 57 selected loci and two fossil constraints (the root and the MRCA of *Colomys*
1265 and *Zelotomys*; see text and SM1 for more details). The topology was fixed to the ASTRAL solution of
1266 the species tree based on all 395 loci (the support of particular nodes is described in the text). The
1267 numbers in circles are TMRCAs of particular clades in million years ago (Ma). The names of newly
1268 delimited genera are shown in red on the right side of the figure. We also suggest to move *Myomyscus*
1269 *angolensis* in the genus *Mastomys* based on its phylogenetic position and evolutionary distances (see
1270 text for more details).

1271
1272 **Fig. 3.** Parsimony (branch coloration) and likelihood (pie charts) reconstruction of ancestral habitats
1273 across Praomyini mapped on the chronogram resulting from our divergence dating of the species tree
1274 in StarBEAST 2. White = forest, grey = open lowland savannah-like vegetation, black = open montane
1275 habitats. Pictures on the right side of the figure illustrate these habitats.

1276
1277 **Fig. 4.** (A) Ventral, dorsal and lateral view of *Serengetimys pernanus* from northern Tanzania (specimen
1278 TZ27869, adult male, locality Ikona). (B) All known localities of this species (based on Van der Straeten
1279 1999, Stanley et al. 2007, and our unpublished data). Note that the specimen from the southernmost
1280 locality (Dakawa) has an aberrant morphology (Van der Straeten 1999), but another genotyped
1281 individual from the same locality differentiated from remaining sympatric *Mastomys* (Lecompte et al.
1282 2005) and clustered with our new samples from northern Tanzania and southern Kenya (not shown).
1283 An inset shows the map of Africa and the red frame indicates its zoomed part.

1284
1285 **Fig. 5.** Dorsal (above) and ventral (below) views of *Chingawaemys* gen. nov. and *Stenocephalemys*
1286 skins. (A) *Chingawaemys rarus* sp. nov. ZMMU S-181580 (holotype), (B) *Stenocephalemys albipes*
1287 ZMMU S-181579, (C) *Stenocephalemys ruppi* ZMMU S-181704. All specimens collected in the Chingawa
1288 Forest in April-May 2007.

1289

1290 **Fig. 6.** Dorsal (above), ventral (middle) and lateral (below) views of *Chingawaemys* gen. nov. and
1291 *Stenocephalemys* skulls. (A) *Chingawaemys rarus* sp. nov. ZMMU S-181580 (holotype), (B)
1292 *Stenocephalemys albipes* ZMMU S-181579, (C) *Stenocephalemys ruppi* ZMMU S-181704. All specimens
1293 collected in the Chingawa Forest in April-May 2007.

1294

1295 **Fig. 7.** Panoramic view of the type locality of *Chingawaemys rarus* sp. nov., the Chingawa Forest
1296 (southwestern Ethiopia).

1297

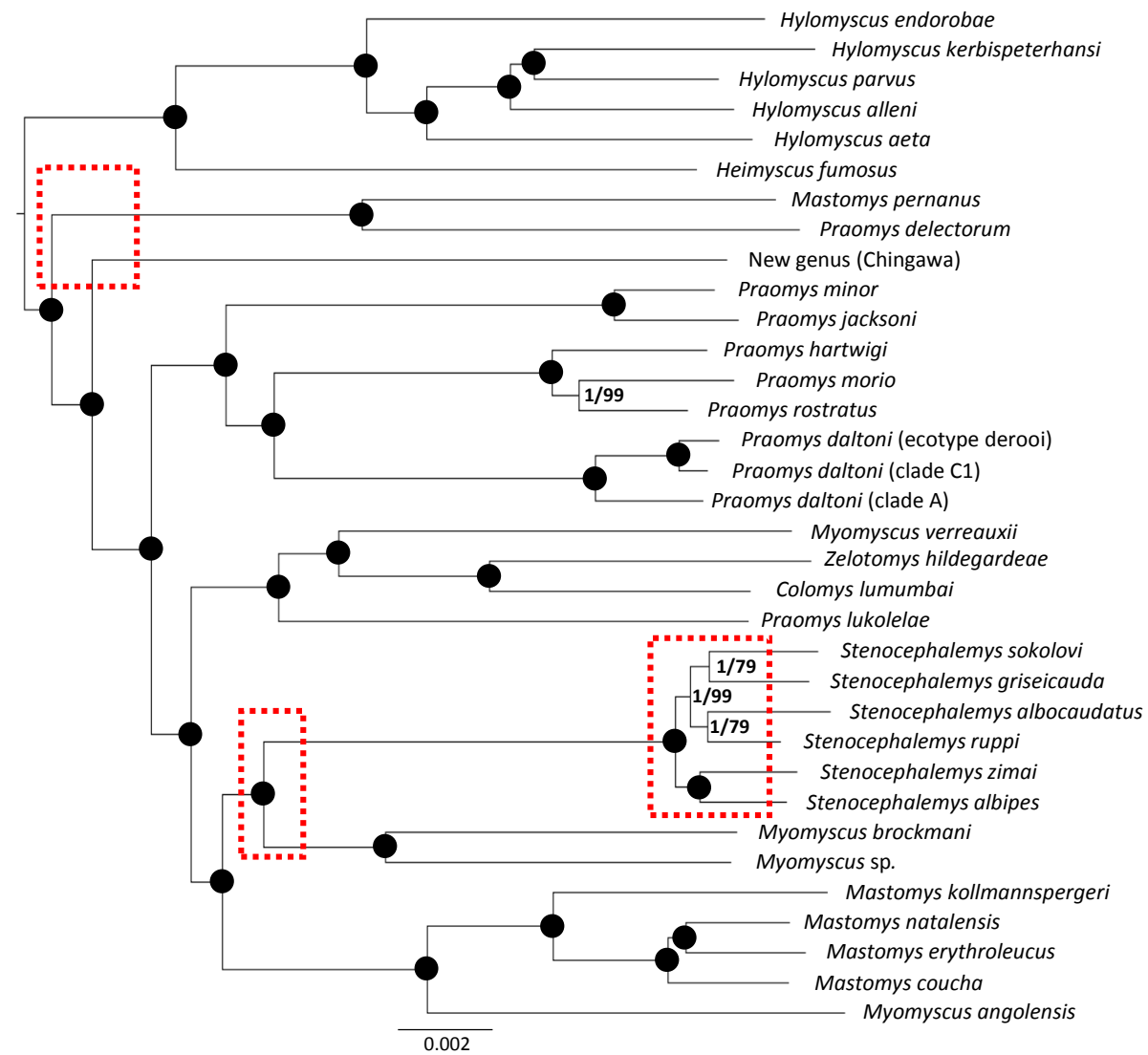
1298

1299 **Table 1.** List of material of Praomyini (+ four outgroups) used in phylogenomic analyses, their current/proposed generic classification, and the GenBank
 1300 accession numbers of mitogenomes.
 1301

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

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

(A) 395 concatenated loci



(B) complete mitogenomes

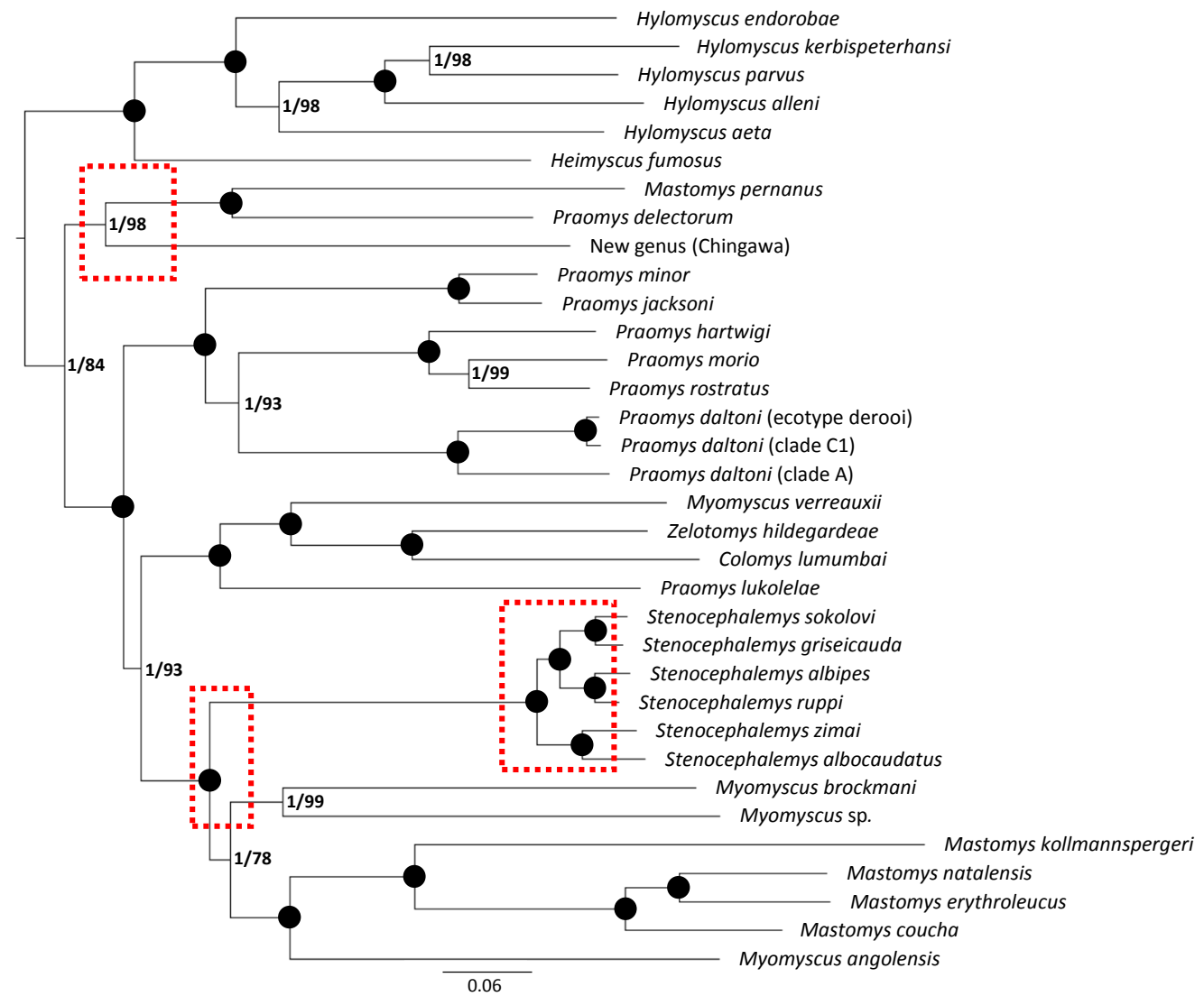


Figure 1

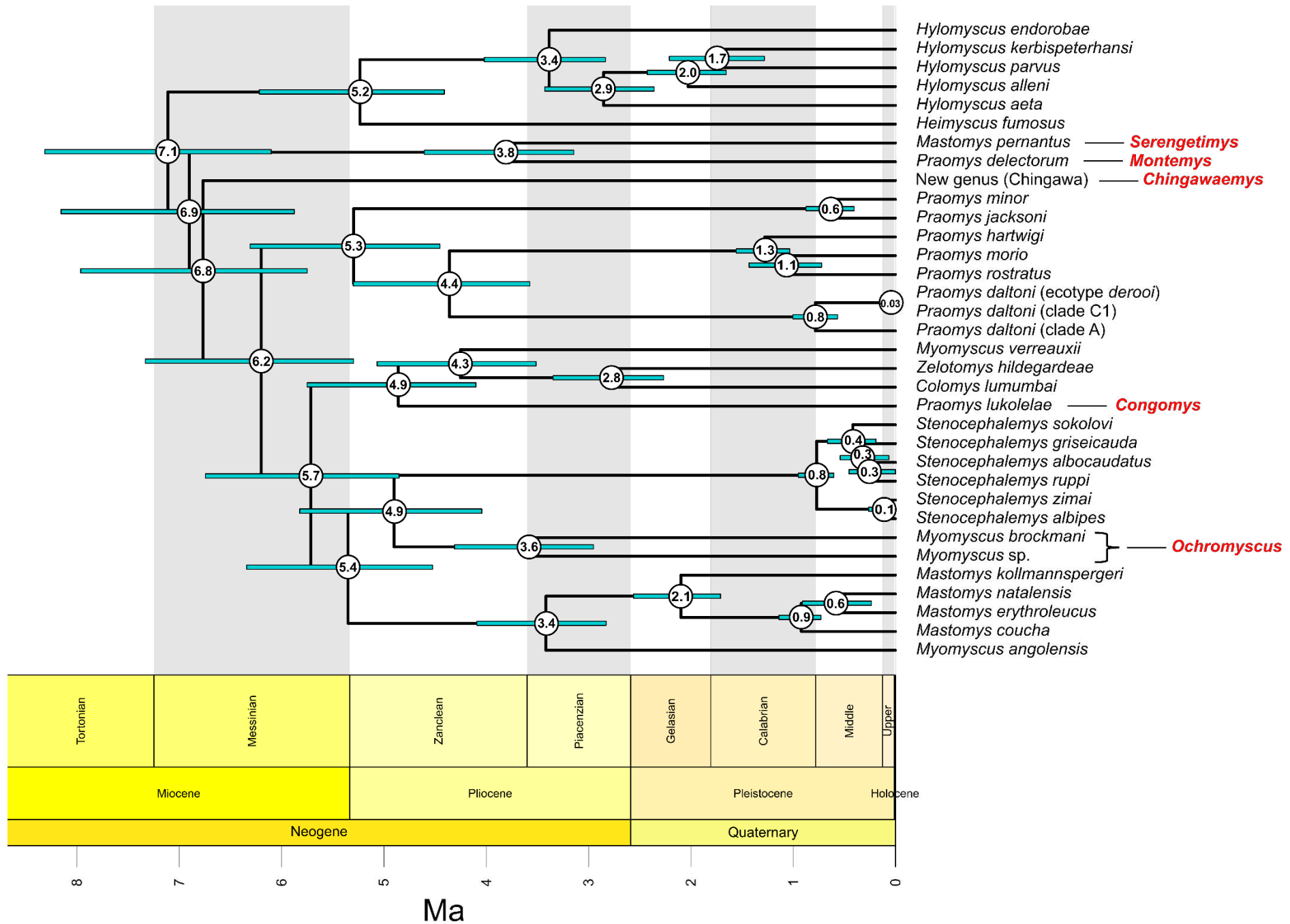


Figure 2

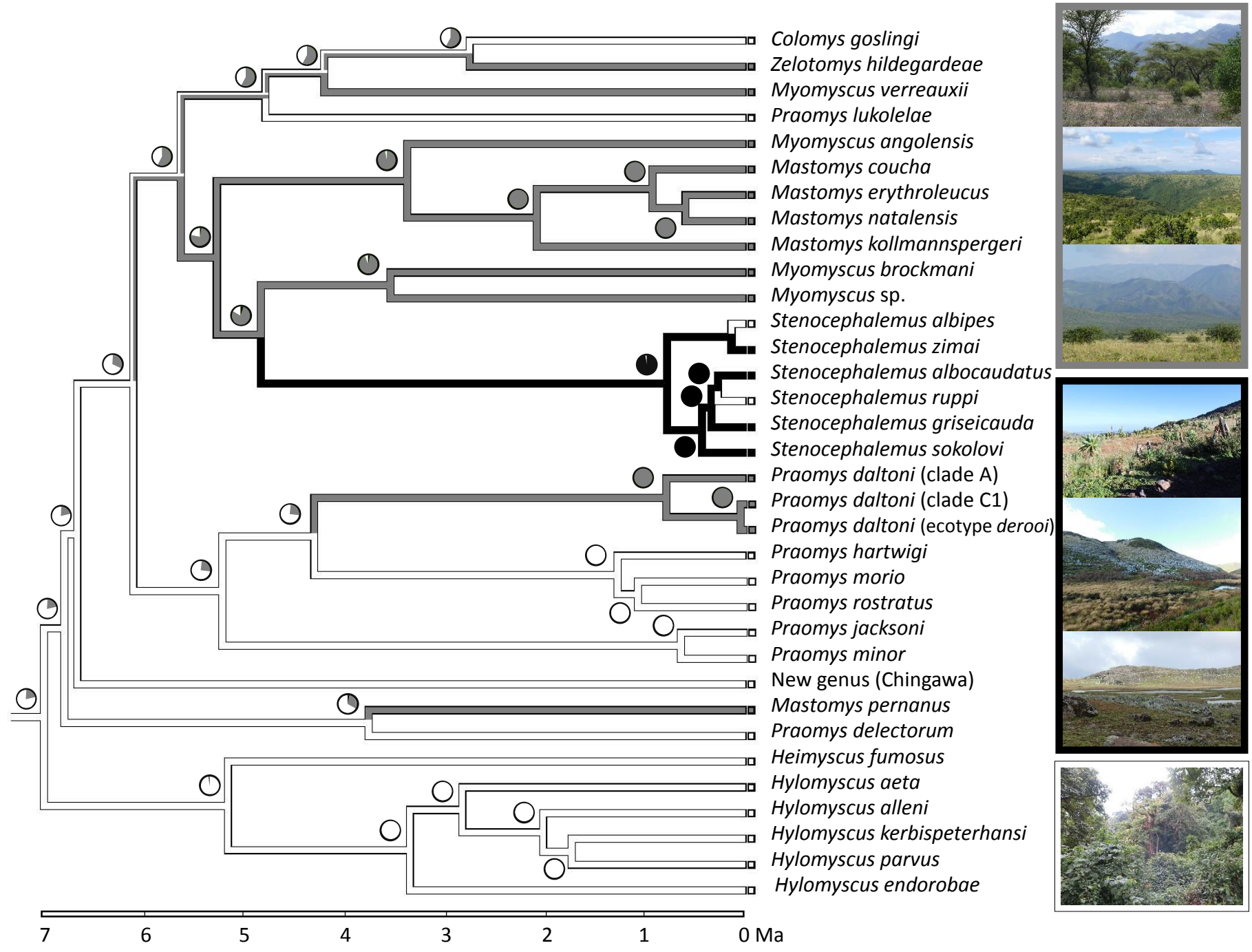


Figure 3

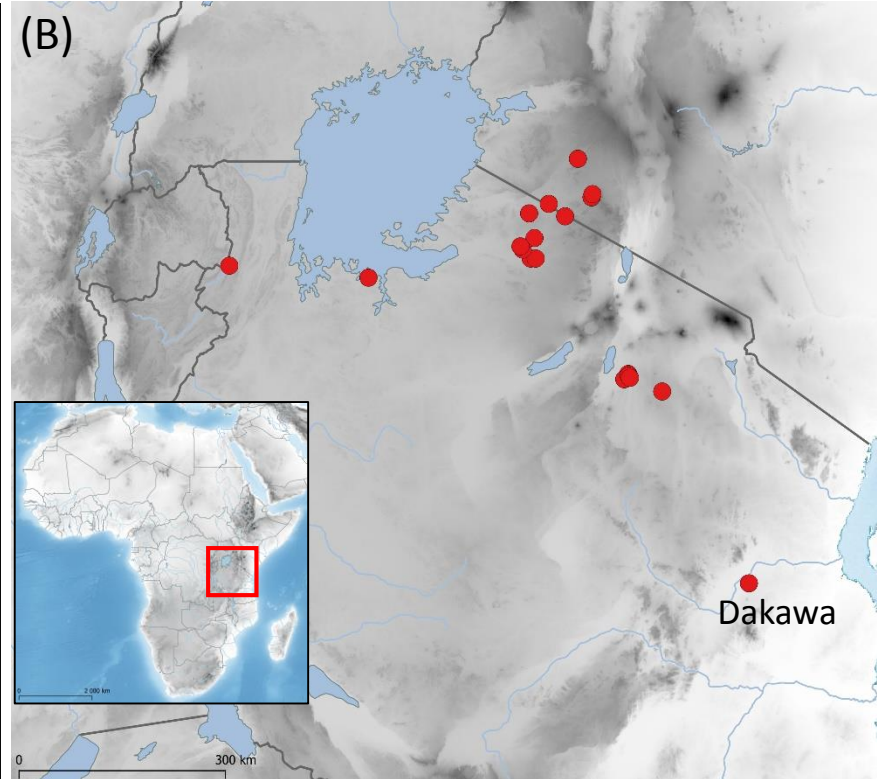
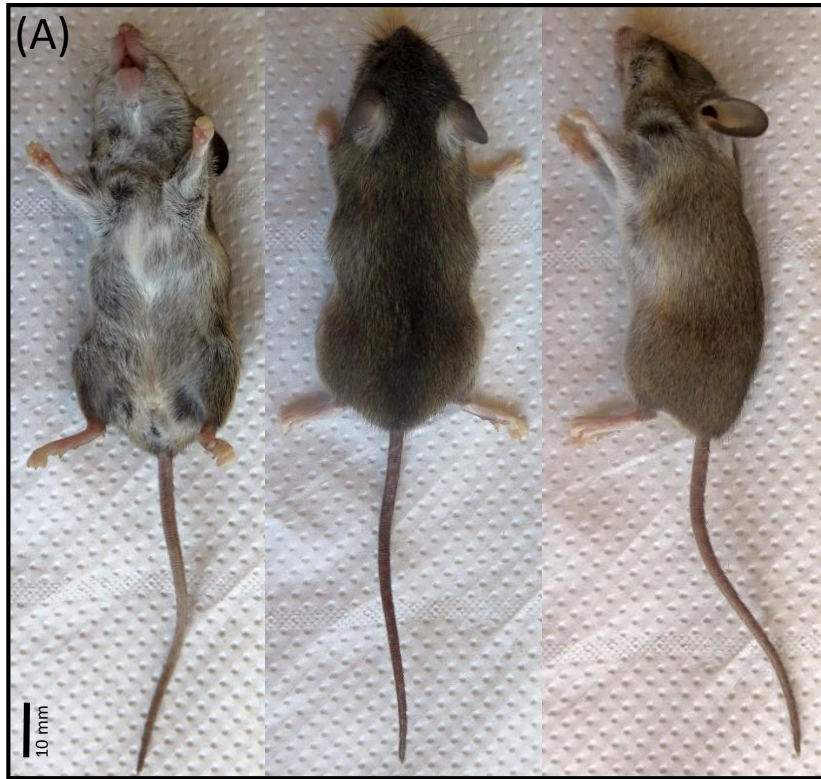


Figure 4

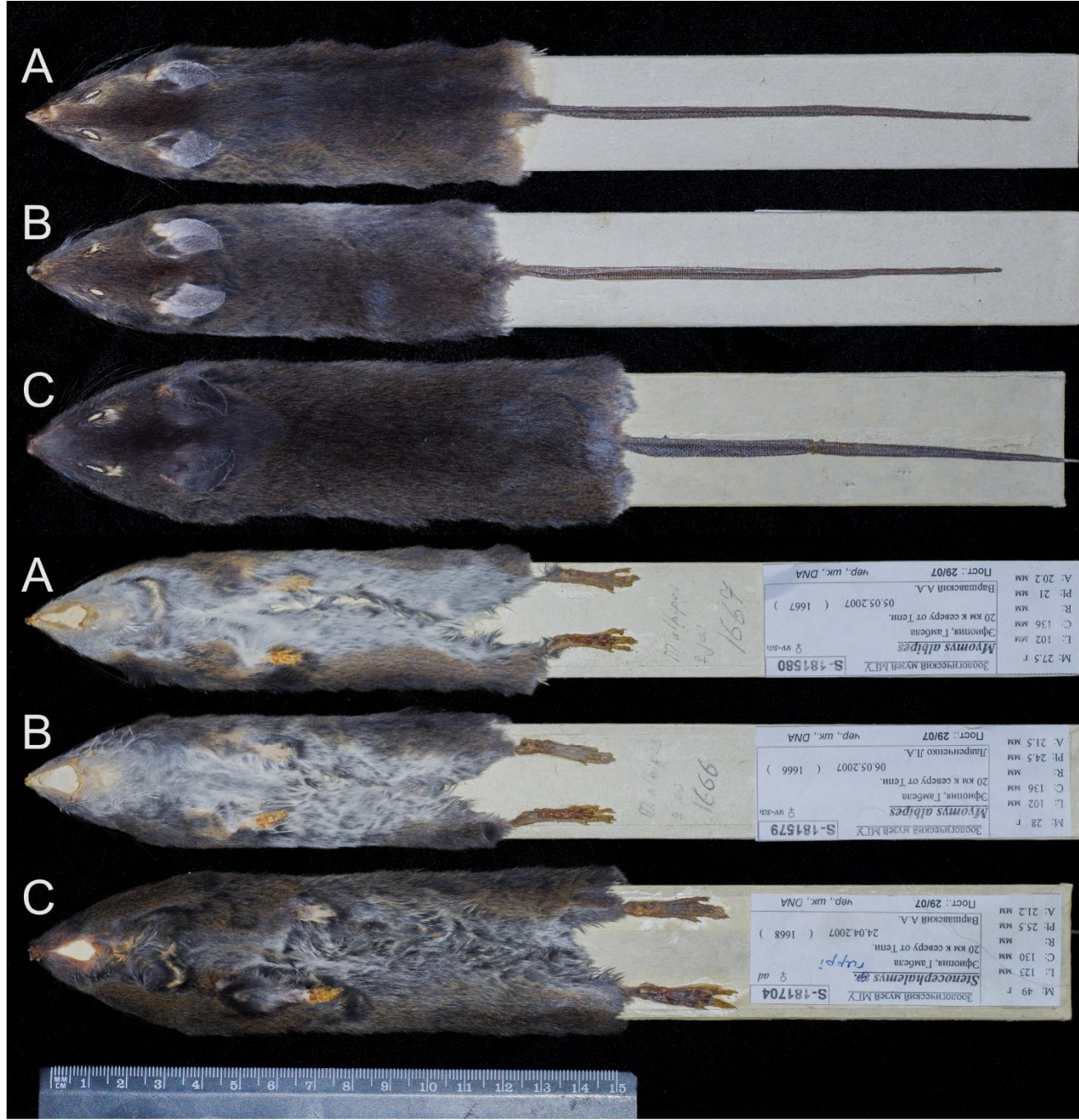


Figure 5



Figure 6



Figure 7



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