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Fossils know it best: Using a new set of fossil calibrations to improve the temporal phylogenetic framework of murid rodents (Rodentia: Muridae)

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1 ***Title***

2 **Fossils know it best: using a new set of fossil calibrations to improve the temporal**
3 **phylogenetic framework of murid rodents (Rodentia: Myomorpha: Muroidea:**
4 **Muridae)**

6 ***Authors***

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24

25 ***Running title:*** Dated phylogeny of Muridae

26 **Abstract**

27 Murid rodents (Rodentia: Myomorpha: Muroidea: Muridae) represent the most diverse and
28 abundant mammalian group. In this study, we reconstruct a dated phylogeny of the family using
29 a multilocus dataset (six nuclear and nine mitochondrial gene fragments) encompassing 160
30 species representing 82 distinct murid genera from four extant subfamilies (Deomyinae,
31 Gerbillinae, Lophiomyinae, and Murinae). In comparison with previous studies on murid or
32 muroid rodents, our work stands out for the implementation of multiple fossil constraints within
33 the Muridae thanks to a thorough review of the fossil record. Before being assigned to specific
34 nodes of the phylogeny, all potential fossil constraints were carefully assessed; they were also
35 subjected to several cross-validation analyses. The resulting phylogeny is consistent with
36 previous phylogenetic studies on murids, and recovers the monophyly of all sampled murid
37 subfamilies and tribes. Based on nine controlled fossil calibrations, our inferred temporal
38 timeframe indicates that the murid family likely originated in the course of the Early Miocene,
39 23.0-16.0 million years ago (Ma), and that most major lineages (i.e. tribes) have started
40 diversifying *ca.* 10 Ma. Historical biogeography analyses support the Paleotropical origin for
41 the family, with an initial internal split (vicariance event) followed by subsequent migrations
42 between Afrotropical and Indomalayan lineages. During the course of their diversification, the
43 biogeographic pattern of murids is marked by several dispersal events toward the Australasian
44 and the Palearctic regions, mostly from the Indomalaya. The Afrotropical region was also
45 secondarily colonized at least three times from the Indomalaya, indicating that the latter region
46 has acted as a major centre of diversification for the family.

47

48 **Keywords**

49 Fossils, historical biogeography, molecular dating, Muridae, *Mus*, *Rattus*

50

51 **1. Introduction**

52 With about 150 genera and more than 730 recognized species, Muridae is the most diverse
53 family of mammals (Musser and Carleton, 2005). Collectively murids have colonized highly
54 distinct ecological niches, adapting to a wide array of environments ranging from warm (deserts
55 or tropical forests) to cold habitats (high altitude mountain ranges, tundra; Vaughan et al.,
56 2011). Life habits in murids are also diverse, as the family encompasses amphibious, arboreal,
57 fossorial, or terrestrial taxa (Michaux et al., 2007; Musser and Carleton, 2005).

58 All murid species are native to the Old World (Musser and Carleton, 2005), but some
59 species (especially the black rat *Rattus rattus* Linnaeus, the Norway rat *Rattus norvegicus*
60 (Berkenhout) and the house mouse *Mus musculus* Linnaeus) now have a worldwide distribution
61 due to commensalism and dissemination by humans. Murid species diversity is especially high
62 in the Australasian and Indomalayan regions which accommodate half of the species diversity
63 of the family (Rowe et al., 2016a). Second to that is the species diversity in the Afrotropical
64 region (more than 200 species; Musser and Carleton, 2005). By contrast, there are much less
65 native murid taxa in the Palearctic region (e.g. *Apodemus* Kaup, *Diplothrix* Thomas, or
66 *Tokudaia* Kuroda).

67 The history of murid systematics is complex and convoluted with numerous changes
68 occurring in the past sixty years (see Table 1 for a summary). Simpson (1945) divided
69 representatives of family Muridae (as currently understood) into two separate families:
70 Cricetidae (with subfamilies Gerbillinae, Lophiomyinae and others) and Muridae (subfamilies
71 Murinae and Otomyinae). Chaline et al. (1977) considered “murid” rodents to belong to four
72 families: Cricetidae (including Lophiomyinae), Gerbillidae, Muridae (exclusively Murinae)
73 and Nesomyidae (including Otomyinae). Lavocat (1978) simplified this classification by
74 recognizing only two families: Muridae (Murinae) and Nesomyidae (in which he included
75 Gerbillinae, Lophiomyinae and Otomyinae). Another major change was later made by Carleton

76 and Musser (1984), who defined family Muridae in the broad sense with no less than 14
77 subfamilies (including Gerbillinae, Lophiomyinae, Murinae and Otomyinae). Following the
78 introduction of molecular systematics, changes in the classification of family Muridae
79 continued at a fast rate. Using molecular phylogenetics Chevret et al. (1993a) demonstrated that
80 *Acomys* I. Geoffroy is not a member of the subfamily Murinae but belongs to a separate
81 monophyletic clade including *Deomys* Thomas, *Lophuromys* Peters and *Uranomys* Dollman.
82 All four genera were assigned to the subfamily Deomyinae, which is closely related to the
83 Gerbillinae. In another study, Chevret et al. (1993b) showed that Otomyinae are closely allied
84 to the tribe Arvicanthini, thus unequivocally constituting a subset of the subfamily Murinae at
85 the tribe level (Ducroz et al., 2001; Jansa and Weksler, 2004). Jansa and Weksler (2004) also
86 strongly suggested that Lophiomyinae belonged to the Muridae. Only part of these proposals
87 was followed by Musser and Carleton (2005) who recognized the following five subfamilies in
88 the family Muridae: Deomyinae, Gerbillinae, Leimacomyinae, Murinae and Otomyinae.
89 Nowadays the most consensual classification agrees on five subfamilies: Deomyinae (four
90 genera and *ca.* 42 species), Gerbillinae (16 genera and *ca.* 103 species), Leimacomyinae (only
91 one species, possibly extinct; Kingdon, 2015), Lophiomyinae (only one species) and Murinae
92 (129 genera and *ca.* 584 species; see the review of Granjon and Montgelard, 2012).

93 Musser and Carleton's (2005) comprehensive catalogue listed 730 species in the family
94 Muridae. Estimates of species diversity in this family are very likely not definitive, as new
95 murid taxa are being regularly described (e.g. Carleton et al., 2015; Esselstyn et al., 2015;
96 Missoup et al., 2016; Mortelliti et al., 2016; Rowe et al., 2016a). Expected and ongoing raise in
97 species number can be accounted for by an increased focus on poorly known regions with high
98 levels of endemism, especially in tropical Asia and Africa. It is also linked with the
99 development of integrative taxonomy studies, where molecular genetic approaches are able to

100 detect taxa and geographical regions with high cryptic diversity (e.g. Bryja et al., 2014, 2017;
101 Ndiaye et al., 2016).

102 Because of the high species richness of the family, determining the precise timing of its
103 radiation is of particular paleobiogeographic interest. Several dated estimates for the age of
104 Muridae are available owing to studies either focusing on the order Rodentia (Adkins et al.,
105 2001, 2003; Fabre et al., 2012; Montgelard et al., 2008), on the superfamily Muroidea
106 (Muroidea; Schenk et al., 2013 ; Stepan et al., 2004) or on various murid subsets (e.g. Bryja
107 et al., 2014; Chevret and Dobigny, 2005; Dobigny et al., 2013; Fabre et al., 2013; Pagès et al.,
108 2016; Rowe et al., 2008, 2011, 2016b). However, no clear consensus could be reached for the
109 age of the family Muridae. Indeed, age estimates derived from all aforementioned studies are
110 far from being congruent, likely because their datasets have not been designed for this particular
111 purpose. In addition, all these studies used very diverse dating procedures, some of them relying
112 on substitution rate calibrations (e.g. Arbogast et al., 2001; Nicolas et al., 2008) whereas others
113 used fixed ages (e.g. the putative *Mus/Rattus* split at 12 Ma; Stepan et al., 2004), very distant
114 fossil constrains (Adkins et al., 2003; Fabre et al., 2012; Montgelard et al., 2008) or primary
115 calibrations using various fossil constraints within or outside the family Muridae (e.g. Bryja et
116 al., 2014; Pagès et al., 2016; Rowe et al., 2016b; Schenk et al., 2013).

117 For fossil-based calibrations of molecular clocks, it is crucial: (i) to properly assign and
118 place fossils on the tree, and (ii) to correctly estimate the age of fossil-bearing formations
119 (Parham et al., 2012; Sauquet et al., 2012). Unfortunately the fossil record of oldest murids is
120 quite fragmentary and mostly consists of isolated teeth and mandible remains, thus sometimes
121 making taxonomic identification difficult. The earliest representatives for the family Muridae
122 include the tribe Myocricetodontini with genera such as †*Myocricetodon* Lavocat, †*Dakkamys*
123 Jaeger and †*Mellalomys* Jaeger (Jacobs and Flynn, 2005; Lazzari et al., 2011). Extinct members
124 of the genus †*Potwarmus* Lindsey could be considered as a stem group of the subfamily

125 Murinae based on detailed analyses of dental morphology (Lazzari et al., 2011; López
126 Antoñanzas, 2009; Wessels, 2009). The earliest unequivocal representative of the subfamily
127 Murinae is the genus †*Antemus* Jacobs (Jacobs and Downs, 1994; Jacobs and Flynn, 2005;
128 Kimura et al., 2015). †*Antemus* possesses a new cusp (anterostyle, also known as t1), which is
129 a synapomorphy of Murinae. The earliest record of †*Antemus chinjiensis* is dated at 13.8 Ma
130 (Jacobs et al., 1990) based on specimens from the locality YGSP 491, Chinji Formation in the
131 Potwar Plateau, Pakistan (Jacobs, 1977). In the fossil record of the Potwar Plateau, two more
132 derived fossil genera are of particular interest: †*Karnimata* Jacobs and †*Progonomys* Schaub.
133 Based on the relative position of the anterostyle to the lingual anterocone on M1, Jacobs (1978)
134 hypothesized that †*Karnimata* is related to *Rattus* and that †*Progonomys* is a member of the
135 lineage including *Mus*. Hence, their first stratigraphic occurrence has been used to define the
136 widely used *Mus/Rattus* calibration (ca. 12 My; Jacobs and Downs, 1994). However, in 2015,
137 Kimura et al. revisited these fossils from a paleontological perspective and proved this
138 calibration point to be controversial. They showed that †*Karnimata* is a member of the
139 Arvicanthini-Millardini-Otomyini clade rather than a member of the lineage encompassing the
140 genus *Rattus* and its relatives (i.e. tribe Rattini). Therefore, they demonstrated that the
141 continuous fossil record of the murine rodents from the Potwar Plateau actually provides a
142 minimum age for the most recent common ancestor of the lineages leading to *Arvicanthis*
143 Lesson and *Mus* (= *Mus/Arvicanthis* split).

144 Recent progresses in divergence dating analyses lead us to revisit results previously
145 obtained by favouring the implementation of a new set of well-justified primary fossil
146 calibrations within a Bayesian framework. In comparison to previous studies (listed above), our
147 study can be considered as medium-sized in terms of taxonomic sampling, and essentially
148 focused on the family Muridae. But our study stands out for rigorous evaluation of the fossil
149 data for this highly diverse mammalian family. The present study has four main objectives: (i)

150 to design a comprehensive multi-marker molecular dataset for the family Muridae, (ii) to review
151 the murid fossil record in order to identify reliable and suitable primary fossil calibrations, (iii)
152 to provide a reliable estimate of the timing of diversification of the family using multiple fossil
153 calibrations, and (iv) to lean on the resulting dated phylogeny to reconstruct the biogeographic
154 history of the family using up-to-date analytical approaches.

155

156 **2. Material and Methods**

157 *2.1. Taxon sampling*

158 For this study, new DNA sequences were generated for five murid species (*Acomys* cf.
159 *cineraceus*, *Acomys subspinosus* (Waterhouse), *Acomys wilsoni* Thomas, *Arvicanthis niloticus*
160 (Desmarest), *Arvicanthis neumanni* (Matschie) see Appendix A). Though we largely relied on
161 GenBank data for this work, it is worth underlining that our research group generated thousands
162 of murid sequences (all deposited in GenBank) in the past 15 years (we used some of these
163 sequences for 44 species included in this study). In total, our dataset (Appendix A) encompasses
164 160 murid species representing 82 of the 151 known murid genera. All four extant subfamilies
165 (if considering the Togo mouse from Leimacomyinae to be extinct) of Muridae are included.
166 For the largest subfamily Murinae, we included representatives of all 10 tribes that have been
167 defined by Lecompte et al. (2008): Apodemini, Arvicanthini, Hydromyini, Malacomyini,
168 Millardini, Murini, Otomyini, Phloeomyini, Praomyini and Rattini. As outgroup taxa, we
169 selected five species of the family Cricetidae (from subfamilies Arvicolinae, Cricetinae,
170 Neotomyinae and Tylomyinae), which constitutes the sister group of Muridae (Fabre et al.,
171 2012). Finally, the tree was rooted using *Calomyscus baluchi* Thomas, a representative of the
172 more distant family Calomyscidae (Fabre et al., 2012). All species names followed Musser and
173 Carleton (2005) and Monadjem et al. (2015).

174

175 2.2. DNA extraction, sequencing and molecular matrix

176 DNA was extracted using a Qiagen[®] DNeasy Blood and Tissue kit (Qiagen, Hilden,
177 Germany) following the manufacturer's instructions. Two nuclear gene fragments were
178 targeted using the following combinations of polymerase chain reactions (PCR) primers:
179 IRBP217 and IRBP1531 (Stanhope et al., 1992) for the fragment of the 'interphotoreceptor
180 retinoid binding' (IRBP) gene; RAG1F1705 and RAG1R2951 (Teeling et al., 2000) for a
181 fragment of the 'recombination activating gene 1' (RAG1) gene. For PCR protocols, see Bryja
182 et al. (2017) and Teeling et al. (2000), respectively. PCR products were Sanger sequenced in
183 both directions using the BigDye[®] Terminator chemistry (Thermo Fisher Scientific) either in
184 the Institute of Vertebrate Biology on an 'Applied Biosystems[®] 3130xl Genetic Analyzer', or
185 commercially through the GATC Biotech company (Konstanz, Germany). New sequences were
186 deposited in GenBank under accession numbers KY634246 to KY634250.

187 The newly generated sequences were further combined with data from GenBank. The
188 resulting matrix (see Appendix A) encompasses the following six nuclear and nine
189 mitochondrial gene fragments: 'acid phosphatase 5' (AP5), BRCA1, intronic portion of
190 'Peripheral benzodiazapine receptor variant' (BZRP), 'growth hormone receptor' (GHR), IRBP
191 and RAG1, for the nuclear genes, and '12S ribosomal RNA' (12S), '16S ribosomal RNA'
192 (16S), 'ATP synthase 8' (ATPase8), 'cytochrome c oxidase I' (COI), 'cytochrome oxidase II'
193 (COII), 'cytochrome *b*' (Cytb), 'Aspartic acid transfer RNA' (tRNA-Asp), 'Lysine transfer
194 RNA' (tRNA-Lys), 'Serine transfer RNA' (tRNA-Ser), for the mitochondrial genes. For nine
195 taxa (*Acomys* cf. *cineraceus*, *Acomys wilsoni* Thomas, *Aethomys chrysophilus* (de Winton),
196 *Aethomys hindei* (Thomas), *Aethomys kaiseri* (Noack), *Aethomys silindensis* Roberts,
197 *Arvicanthis nairobae* J.A. Allen, *Arvicanthis neumanni* and *Thallomys paedulus* (Sundevall),
198 gene fragments were concatenated from two individuals to minimize the amount of missing
199 data. For all protein-coding genes, we used Mesquite 3.2 (Maddison and Maddison, 2007) to

200 check the coding frame for possible errors or stop codons. The sequences of several markers
201 (i.e. 12S, 16S, intronic portion of BZRP, tRNA-Asp, tRNA-Lys and tRNA-Ser) were variable
202 in length; their alignment was accomplished using MUSCLE (Edgar, 2004) with default
203 settings.

204

205 *2.3. Phylogenetic analyses*

206 Phylogenetic analyses were conducted using both Bayesian inference (BI) and
207 maximum likelihood (ML). Analyses were performed on the online computer cluster CIPRES
208 Science Gateway (Miller et al., 2010; www.phylo.org) and on the high performance computing
209 (HPC) cluster hosted in the Centre de Biologie pour la Gestion des Populations (CBGP) in
210 Montferrier-sur-Lez, France. For both phylogenetic analytical approaches, we carried out
211 partitioned analyses to improve phylogenetic accuracy (Nylander et al., 2004). The molecular
212 dataset was divided *a priori* into 33 partitions: we used three partitions for each of the protein-
213 coding genes (AP5, ATPase8, BRCA1, COI, COII, Cytb, GHR, IRBP and RAG1) and one
214 partition for each of the rRNA-tRNA genes (12S, 16S, tRNA-Asp, tRNA-Lys and tRNA-Ser)
215 as well as the BZRP intronic portion. The best partitioning scheme and substitution models
216 were determined with PartitionFinder 1.1.1 (Lanfear et al., 2014) using a greedy heuristic
217 algorithm; because of the risk of over-parameterization associated with the high number of
218 specified partitions, the ‘unlinked branch lengths’ option was chosen over the ‘linked branch
219 lengths’ option. The Bayesian information criterion (BIC) was also preferentially used to
220 compare partitioning schemes and substitution models following the recommendation of
221 Ripplinger and Sullivan (2008).

222 PartitionFinder (based on BIC) identified the same three partitions for both BI and ML
223 analyses: two partitions are associated with a Generalized-Time-Reversible (GTR + Γ +I) model

224 and one partition is associated with a Hasegawa-Kishino-Yano (HKY + Γ +I) model (see Table
225 2).

226 Bayesian inference analyses were carried out using MrBayes v3.2.6 (Ronquist et al.,
227 2012b). Two independent runs with four MCMC (one cold and three incrementally heated
228 chains) were conducted: they ran for 50 million generations, with trees sampled every 1,000
229 generations. A conservative 25% burn-in was applied after checking for stability on the log-
230 likelihood curves and the split-frequencies of the runs. Support of nodes for MrBayes analyses
231 was provided by clade posterior probabilities (PP) as directly estimated from the majority-rule
232 consensus topology. Following Erixon et al. (2003), nodes supported by $PP \geq 0.95$ were
233 considered strongly supported.

234 Maximum likelihood analyses were performed using RAxML v8.2.8 (Stamatakis, 2014).
235 Because this software does not allow simpler substitution models, we used three partitions with
236 a General Time Reversible (GTR + Γ +I) model (see Table 2). The best ML tree was obtained
237 using heuristic searches with 100 random addition replicates. Clade support was then assessed
238 using a non-parametric bootstrap procedure with 1,000 replicates. Following Hillis and Bull
239 (1993), nodes supported by bootstrap values (BV) ≥ 70 were considered strongly supported.

240

241 *2.4. Evaluation of suitable fossil calibrations*

242 Following the recommended criteria of Parham et al. (2012) for fossil calibrations, we
243 rigorously compiled a list of potential candidates from the paleontological literature and
244 eventually retained 18 candidate fossils (see Table 3). The candidate fossils possess the
245 information for the collection site, unique identification number, and the state of preservation
246 along with justification for the age of the fossil (i.e., age of fossil-bearing formation and
247 stratigraphic level, preferably with an absolute age by radiometric dating and/or reliable relative
248 age estimates, for example, by magnetostratigraphy).

249 In the next step, diagnostic morphological characters were reassessed to determine
250 whether they could be reliably used as minimum age constraints in our phylogeny, either as
251 crown or stem calibrations. Seven fossils were discarded following this step (see the ‘Results’
252 section).

253 For the remaining 11 fossils, we used the cross-validation procedure developed by Near
254 and Sanderson (2004) and Near et al. (2005). The following approach was used: (i) we
255 identified potential inconsistencies within the 11 remaining fossil calibrations, and (ii) we
256 explored the impact of the inclusion of each of these fossils on our divergence time estimates.
257 Each of the 11 fossil constraints was enforced at a time in a specific Bayesian relaxed-clock
258 (BRC) analysis to estimate the ages of the remaining nodes (see also section 2.5). First, the sum
259 of the squared differences between the molecular and fossil age estimates (SS) was calculated
260 (for more details see Near and Sanderson, 2004). All calibration points were then ranked based
261 on the magnitude of its SS score; here the fossil with the greatest SS score is assumed to be the
262 most inconsistent with respect to all other fossils in the analysis (Near and Sanderson, 2004).
263 Second, we calculated the average squared deviation, s , for all fossil calibrations in the analysis.
264 Following the method of Near et al. (2005), we removed the fossil with the greatest SS score
265 and recalculated s with the remaining fossil calibration points. This process was pursued until
266 only the two fossil calibration points with the lowest and second lowest magnitudes of SS
267 remained (Near and Sanderson, 2004). The rationale behind this procedure is to assess whether
268 calibration points are approximately equally informative and accurate (Near et al., 2005): if it
269 is the case the magnitude of s should only decrease by a small fraction whenever a fossil
270 calibration is removed.

271

272 *2.5. Bayesian relaxed-clock analyses*

273 Although divergence time dating is now a well-established cornerstone of evolutionary
274 biology, there is still no widely accepted objective methodology for converting data from the
275 fossil record to calibration information of use in molecular phylogenies (Drummond and
276 Bouckaert, 2015). In the last few years, several methodological approaches to better implement
277 fossil calibrations have been developed, for instance allowing one to directly include fossil
278 lineages in phylogenies ('total-evidence dating'; Pyron, 2010; Ronquist et al. 2012a) or to
279 account for information on the density of the fossil record ('fossilized birth-death (FBD)
280 process'; Stadler, 2010; Heath et al., 2014). However, for our study, a 'total evidence dating'
281 approach was not applicable since it would have required the coding of a morphological matrix
282 for both fossils and extant taxa, which is problematic given the fragmentary nature of murid
283 fossils. The use of the FBD methodology was also not envisioned because the fossil record of
284 murid rodents is too sparse. Instead, we relied on a node-dating approach in which fossil
285 information is enforced on specific nodes through the use of parametric distributions.

286 Following our assessment of the murid fossil record and the results of cross-validation
287 analyses, nine fossil calibrations were finally retained for the dating procedure (for more
288 information, see Tables 3 and 4, and Appendix B). Five of them were defined based on fossil
289 material collected in the Siwalik Group of Pakistan (†*Antemus chinjiensis*, †*Karnimata darwini*
290 Jacobs, †cf. *Karnimata* sp., †*Mus* sp. and †*Abudhabia pakistanensis* Flynn and Jacobs). Three
291 additional accepted fossils originate from 6.1 Ma fossils discovered in the Lemudong'o locality
292 in Kenya (†*Aethomys* sp., †*Arvicanthis* sp. and †*Gerbilliscus* sp.), and the last retained fossil
293 calibration constraint is defined by the 9.6 Ma fossil of †*Parapodemus lungdunensis* Schaub.
294 Priors for fossil constraints were defined by using either uniform or lognormal statistical
295 distributions in two separate analyses. Statistical distributions were bounded by the minimum
296 ages provided by the fossil constraints and a conservative maximum age (*ca.* 25 Ma) for the
297 root derived from the study of Schenk et al. (2013; see Table 4). In a preliminary way (see

298 section 2.4 of the Material and Methods), BRC analyses were also conducted using one fossil
299 constraint at a time to carry out cross-validation analyses.

300 Bayesian relaxed-clock analyses were conducted with BEAST v1.8.4 (Drummond et al.,
301 2012) using uncorrelated lognormal relaxed clocks (Drummond et al., 2006). To limit the risk
302 of over-parameterization: (i) we used three clock models (based on PartitionFinder results,
303 Table 2); and (ii) we enforced a guide tree that corresponds to the topology with the best clade
304 support (this topology corresponds to the topology obtained with MrBayes; see the ‘Results’
305 section). For the tree speciation model, a birth death process (Gernhard, 2008) was used in order
306 to better account for extinct and missing lineages.

307 BEAST .xml files were modified to implement the path-sampling procedure for Bayes
308 factor (B_F) estimation following the recommendations of Baele et al. (2013). Out of the two
309 calibrations, the calibration procedure with lognormal prior has the best harmonic mean (-
310 208117.74 *versus* -208262.58 for the procedure with a uniform prior) and is recovered as the
311 best-fit calibration procedure with a statistically significant B_F of 289.68 ($B_F > 10$, Kass and
312 Raftery, 1995). The final analysis (with nine verified fossil constraints and lognormal prior
313 distribution for calibration constraints) was carried out by two independent runs each with 50
314 million generations and trees sampled every 5,000 generations. We used a conservative burn-
315 in of 12.5 million generations per run. Post burn-in trees from both analyses were further
316 combined using the LogCombiner module of BEAST. Convergence of runs was assessed
317 graphically under Tracer v.1.6 and by examining the ESS of parameters.

318

319 *2.6. Historical biogeography*

320 Ancestral biogeography was reconstructed using the R package ‘BioGeoBEARS’
321 (Matzke, 2013). Data for species’ ranges were obtained from the International Union for
322 Conservation of Nature website (<https://www.iucn.org/>). Five major biogeographic areas were

323 defined on the basis of Olson et al. (2001): A, West Palearctic (from Western Europe to the
324 Ural Mountains, including North Africa); B, East Palearctic (from the Urals to Japan); C,
325 Indomalaya (from Afghanistan through the Indian subcontinent and Southeast Asia to lowland
326 southern China, and through Indonesia as far as Java, Bali, and Borneo, west of the Wallace
327 line); D, Australasia (Australia, New-Zealand, Papua-New-Guinea and neighbouring small
328 islands); E, Afrotropics (Africa, northern part excluded). Dispersal rate between adjacent areas
329 was fixed to 1 (A-B; B-C), whereas the dispersal of 0.7 (A-E; C-D) and 0.3 (B-D; B-E) was
330 specified for long-distance dispersal or whenever a geographical barrier had to be crossed.
331 Dispersal was disallowed between geographical areas separated by two or more areas (A-D; D-
332 E). Six models of geographic range evolution were compared in a likelihood framework: (i)
333 Dispersal-Extinction Cladogenesis model (DEC) similar to Lagrange (Ree and Smith, 2008),
334 which parameterizes dispersal and extinction; (ii) DEC +J model (Matzke, 2013; 2014), which
335 adds founder-event speciation with long-distance dispersal (cladogenesis, where daughter
336 lineage is allowed to jump to a new range outside the range of the ancestor; Matzke, 2013) to
337 the DEC framework; (iii) Dispersal Vicariance Analysis (DIVA; Ronquist, 1997); (iv) DIVA
338 with long-distance dispersal (DIVA +J; Matzke, 2013); (v) Bayesian inference of historical
339 biogeography for discrete areas (BayArea; Landis et al., 2013); and (vi) BayArea with long-
340 distance dispersal (BayArea +J; Matzke, 2013). Model fit was assessed using the Akaike
341 information criterion (AIC) and likelihood-ratio tests (LRT).

342

343 **3. Results**

344 *3.1. Phylogeny of Muridae*

345 Our multilocus dataset representing all major lineages of the family Muridae is 10,482 bp
346 long with 42.5% missing data. Both BI and ML analyses yield similar topologies (see Fig. 1 for
347 the topology inferred under BI, and Fig. S1 in Appendix D for the best-fit ML tree), as indicated

348 by a high proportion of shared nodes (160 out of 162). BI and ML analyses differ only in the
349 position of *Pelomys fallax* (Peters) and *Zyzomys argurus* (Thomas), but their placements are
350 not significantly supported in either analysis. Clade support is moderate to high on average; if
351 considering the number of nodes that are supported by $PP \geq 0.95$ or $BV \geq 70\%$, BI analyses
352 yield a slightly more robust topology (135 well-supported nodes) compared to the ML tree (122
353 well-supported nodes).

354 Phylogenetic analyses confirm the monophyly of the family Muridae, of all its four
355 constituent subfamilies, as well as of the previously defined tribes of the subfamily Murinae
356 (Fig. 1). On the contrary, the phylogenetic position of some genera (e.g. *Acomys* I. Geoffroy,
357 *Dasymys* Peters, *Golunda* Gray, *Melomys* Thomas, *Micaelamys* Ellerman, *Pelomys* Peters,
358 *Oenomys* Thomas and *Otomys* F. Cuvier) within particular tribes was only partly supported.

359

360 3.2. Evaluation of suitable fossil calibrations

361 We summarized all fossils considered in this study in Table 3 and Appendix B regarding
362 taxonomic information and specification for prior settings (see also Figure 2 for their respective
363 positions within the tree). Five out of 18 preselected fossils (i.e. †*Parapelomys robertsi* Jacobs,
364 †*Potwarmus primitivus*, †*Preacomys kikiae* Geraads, †cf. *Progonomys* sp. Schaub and †aff.
365 *Stenocephalomys* Frick) were excluded from further analyses because the scarcity of
366 paleontological interpretation about their phylogenetic relationships impeded assigning them to
367 specific nodes of the phylogeny (Appendix B). We also excluded fossils of *Acomys* and
368 *Lemniscomys* Trouessart from the Lemudong'O locality, Kenya (Manthi, 2007), because first
369 upper molars, which possess the most diagnostic characters in the murine dentition, are not
370 described from the locality (Table 3; see more details also in Appendix B). The two-step cross-
371 validation procedure resulted in a further reduction of the fossil set of possible calibration
372 points. Specifically, we excluded two fossils: one is a 2.4 Ma fossil identified as the genus

373 *Gerbillus* Desmarest, while the other one corresponds to a 6.1 Ma fossil identified as the genus
374 *Mastomys* Thomas (Appendix C). The rationale is that (i) these two fossil calibrations exhibited
375 the largest magnitude of SS, and that (ii) their removal also resulted in a very high (fivefold)
376 decrease in s (see Appendix C for more details). As a result of the latter series of selection steps,
377 nine fossils were finally retained for divergence dating (see Figure 2 for their position on the
378 tree, Table 4 for specification of priors, and Appendix B for more details on all considered
379 fossils).

380

381 *3.3 Historical biogeography and divergence dating*

382 Among the six models of geographic-range evolution compared in a likelihood
383 framework in BioGeoBEARS, the Dispersal-Extinction Cladogenesis model with founder-
384 event speciation (DEC +J) was chosen because of its best likelihood and AICc associated scores
385 ($\ln L = -117.1$, $AICc = 240.4$; Table 5).

386 The dated tree resulting from the BRC analyses is shown in Figure 2 while dating
387 estimates for all internal nodes are provided in Table 6, and results of ancestral distribution
388 reconstructions are presented in Figure 3. The most recent common ancestor (MRCA) of
389 Muridae originated during the early Miocene (median age of 19.3 Ma; 95% highest posterior
390 density (HPD): 17.06-21.92 Ma) in the Afrotropical and Indomalayan bioregions.

391 Three subfamilies (Deomyinae, Gerbillinae and Lophiomyinae) belonging to the same
392 clade started their diversification in the Afrotropics. Within this clade, a first split occurred *ca.*
393 18.6 Ma (95% HPD: 16.35-21.11 Ma) between the Lophiomyinae and the clade encompassing
394 the Deomyinae and Gerbillinae. Deomyinae started their diversification *ca.* 14.6 Ma (95%
395 HPD: 12.68-16.82 Ma) while Gerbillinae started theirs *ca.* 12.2 Ma (95% HPD: 10.46-14.16
396 Ma). In Deomyinae and Gerbillinae, several lineages were able to colonize the Palearctic region

397 from the Afrotropics (in our dataset, this concerns *Acomys russatus* (Wagner) and *Gerbillus*
398 *gerbillus* Olivier).

399 The subfamily Murinae originated in the Indomalayan region during the middle Miocene
400 (median age of 14.2 Ma; 95% HPD: 12.70-16.07 Ma); the corresponding basal split separated
401 the Phloeomyini and all remaining murines ('core murines' *sensu* Steppan et al. 2005). The
402 next major split occurred in the Indomalaya between Rattini and the remaining tribes of
403 Murinae (median age of 12.3 Ma; 95% HPD: 11.28-13.62 Ma), with an origin of Rattini
404 estimated at 10.4 Ma (95% HPD: 9.23-11.93 Ma). The ancestral area of Rattini was also
405 inferred to be the Indomalaya; during the course of their diversification, a few taxa colonized
406 Australasia (e.g. *Bunomys andrewsi* (J.A. Allen), *Melasmothrix naso* Miller and Hollister,
407 *Paruromys dominator* Thomas and *Rattus leucopus* (Gray)) as well as the West and East
408 Palearctic (e.g. *Micromys minutus* (Pallas) and *Diplothrix legata* (Thomas)). The Hydromyini
409 split from the remaining Murinae at *ca.* 11.9 Ma (95% HPD: 10.95-13.10 Ma); although basal
410 lineages of this tribe are currently found in the Indomalaya (e.g. *Archboldomys luzonensis*
411 Musser, *Apomys datae* (Meyer), *Apomys hylocoetes* Mearns, *Chrotomys gonzalesi* Rickart and
412 Heaney, *Chiropodomys gliroides* (Blyth) and *Rhynchomys isarogensis* Musser and Freeman),
413 a specific and diverse lineage of Hydromyini also colonized and radiated in the Australasia *ca.*
414 8.1 Ma (95% HPD: 7.22-9.09 Ma). The clade gathering Apodemini, Malacomyini, Murini and
415 Praomyini likely originated in the Afrotropics, with several lineages secondarily colonizing the
416 Indomalaya and the West and East Palearctic. The split between Malacomyini (which remained
417 in the Afrotropics) and Apodemini (which dispersed and differentiated mainly in the West and
418 East Palearctic) is estimated at *ca.* 10.2 Ma (95% HPD: 9.33-11.39 Ma). Murini started to
419 diversify in the Indomalaya at *ca.* 7.2 Ma (95% HPD: 6.24-9.29 Ma). The intense radiation (51
420 extant species, Monadjem et al., 2015) of Praomyini occurred in the Afrotropics (median age
421 of 6.8 Ma for the MRCA of Praomyini; 95% HPD: 6.06-7.77 Ma). The Indomalayan Millardini

422 split from the predominantly Afrotropical Arvicanthini + Otomyini tribes at *ca.* 10.8 Ma (95%
423 HPD: 9.88-12.04 Ma). The respective first diversifications within Arvicanthini, Millardini and
424 Otomyini are estimated at *ca.* 8.8 Ma (95% HPD: 7.92-9.72 Ma), 9.2 Ma (95% HPD: 7.72-
425 10.75 Ma) and 4.9 Ma (95% HPD: 4.12-5.98 Ma), respectively. The position of Asian *Golunda*
426 within Arvicanthini is not resolved (Fig. 1); the dispersal to Indomalaya of the lineage leading
427 to the extant *Golunda* species at *ca.* 8.5 Ma (95% HPD: 7.33-9.57 Ma; as suggested in Fig. 3)
428 should therefore be taken with caution.

429 **4. Discussion**

430 *4.1. Selection of taxa and molecular markers*

431 Our sampling of 160 species from 82 genera represents 22% of known murid species
432 diversity and more than half of the generic diversity of the family Muridae. When one compares
433 our sampling effort to previous studies (Table 7), only the study of Fabre et al. (2012) relied on
434 a better sampling for the family Muridae (302 species from 105 genera, i.e. about 41% of known
435 species diversity). In the study of Schenk et al. (2013), 18% of murid species are included. The
436 number of sampled murid species is also lower in Lecompte et al. (2008) and Rowe et al. (2008)
437 because their studies focussed on specific tribes and subfamilies.

438

439 *4.2. Calibration of molecular clock and divergence dating*

440 Using the classical *Mus/Rattus* calibration as prior for divergence dating often lead to an
441 underestimation of the age of the subfamily Murinae, inferring median ages that are generally
442 comprised between 13.3 to 12.0 Ma. Only the most recent studies (e.g. Rowe et al., 2016b) used
443 the correct *Mus/Arvicanthis* calibration with a prior median age of 11.1 Ma (as suggested by
444 Kimura et al., 2015). This resulted in the estimation of Murinae age of *ca.* 14.0 Ma (Rowe et
445 al., 2016b), which is consistent with our study (Table 6).

446 Other fossils frequently used for molecular clock calibration are from the genus
447 †*Parapodemus*. Recent studies used these fossils in two ways: the first occurrence of
448 †*Parapodemus* sp. (Martín-Suárez and Mein, 1998) in the late Miocene in Europe (Lungu,
449 1981; see Appendix B) was used to calibrate the MRCA of ‘Apodemurini’ (representing the
450 split between Apodemini+Malacomyini and Murini+Praomyini; Fabre et al., 2013; Rowe et al.,
451 2011). Another calibration point is based on the discovery of †*Parapodemus pasquierae*
452 Aguilar and Michaux, from ‘Lo Fournas 6’ site (Roussillon, France). Authors postulated that
453 the latter species and the smaller †*Parapodemus lugdunensis* co-occurred during the same time
454 period ‘MN10’ (Aguilar et al., 1999; Montuire et al., 2006), dated approximately at 9.7 Ma
455 (Mein, 2003). Michaux et al. (2002) considered the differences between these two species as
456 representative of the split between the large *Apodemus mystacinus* Danford and Alston and all
457 smaller *Apodemus* species from the subgenus *Sylvaemus*, but they used a younger age of 7.0
458 Ma as a prior for their divergence. Numerous authors followed this calibration (e.g. Bryja et al.,
459 2014; Fabre et al., 2013; Lecompte et al., 2008; Schenk et al., 2013) even if there is no clear
460 rationale for it. The estimated dates of MRCA of Apodemini range from 7.5 Ma (Rowe et al.
461 2016b; Schenk et al., 2013) to 9.6 Ma (Bryja et al., 2014; Michaux et al., 2002; Lecompte et
462 al., 2008). In our study, we conservatively used the †*Parapodemus lugdunensis* fossil as a stem
463 constraint for Apodemini and this placement resulted in an estimation of their MRCA at 9.0 Ma
464 (95% HPD: 7.92-10.13 Ma).

465 There are several localities in Africa (e.g. Lukeino Formation, Winkler, 2002;
466 Lemudong’o, Ambrose et al., 2007; Manthi, 2007) where fossil representatives of *Arvicanthis*
467 were identified. These fossils were used for molecular clock calibration in several studies with
468 a prior MRCA for the genus at 6.1 Ma (e.g. Fabre et al., 2013; Rowe et al., 2011). The fossils
469 from Lemudong’o were also used, in a less conservative way, by Bryja et al. (2014): based on
470 early records of †*Otomys* sp. (ca. 5.0 Ma; Denys, 1990), †*Aethomys* sp., †*Arvicanthis* sp.,

471 †*Lemniscomys* sp. (from Lemudong' o = 6.1 Ma; Ambrose et al., 2007; Manthi et al., 2007) and
472 other relevant samples where these and related genera were absent (9.50-10.50 Ma; Mein et al.
473 2004), they set the split between Arvicanthini and Otomyini within 6.08-9.54 Ma. This
474 calibration resulted in an estimation of the MRCA for the tribe Arvicanthini at 7.8 Ma (Bryja
475 et al., 2014), which is about 1 million year younger than our own estimate (Table 6). Rowe et
476 al. (2016b) used as minimum age 8.7 Ma for the split between *Arvicanthis* and *Otomys* based
477 on the study of Kimura et al. (2015) that set minimum and maximum ages for locality Y388,
478 where †*Karnimata darwini* was found. This calibration resulted in an estimated MRCA of
479 Arvicanthini at 8.5 Ma. In our study, we instead used the age of an older locality (Y182; median
480 age of 9.2 Ma) where †*Karnimata darwini* was also found (Jacobs, 1978; Kimura et al., 2015),
481 in order to set a crown calibration for the Arvicanthini/Millardini/Otomyini clade. This
482 placement resulted in an estimation of their MRCA at 8.8 Ma (95% HPD: 7.92-9.72 Ma) (Table
483 6).

484

485 4.3. Historical biogeography with focus on faunal exchanges between the Afrotropics and 486 the Indomalaya

487 Our study could not resolve the origin of murid rodents, but it was either in the Afrotropics
488 or in the Indomalaya. Our inferred ancestral tropical range for the MRCA of murids is consistent
489 with the fact that most extant murid taxa are still distributed in warm and moist tropical areas.
490 During the Early Miocene (23.0-16.0 Ma), the rotation of Africa and Arabia, and finally the
491 collision with Eurasia formed a landbridge between Africa and Eurasia (the so-called
492 'Gomphotherium landbridge'; Rögl, 1999). During this time period, early murids colonized
493 both geographical regions. The subsequent reopening of the Mediterranean-Indo-Pacific
494 seaway ('Indo-Pacific recurrence'; Rögl, 1999) separated Africa from Eurasia again, thus
495 giving rise to the main clades of Afrotropics and Indomalaya rodents. Three subfamilies,

496 Deomyinae, Gerbillinae and Lophiomyinae, then likely diversified in the Afrotropics (Chevret
497 and Dobigny, 2005; Ndiaye et al., 2016; Schenk et al., 2013, this study; Figure 3). This
498 hypothesis is supported by paleontological records since the oldest fossils tied to these
499 subfamilies were found in the Afrotropics (e.g. late Miocene *Acomys*, *Gerbilliscus*, *Lophiomyis*
500 and †*Preacomys* from East Africa; Winkler et al. 2010 and references therein). The subfamily
501 Murinae started to diversify in Indomalaya, most probably in Southeast Asia, where we can
502 also find the hitherto highest phylogenetic diversity, including the oldest offshoots of this clade
503 (e.g. the ancestor of Phloeomyini probably lived in the Philippines, those of Rattini and
504 Hydromyini in South-east Asia, etc.; Fabre et al., 2013).

505 During the Middle Miocene (16.0-11.6 Ma), the Mediterranean-Indo-Pacific seaway
506 closed again at the beginning of the Serravallian *ca.* 13.8 Ma ('Parathethys Salinity Crisis';
507 Rögl, 1999), co-incidentally with a global cooling that caused vegetation shifts and a general
508 aridification (Prista et al., 2015). The newly formed landbridge (Rögl, 1999) allowed repeated
509 dispersals of murine rodents from Asia to both Africa and Eurasia. Murine fossil records
510 provide clear evidence for connections between the Indomalaya, the Palearctic, and the
511 Afrotropics. Among them, there are two conspicuous examples: (i) †*Progonomys* was recorded
512 in many Indomalayan Middle Miocene localities (Jacobs and Flynn, 2005) as well as in the
513 Palearctic region (Algeria: Wessels, 2009; China: Qiu et al., 2004; Egypt: Heissig, 1982;
514 France: Mein et al., 1993; Spain: Weerd, 1976); and (ii) the oldest records of †*Parapelomys*
515 spp. were found synchronously in Africa (8.5 Ma; Chorora, Ethiopia; Geraads, 2001) and in
516 Pakistan (*ca.* 8.0 Ma; Jacobs and Flynn, 2005). During this period, representatives of several
517 murine tribes occurred in the Afrotropics (Arvicanthini, Malacomyini, Otomyini and
518 Praomyini) and the Indomalaya (Millardini, Murini, Rattini, and basal lineages of Hydromyini).

519 The last faunal interchange of murid taxa between Africa, Asia and Western Palearctic
520 (Benammi et al., 1996; Sabatier, 1982; Sen, 1977, 1983; Winkler, 2002) is coincident with

521 Messinian Salinity Crisis *ca.* 6 Ma during the Late Miocene (Hsü et al., 1973, 1978). During
522 this period of global sea level depression (Haq et al., 1987) Africa and Arabia were reconnected
523 through Neguev-Sinai landbridge ('Levantine corridor', Fernandes et al., 2006) and landbridge
524 in the Bab-el-Mandeb (Bosworth et al., 2005). In murids, evidence to support this faunal
525 exchange can be found in the African subgenus *Nannomys* (genus *Mus*), which colonized
526 Afrotropics and started there its radiation *ca.* 5.2 Ma (Bryja et al., 2014). A possible example
527 for an opposite west-to-east migration is the genus *Golunda*, which belongs to the Arvicanthini
528 tribe. In a predominantly Afrotropical clade, *Golunda* is the only genus that occurs in the
529 Indomalaya, probably since the end of Miocene (Ducroz et al., 2001; Fig. 3). However, one
530 should be cautious with this scenario since the position of *Golunda* within Arvicanthini is not
531 well supported (Fig. 1). Africa-to-Asia dispersals at the Miocene/Pliocene boundary have been
532 also recorded in other taxa, such as rodents (e.g. *Myomyscus yemeni* (Sanborn and Hoogstraal);
533 our unpubl. data), reptiles (e.g. *Varanus yemenensis*: Böhme et al., 2003, Portik and Papenfuss
534 2012; *Hemidactylus* geckos: Šmíd et al. 2013; *Echis* vipers: Pook et al. 2009) and hamadryas
535 baboons (Winney et al. 2004).

536

537 **5. Conclusion and perspectives**

538 In this study, we provided an improved multilocus dated phylogeny for the highly
539 speciose family Muridae. Both our dating and historical biogeography analyses suggest that the
540 family originated during the Early Miocene, and subsequently gave rise to four extant
541 subfamilies: three in the Afrotropical region (Deomyinae, Gerbillinae and Lophiomyinae) and
542 one in the Indomalaya (Murinae). Our study also supports a dynamic biogeographic scenario
543 in which repeated colonisation events occurred in the Australasian (Hydromyini, Rattini),
544 Afrotropical (Malacomyini, Praomyini, Arvicanthini, Otomyini) and Palearctic (Apodemini)
545 regions. One of the strong aspects of this study lies in the assessment and treatment of fossil

546 data (Appendix B); such data is likely to be useful for further studies investigating the timing
547 of diversification of rodents, or even mammals in general. For an easy access to all
548 corresponding fossil records, we have made data available on the Date-a-Clade Website
549 (<http://palaeo.gly.bris.ac.uk/fossilrecord2/dateaclade/index.html>), Paleobiology Database
550 (<http://fossilworks.org/>) and TimeTree Database (<http://timetree.org>).

551

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564

565 **Authors' contributions:** GJK, GD, LG, JB conceived the ideas; TA collected genetic
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567 GJK performed phylogenetic analyses; TA, JB, GJK wrote the first version of the manuscript
568 that was then implemented by all authors.

569

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923 **Figure titles**

924 **Figure 1.** Molecular phylogeny of family Muridae based on Bayesian inference (BI) in
925 MrBayes. Very similar topology was obtained also by maximum likelihood (ML)
926 analysis in RAxML (see Appendix D). Red points show nodes supported in BI
927 analysis (posterior probability $PP \geq 0.95$), blue points show high bootstrap support
928 in ML analysis (bootstrap $BV \geq 0.70$). Violet nodes are supported by both analyses.

929 **Figure 2.** Divergence dating analysis of family Muridae. Nodes show medians of times to most
930 recent common ancestor (MRCA), node bars indicate 95% HPD intervals. Latin
931 numbers in yellow squares indicate positions of fossil constrains selected by
932 multiple-step evaluation and used for final analysis (see Table 4 for more details).

933 **Figure 3.** Ancestral reconstruction for family Muridae with BioGeoBEARS (DEC+J; $d=0.008$;
934 $e=0$; $j=0.0246$; $\text{LnL}=-117.11$). Five biogeographical areas are represented using
935 different colours: A, West Palearctic (dark blue); B, East Palearctic (light blue); C,
936 Indomalaya (green); D, Australasia (yellow); E, Afrotropics (red).

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940 **Tables:**

941 **Table 1:** Brief summary of taxonomic changes in the family Muridae. The taxonomic position
942 of particular lineages has changed significantly and they were either considered as
943 separate families, or included in other families outside Muridae (names of families
944 are in bold).

945 **Table 2:** PartitionFinder results showing optimum partitioning schemes and best fit models
946 for each analysis (RAxML, MrBayes, BEAST). Settings: BIC, unlinked branch
947 lengths, greedy algorithm.

948 **Table 3:** Overview of 18 candidate fossils with stratigraphic age, locality and relevant references. For
949 more details see Appendix B.

950 **Table 4:** Overview of fossils finally selected for divergence dating, with parameters of uniform
951 and lognormal prior distribution.

952 **Table 5:** Comparison of models used for BioGeoBEARS; likelihood scores (LnL), number of
953 parameters (numparams), dispersal rate (d), extinction rate (e), free parameter controlling
954 the relative probability of founder-event speciation events at cladogenesis (j), corrected
955 Akaike Information Criterion (AICc), and AICc model weights.

956 **Table 6:** Results of divergence dating analysis. Time to the most common ancestor (MRCA) is
957 shown as median in Ma, with 95% highest posterior density (HPD). Estimates from
958 previous studies dealing with divergence dating of murid rodents are reviewed here
959 for comparison.

960 **Table 7:** Comparison between previous relevant studies.

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963 **Supplementary material**

964 **Appendix A.** List of taxa and genetic markers.

965 **Appendix B.** Description of considered fossils.

966 **Appendix C.** Results of cross-validation of fossil constraints.

967 **Appendix D.** Maximum likelihood phylogenetic tree.

Table 1: Brief summary of taxonomic changes in the family Muridae, The taxonomic position of particular lineages has changed significantly and they were either considered separate families or included in other families outside Muridae (name of families are in bold).

Simpson (1945)		Chaline et al. (1977)		Lavocat (1978)	
Cricetidae	Lophiomyinae	Cricetidae	Lophiomyinae	Nesomyidae	Lophiomyinae
	Gerbillinae	Gerbillidae			Gerbillinae
Muridae	Murinae	Muridae	Murinae		Otomyinae
	Otomyinae	Nesomyidae	Otomyinae	Muridae	
Carleton and Musser (1984)		Musser and Carleton (2005)		Granjon and Montgelard (2012)	
Muridae	Lophiomyinae	Cricetidae	Lophiomyinae	Muridae	Lophiomyinae
	Gerbillinae	Muridae	Otomyinae		Gerbillinae
	Murinae		Gerbillinae		Murinae
	Otomyinae		Murinae		Deomyinae
			Deomyinae		Leimacomyinae
			Leimacomyinae		

Table 2: PartitionFinder results showing optimum partitioning schemes and best fit models for each analysis (RAxML, MrBayes, BEAST). Settings: BIC, unlinked branch lengths, greedy algorithm.

Analysis	N. of part	Best sub. model	Subsets
RAxML	3	GTR+I+G	12S, 16S, ATPase8_pos1-pos2, COII_pos1-pos2, COI_pos1-pos2, CYTB_pos1-pos2, tRNA-Asp, tRNA-Lys, tRNA-Ser
		GTR+I+G	ATPase8_pos3, COII_pos3, COI_pos3, CYTB_pos3
		GTR+I+G	AP5_pos1-pos3, BRCA_pos1-pos3, BZRP, GHR_pos1-pos3, IRBP_pos1-pos3, RAG_pos1-pos3
MrBayes and BEAST	3	GTR+I+G	12S, 16S, ATPase8_pos1-pos2, COII_pos1-pos2, COI_pos1-pos2, CYTB_pos1-pos2, tRNA-Asp, tRNA-Lys, tRNA-Ser
		HKY+I+G	ATPase8_pos3, COII_pos3, COI_pos3, CYTB_pos3
		GTR+I+G	AP5_pos1-pos3, BRCA_pos1-pos3, BZRP, GHR_pos1-pos3, IRBP_pos1-pos3, RAG_pos1-pos3

Table 3: Overview of 18 candidate fossils with stratigraphic age, locality and relevant references. For more details see Appendix B.

Fossil	Final analysis	Reason for excluding	Age (Ma)	Dating		Fossils	
				Method	References	Site	References
† <i>Potwarmus primitivus</i> (Wessels)	No	Equivocal placement	16.0	magnetostratigraphy	time scale of Ogg and Smith (2004)	Pakistan, Potwar Plateau, YGSP591	Lindsay (1988), Wessels (2009)
† <i>Antemus chinjiensis</i> Jacobs	Yes (1)		13.8	magnetostratigraphy	Jacobs and Flynn (2005)	Pakistan, Potwar Plateau, YGSP 491	Jacobs et al. (1989)
†cf. <i>Progonomys</i> sp. Schaub	No	Equivocal placement	11.6	magnetostratigraphy	time scale of Ogg and Smith (2004)	Pakistan, Potwar Plateau, YGSP 83, YGSP 504	Jacobs and Flynn (2005), Cheema et al. (2000), Kimura et al. (in prep.)
†cf. <i>Karnimata</i> sp. Jacobs	Yes (2)		11.2	magnetostratigraphy	Kimura et al. (2015) by time scale of Ogg and Smith (2004)	Pakistan, Siwalik Group, Nagri Formation, YGSP 791, YGSP 797,	Jacobs and Flynn (2005); Kimura et al. (2015)
† <i>Parapodemus lungdunensis</i> Schau	Yes (3)		9.6	magnetostratigraphy	Daxner-Höck (2003)	France, Dionay	Lungu (1981), Mein et al. (1993), Renaud et al. (1999)
† <i>Karnimata darwini</i> Jacobs	Yes (4)		9.2	magnetostratigraphy	Kimura et al. (2015) by time scale of Ogg and Smith (2004)	Pakistan, Siwalik Group, Dhok Pathan Formation, YGSP 182	Jacobs (1978); Kimura et al. (2015)
† <i>Abudhabia pakistanensis</i> Flynn and Jacobs	Yes (5)		8.7	magnetostratigraphy	Flynn and Jacobs (1999) by time scale of Ogg and Smith (2004)	Pakistan, Siwalik Group, Dhok Pathan Formation, YGSP387	Flynn and Jacobs (1999)
†aff. <i>Stenocephalomys</i> Frick	No	Equivocal placement	8.5	$^{40}\text{K}/^{40}\text{Ar}$	Geraads et al. (2002), Suwa et al. (2015)	Ethiopia, Chorora	Geraads (2001)
†cf. <i>Parapelomys</i> Jacobs	No	Equivocal placement	8.5	$^{40}\text{K}/^{40}\text{Ar}$	Geraads et al. (2002), Suwa et al. (2015)	Ethiopia, Chorora	Geraads (2001)

Table 3 (continued)

Fossil	Final analysis	Reason for excluding	Age (Ma)	Dating		Fossils	
				Method	References	Site	References
† <i>Preacomys kikiæ</i> Geraads	No	Equivocal placement	8.5	$^{40}\text{K}/^{40}\text{Ar}$	Geraads et al. (2002), Suwa et al. (2015)	Ethiopia, Chorora	Geraads (2001)
† <i>Mus</i> sp. Linneaus	Yes (6)		8.0	magnetostratigraphy	Kimura et al. (2015) by time scale of Ogg and Smith (2004)	Pakistan, Siwalik Group, Dhok Pathan Formation, YGSP 547	Kimura et al. (2013; 2015)
† <i>Acomys</i> sp. I. Geoffroy	No	missing M1	6.1	$^{40}\text{Ar} / ^{39}\text{Ar}$	Deino and Ambrose (2007)	Kenya, Lemudong'o, locality 1	Manthi (2007)
† <i>Aethomys</i> sp. Thomas	Yes (7)		6.1	$^{40}\text{Ar} / ^{39}\text{Ar}$	Deino and Ambrose (2007)	Kenya, Lemudong'o, locality 1	Manthi (2007)
† <i>Arvicanthis</i> sp. Lesson	Yes (8)		6.1	$^{40}\text{Ar} / ^{39}\text{Ar}$	Deino and Ambrose (2007)	Kenya, Lemudong'o, locality 1	Manthi (2007)
† <i>Gerbilliscus</i> sp. (Thomas)	Yes (9)		6.1	$^{40}\text{Ar} / ^{39}\text{Ar}$	Deino and Ambrose (2007)	Kenya, Lemudong'o, locality 1	Manthi (2007)
† <i>Lemniscomys</i> sp. Trouessart	No	missing M1	6.1	$^{40}\text{Ar} / ^{39}\text{Ar}$	Deino and Ambrose (2007)	Kenya, Lemudong'o, locality 1	Manthi (2007)
† <i>Mastomys</i> sp. Thomas	No	cross-validation	6.1	$^{40}\text{Ar} / ^{39}\text{Ar}$	Deino and Ambrose (2007)	Kenya, Lemudong'o, locality 1	Manthi (2007)
† <i>Gerbillus</i> sp. Desmarest	No	cross-validation	2.4	geochronology (BKT-3 tephra), $^{40}\text{K}/^{40}\text{Ar}$, $^{40}\text{Ar} / ^{39}\text{Ar}$; sedimentology	Kimbel et al. (1996), Campisano and Feibel (2008)	Ethiopia, Hadar, AL894	Reed (2011)

Table 4: Overview of fossils finally selected for divergence dating, with parameters of uniform and lognormal prior distribution.

	Fossil	Position	Stem/Crown	Age (Ma)	Uniform distribution		Lognormal distribution		
					Min	Max	Offset	Log	Mean
1	† <i>Antemus chinjiensis</i>	crown Murinae	crown	13.8	13.24	25.29	13.24	1.0	3.2
2	†cf. <i>Karnimata</i> sp.	<i>Mus/Arvicanthis</i> split	crown	11.2	10.47	25.37	10.47	1.0	4.0
3	† <i>Parapodemus lugdunensis</i>	<i>Apodemus/Tokudaia</i> split	stem	9.6	8.93	25.41	8.93	1.0	4.5
4	† <i>Karnimata darwini</i>	TMRCA Millardini/Otomyini/Arvicanthini	crown	9.2	8.52	25.42	8.52	1.0	4.6
5	† <i>Abudhabia pakistanensis</i>	<i>Gerbilliscus/Desmodillus</i> split	crown	8.7	8.01	25.43	8.01	1.0	4.7
6	† <i>Mus</i> sp.	Murini	stem	8.0	7.29	25.45	7.29	1.0	4.9
7	† <i>Aethomys</i> sp.	<i>Aethomys</i>	stem	6.1	5.34	25.50	5.34	1.0	5.5
8	† <i>Arvicanthis</i> sp.	<i>Arvicanthis</i>	stem	6.1	5.34	25.50	5.34	1.0	5.5
9	† <i>Gerbilliscus</i> sp.	<i>Gerbilliscus</i>	stem	6.1	5.34	25.50	5.34	1.0	5.5

Table 5: Comparison of models used for BioGeoBEARS; likelihood scores (LnL), number of parameters (numparams), dispersal rate (d), extinction rate (e), free parameter controlling the relative probability of founder-event speciation events at cladogenesis (j), corrected Akaike Information Criterion (AICc), and AICc model weights.

	LnL	numparams	d	e	j	AICc	AICc wt
DEC	-133.724	2	0.005	0.000	0.000	271.525	0.05181
DEC +J	-129.826	3	0.004	0.000	0.008	265.806	0.90415
DIVALIKE	-146.958	2	0.007	0.000	0.000	297.993	9.2665e-08
DIVALIKE +J	-132.856	3	0.004	0.000	0.012	271.866	0.04369
BAYAREALIKE	-178.311	2	0.005	0.036	0.000	360.698	2.2423e-21
BAYAREALIKE +J	-137.687	3	0.003	0.000	0.014	281.528	0.00035

Table 6: Results of divergence dating analysis. Time to the most common ancestor (TMRCA) is shown as median in Ma, with 95% highest posterior density (HPD). Estimates from previous studies dealing with divergence dating of murid rodents are reviewed here for comparison.

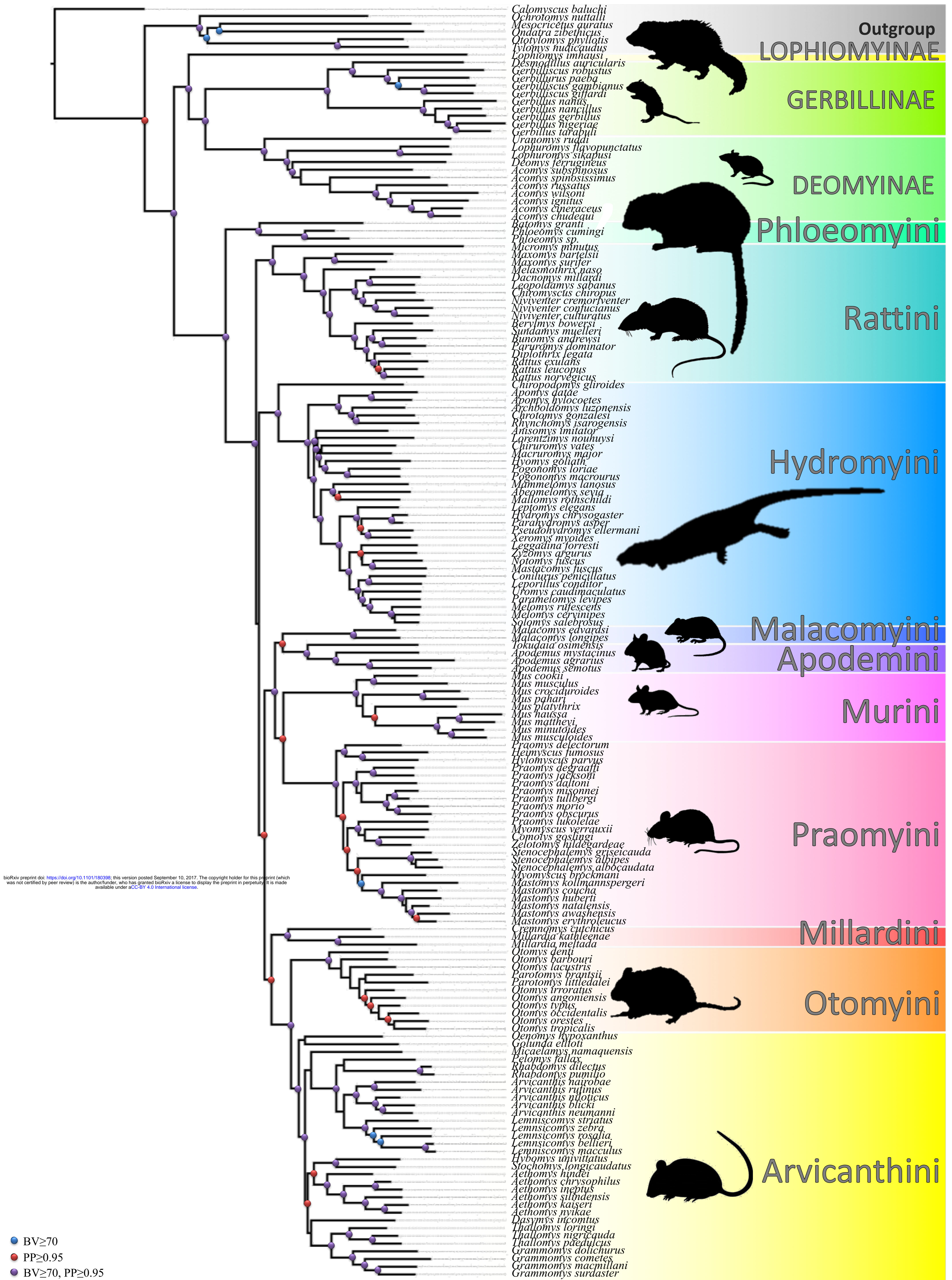
TMRCA	median	2.5%	97.5%	Steppan et al. (2004)	Lecompte et al. (2008)	Rowe et al. (2011)	Fabre et al. (2012)	Fabre et al. (2013)	Schenk et al. (2013)	Bryja et al. (2014)	Rowe et al. (2016b)
Muridae	19.3	17.06	21.92	22.5			~33-23		~21.0		
Lophiomyinae*	18.6	16.35	21.11								
Gerbillinae	12.2	10.46	14.16	9.3			~23-5		~10.0		
Deomyinae	14.6	12.68	16.82	13.1			~23-5		~13.0		
Murinae	14.2	12.70	16.07	12.0	12.3	13.3	~23-5		~14.5		~14.0
"core Murinae"	12.3	11.28	13.62	10.3	11.3			11.60	~12.5		~12.5
Phloeomyini	9.8	7.72	11.85		8.6				~10.0		~10.5
Rattini	10.4	9.23	11.93		9.7			8.70	~11.0		~11.0
Hydromyini	10.4	9.31	11.71		8.9				~11.0		~11.0
Malacomyini	3.4	2.35	4.60							4.4	
Apodemini	9.0	7.92	10.13		9.6				~7.5	9.5	~7.5
Murini	7.2	6.24	8.29		6.6	5.3			~6.0	7.4	~6.5
Praomyini	6.8	6.05	7.77		7.6				~5.0	6.8	~6.0
Millardini	9.2	7.72	10.75								
Otomyini	4.9	4.12	5.98						~6.0	3.8	~3.0
Arvicanthini	8.8	7.92	9.72		8.4	7.3			~7.5	7.8	~8.5

* offshoot from Gerbillinae + Deomyinae

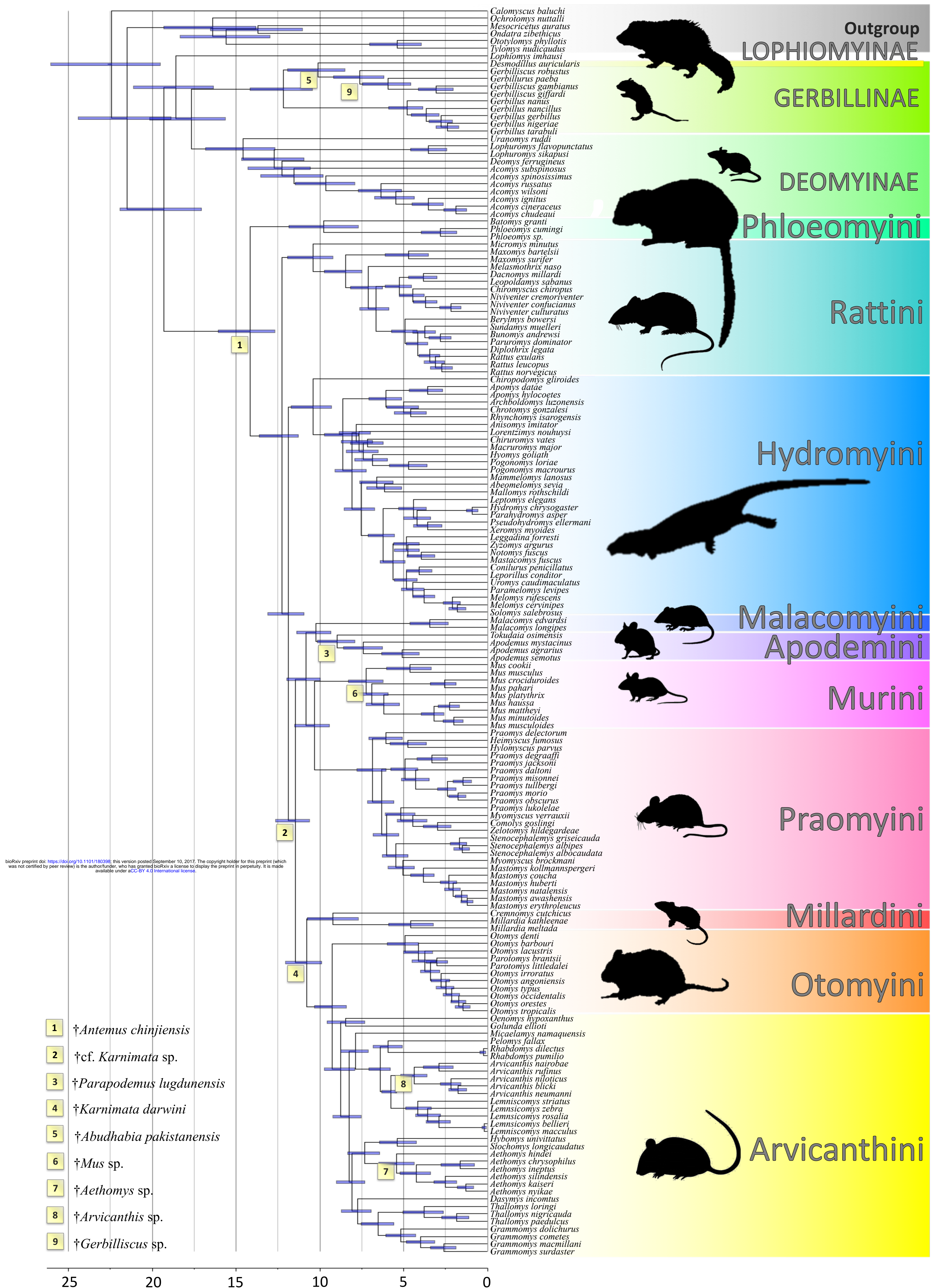
Table 7: Comparison between previous relevant studies.

Author	Focus	Subfamilies	# genera	# species	Fossils in Muridae	# genetic markers
Fabre et al. (2012)	Rodentia	4	105	302	0	11 (8)*
Schenk et al. (2013)	Muroidea	4	85	136	4	4
our study	Muridae	4	82	160	9	15
Rowe et al. (2008)	Hydromyini (outgroup all Murinae + Gerbillinae+Deomyinae)	3	66	78	2	8
Lecompte et al. (2008)	Murinae	3	46	83	2	3

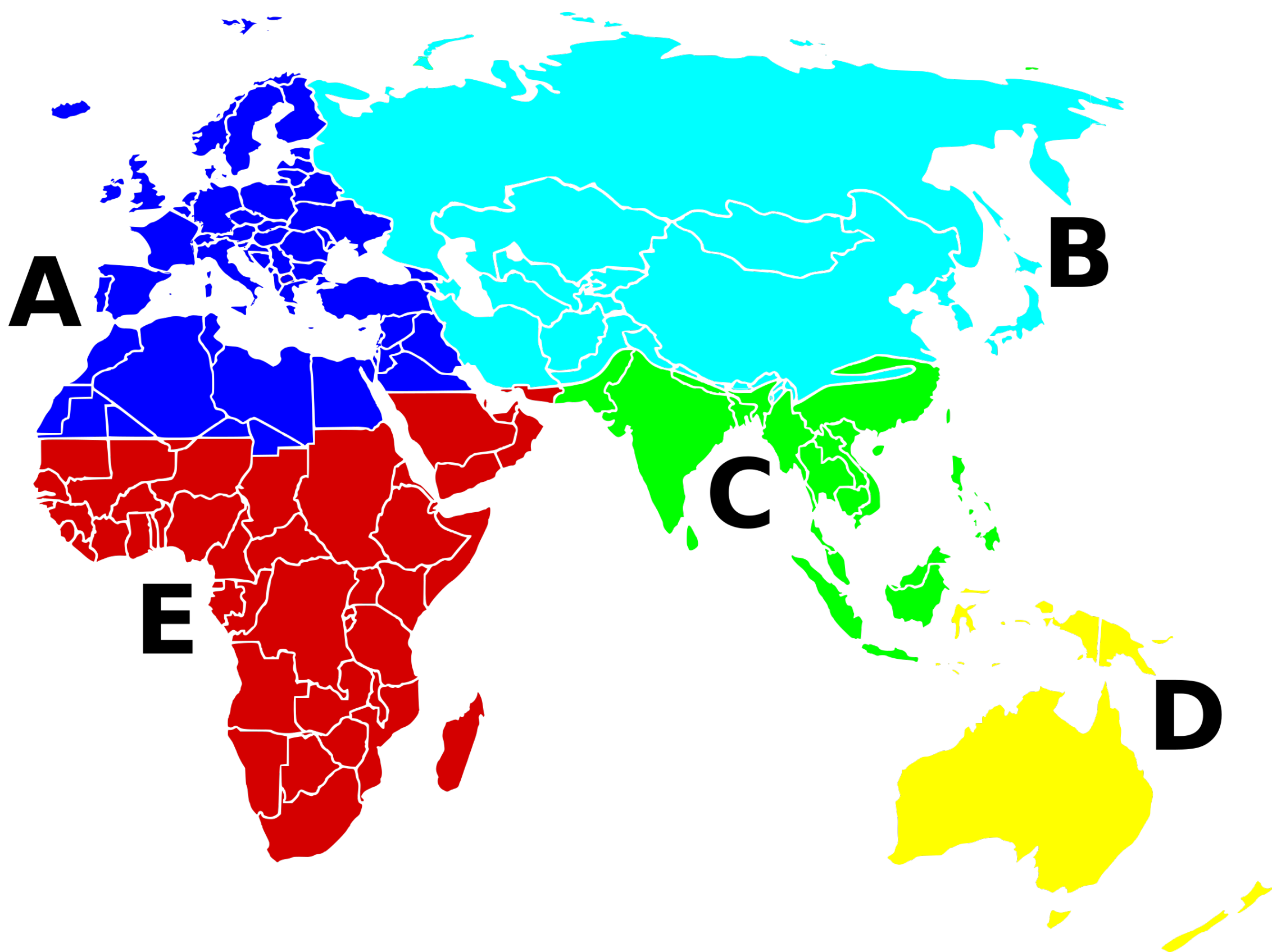
* 11 genetic markers for Rodentia, only 8 for Muridae



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