

Molecular phylogeny of Southeast Asian arboreal murine rodents

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Abstract

Recent phylogenetic studies and taxonomic reviews have led to nearly complete resolution of the phylogenetic divisions within the old world rats and mice (Muridae, Murinae). The *Micromys* division and *Pithecheir* division are two notable exceptions where groupings of species into these divisions based on morphology and arboreal lifestyle have not been supported by phylogenetic evidence. Several enigmatic species from these divisions have been missing from molecular studies, preventing a rigorous revision of phylogenetic relationships. In this study, we sequenced for the first time one mitochondrial and three nuclear genes from Southeast Asian keystone species of these two arboreal divisions: *Hapalomys delacouri* (*Micromys* division), *Lenothrix canus* and *Pithecheir parvus* (*Pithecheir* division). We also complemented the molecular data already available for the two divisions with new data from Sundaic *Chiropodomys*, Indian *Vandeleuria oleracea* and the recently described Sulawesi *Margaretamys christinae*. Using this new phylogenetic framework and molecular dating methodologies, our study allows some more detailed classification of the former *Micromys* and *Pithecheir* divisions, while confirming their polyphyletic status. Specifically, the former *Micromys* division should now be split into four monotypic divisions: *Chiropodomys*, *Hapalomys*, *Micromys*, and *Vandeleuria* divisions. The former *Pithecheir* division is likely to be refined and restricted to *Pithecheir* and probably *Pithecheirops*, whereas *Lenothrix* and *Margaretamys* should now be recognized as representatives of the *Dacnomys* division. Our findings have profound implications with regard to the systematics of Murinae, as well as to the early evolution of murine morphology and dental characters.

Introduction

The old world rats and mice, subfamily Murinae (Muridae), contain 584 described and extant species (Aplin & Helgen, 2010; Misonne, 1969; Musser & Carleton, 2005). Southeast Asia constitutes the major hotspot of biodiversity for Old World Murine rodents (Aplin & Helgen, 2010; Misonne, 1969; Musser & Carleton, 2005). Since the Miocene, the Murinae have spread out of Asia into the Indo-Australian, African, Indian and Palearctic regions, where they underwent repeated radiations. Current systematic and phylogenetic studies of murines largely reflect a strong biogeographical footprint with many divisions and phylogenetic clades endemic to specific biogeographic regions (Musser & Carleton, 2005; Lecompte *et al.*, 2008; see Table 1). Three tribes (*i.e.* taxonomic rank between subfamily and genus) are considered the dominant murines of Southeast Asian and Indo-Australian areas according to molecular phylogenetic evidence (Lecompte *et al.*, 2008): (1) the Phloeomyini including 17 species endemic to the Philippines, (2) the Hydromyini including 198 species endemic to the Philippines and the Sahul shelf, and (3) the Rattini including 185 species widespread throughout Southeast Asia and the whole Indo-Pacific archipelago. The 23 species of the *Pithecheir* and *Micromys* divisions comprise the remaining species of currently known murines in the Southeast Asian and Indo-Australian areas. They are distributed across Southeast Asia and Sulawesi (Figure S1), but are neither phylogenetically monophyletic (Schenk *et al.*, 2013) nor readily assigned to these tribes on molecular basis.

As currently defined (Musser & Carleton, 2005), the *Pithecheir* division encompasses the genera *Pithecheir*, *Eropeplus*, *Lenomys*, *Lenothrix*, *Margaretamys*, and *Pithecheirops*. These genera are suspected to represent an artificial grouping (Musser & Newcomb, 1983) and are still considered as Murinae *incertae sedis* as their phylogenetic affinities remain unclear (Lecompte *et al.*, 2008). *Margaretamys* was recently found to be nested within the *Dacnomys* division of the tribe Rattini (Schenk *et al.*, 2013). The *Micromys* division, which encompasses the genera *Chiropodomys*, *Hapalomys*, *Haeromys*, *Micromys*, *Vandeleuria*, and *Vernaya* also appears to represent equivocal grouping (Musser & Carleton, 2005). DNA results demonstrated that the *Micromys* division is polyphyletic (Steppan *et al.*, 2005). This division most likely consist of at least 3 distinct and phylogenetic old lineages with (i) *Micromys* being sister to the Rattini, (ii) *Vandeleuria* closely-related to a clade embracing Praomyini, Murini and Apodemini tribes and (iii) *Chiropodomys* affiliated with the Hydromyini tribe (Rowe *et al.*, 2008; Schenk *et al.*, 2013).

The original groupings of these Southeast Asian taxa into *Pithecheir* and *Micromys* divisions *sensu* Musser & Carleton (2005) relied mostly on their likewise adaptations to

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3 arboreal lifestyle and their similar morphologies. Among the considered morphological
4 features were the global patterns of dental morphology (*i.e.* cusp convergences on the upper
5 molar; see hereafter), distinctive skull features as well as the presence/absence of an
6 opposable hallux of various representative species (Musser & Newcomb, 1983). However, in
7 almost all revisions and classifications performed to date, taxonomists have struggled with the
8 difficulty in classifying these arboreal taxa (see Misonne, 1969; Musser & Newcomb, 1983).
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12 A Mid-Miocene origin of Murinae (12-16 Mya) is suggested by the oldest fossil
13 occurrence of modern murines in the Siwalik deposits (*i.e.* *Antemus mancharensis*) (Wessels,
14 2009). This transition in the Siwalik fossil record is defined by changes in upper molar
15 morphology involving reorientations of the masticatory movements (Coillot *et al.*, 2013;
16 Lazzari *et al.*, 2011). This transition is one of the most well characterised transitions in
17 mammal evolution. It is well documented by many extinct species, from *Potwarmus*, the
18 cricetine-like earliest murid to *Progonomys* that has the derived connection of lingual cusps
19 and the murine occlusal pattern shared with modern murines. Historically, this transition was
20 assigned to the divergence of *Mus* and *Rattus*, assuming that they represent the earliest
21 divergence within Murinae, and has been critical to date for a number of biomedical and
22 evolutionary studies (Patnaik, 2014). However, phylogenetic analyses of Murinae have shown
23 that this fossil transition is more appropriately assigned to the divergence of the Phloeomyini
24 tribe from the remaining Murinae, as this is the earliest divergence among taxa with the
25 derived murine molar cusp pattern (Steppan *et al.*, 2004a; Steppan *et al.*, 2005). Thus,
26 disentangling the basal divergences within Murinae appears critical to accurately interpret the
27 fossil record and to accurately calibrate the divergence of taxa, such as the important genera
28 *Mus* and *Rattus*. Recent molecular clues indicated that some species of the enigmatic
29 *Micromys* and *Pithecheir* divisions may have emerged from very early divergence events
30 within the murine tree and could even be among the first (*e.g.* Badenhorst *et al.*, 2011).
31 Consequently, the phylogenetic placement of the involved species appears to be crucial to
32 disentangle the evolution of their ecomorphological traits and also to unravel the entire
33 diversification history of the Murinae subfamily.
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49 In this study, we sequenced for the first time three genera from the Southeast Asian
50 region of both *Micromys* (*Hapalomys delacouri*) and *Pithecheir* (*Lenothrix canus* and
51 *Pithecheir parvus*) divisions. We also provided new molecular data from Sundaic
52 *Chiropodomys*, Indian *Vandeleuria oleracea* and the recently described Sulawesi endemic
53 *Margaretamys christinae* (Mortelliti *et al.*, 2012). Using this new phylogenetic context and
54 molecular dating methodologies, we addressed the following questions: (*i*) how should we
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3 refine the taxonomy of Murinae; (ii) do morphological (*i.e.* dental) characters support our new
4 molecular findings for phylogenetic placement of the members of these divisions? (iii) how
5 often does arboreality evolve in Murinae from the *Micromys* and *Pithecheir* divisions and
6 how does it relate to early evolution in the group? and (iv) where should we place the Siwalik
7 transition in the murine tree and how should we interpret the early murine fossil record?
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11 12 13 **Methods and materials**

14 *Taxon and gene sampling*

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16 We sequenced four molecular markers that have proven valuable for resolving murine
17 phylogenies (Buzan *et al.*, 2011; Fabre *et al.*, 2013; Jansa *et al.*, 2006; Lecompte *et al.*, 2008;
18 Pagès *et al.*, 2010; Rowe *et al.*, 2011; Rowe *et al.*, 2008; Schenk *et al.*, 2013; Steppan *et al.*,
19 2004b; Steppan *et al.*, 2005). These included one mitochondrial gene (cytochrome *b*
20 apoenzyme: *cyt b*) and three nuclear genes (growth hormone receptor exon 10: *GHR*;
21 interphotoreceptor retinoid binding protein exon 1: *IRPB*, breast and ovarian cancer
22 susceptibility protein exon 11: *BRCA1*). DNA sequences were generated for the following
23 species belonging to *Micromys* and to *Pithecheir* divisions *sensu* Musser and Carleton, 2005:
24 *Chiropodomys gliroides*, *Chiropodomys major*, *Hapalomys delacouri* and *Vandeleuria*
25 *oleracea* (*Micromys* division) and *Lenothrix canus*, *Margaretamys christinae* and *Pithecheir*
26 *parvus* (*Pithecheir* division). To break putative long branches within the tribe Rattini, the two
27 karst-specialist genera *Saxatilomys paulinae* and *Tonkinomys daoventieni* from the *Dacnomys*
28 division (Table S1a) were included in this study. We also mined 170 *cytb*, 190 *IRBP*, 137
29 *GHR*, 74 *BRCA1* sequences representing 191 murine species available from previously
30 published studies (see references above; Table S1b). In total, our dataset includes 196 murine
31 species representing a total of 100 genera following Musser & Carleton's classification
32 (2005). We included 17 representatives of Deomyinae, Gerbillinae and Lophiomyinae (Table
33 S1b) as outgroups (Michaux & Catzeflis, 2000; Steppan *et al.*, 2004b).
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46 We used SEAVIEW (Galtier *et al.*, 1996) to align sequences by eye. We translated
47 nucleotide sequences into peptide sequences to exclude putative NUMt copies and to ensure
48 sequence orthology. From these individual alignments, we built four gene matrices; *cyt b* (200
49 taxa and 1140 sites; 5 % of missing character states), *IRBP* (215 taxa and 1239 sites; 21 %
50 missing data), *GHR* (171 taxa and 937 sites; 12 % missing data), *BRCA1* (94 taxa and 2430
51 sites; 23 % missing data) and a nuclear + mitochondrial supermatrix (221 taxa and 5746 sites;
52 41 % missing data).
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DNA extraction and sequencing of ethanol-preserved specimens

Samples were obtained from the collections of the [CeroPath](#) project, University Montpellier collections, as well as personal tissues collections of J.P Quéré, K. Wells, K. Aplin, A. Mortelliti & R. Castiglia (Table S1a). DNA was extracted from tissue with a DNEasy Tissue Kit (QIAGEN), in accordance with the manufacturer's instructions. We sequenced the whole *cyt b* gene and the *IRBP*, *GHR* and *BRCA1* fragments, according to protocols described elsewhere (Irwin *et al.*, 1991; Lecompte *et al.*, 2008; Pagès *et al.*, 2010). Primer sets used for PCR amplifications and sequencing are listed in Table S2. PCR products were sequenced at the sequencing centre Genoscope (Evry, France) using an ABI 3730xl automatic capillary sequencer and the ABI BigDye Terminator v.3.1 sequencing kit. Sequences were analyzed with the CodonCode Aligner v 4.0.3 software (CodonCode Corporation, Dedham, MA, USA).

DNA extraction and sequencing of museum specimens

Samples from four *Pithecheir* specimens were obtained from the French National Museum of Natural History (MNHN) (Table S1a): two specimens of *Pithecheir parvus* (MNHN-ZM-MO 1977-251, MNHN-ZM-MO 1977-252) and two specimens of *P. melanurus* (MNHN-ZM-MO 1900-580, MNHN-ZM-MO 1900-583). As museum samples contain tiny amounts of poorly preserved DNA, pre-amplification steps were achieved in an independent lab dedicated to degraded DNA analysis (degraded DNA platform, Labex CeMEB), following the ancient DNA standard procedures and using specific equipment and personal protections (Paabo *et al.*, 2004). DNA was extracted from small pieces of skins using QIAamp DNA Micro Kit (QIAGEN), in accordance with the manufacturer's instructions. Because of DNA fragmentation, *cyt b*, *IRBP* and *GHR* markers were obtained using three overlapping fragments (ranging from 310 to 472 bp). Additional primers (Table S2) were designed based on the alignment of sequences available for Murinae, Gerbillinae and Deomyinae (Table S1b). At least three independent PCR amplifications were performed in 25 μ L reaction volumes containing 2.5 units of Perkin Elmer Gold *Taq* polymerase (Applied Biosystems), 2 mM MgCl₂, 250 mM of each dNTP, 0.5 mM of primers. For each independent PCR attempt, a range of dilutions was performed to find the best compromise between inhibitor's concentration and targeted DNA molecule concentration. DNA was amplified with a 5 min activation step at 95°C followed by 55 cycles of denaturation (94°C, 30 s), annealing (temperature in Table S2, 30 s) and elongation (72°C, 45 s). To discard artefactual mutations due to DNA degradation (Paabo *et al.*, 2004) and to determine the consensus sequences for

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3 each individual, all the positive PCR products were sequenced (see supplementary
4 information for further details, Text S1). Next, we combined the newly obtained sequences
5 with the DNA matrices described in the previous section.
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8 9 *Phylogenetic analyses on the individual and concatenated genes*

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11 Phylogenetic trees were reconstructed using two probabilistic methods: maximum likelihood
12 (ML) and Bayesian inference (BI). ML analyses were first carried out on each marker
13 independently using RAXML 7.2.8-ALPHA (Stamatakis, 2006). Each gene considered
14 separately does not result in a robust phylogeny of Murinae: mitochondrial marker helps to
15 resolve terminal nodes, while nuclear genes lend support to deepest ones. But, since the 4
16 markers yielded consistent, compatible topologies, sequences were concatenated and
17 phylogenetic analyses were then carried out using the combined dataset. As the model choice
18 is limited in RAXML, the general time-reversible GTR+G model (option -m GTRGAMMA)
19 was selected and robustness of each tree was assessed using the rapid bootstrap (Bp)
20 procedure (option -f a) with 1,000 replications (option -# numberOfRuns) (Stamatakis *et al.*,
21 2008). Bayesian analyses were performed in MRBAYES 3.1.2 (Ronquist & Huelsenbeck,
22 2003), which allows different substitution models to be specified for each gene partition.
23 Using JMODELTEST 2.1.1 (Posada, 2008) and the corrected Akaike Information Criterion
24 (cAIC), the GTR+I+G model was selected as the best-fitting model of DNA sequence
25 evolution for *Cyt b* and *GHR* markers, the GTR+I+G for the *IRBP*, and the GTR+G for
26 *BRCA1*. The best-fit partitioning schemes (considering the three different codon positions of
27 the four coding genes) and models of molecular evolution were deeper investigated using
28 PARTITIONFINDER (Lanfear *et al.*, 2012). The best-fit partitioning scheme consisted in 3
29 subsets: 1) the first and the second positions of the *Cyt b* codon were merged together, 2) the
30 third position of the *Cyt b* codon was treated separately, 3) all the positions of the nuclear
31 genes were merged together. 56 different substitution models for these three subsets were
32 compared using the *greedy* algorithm. The best-fit substitution model was the GTR+I+G
33 model for each subset according to cAIC values. MRBAYES parameters were set accordingly
34 (see supplementary information). All parameters except the topology were unlinked across
35 partitions, and two independent runs, each with 4 Markov chains Monte Carlo (MCMC)
36 samples comprising one cold and three heated chains, were computed simultaneously. The
37 MRBAYES analyses were run for 50×10^6 generations with trees sampled every 1,000
38 generations. In all cases, both the log-likelihood and model parameter values had reached
39 convergence prior to posterior sampling (effective sample size of the trace of each parameter
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3 checked using Tracer 1.5 (<http://tree.bio.ed.ac.uk/software/tracer/>), and potential scale
4 reduction factors checked reaching 1). The consensus tree was then computed subsequent to a
5 burn-in of 10×10^6 generations (option “allcompat”). The node supports were estimated using
6 posterior probabilities (PP).
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10 Molecular results were further evaluated in light of the morphological characters. As
11 the most abundant material of the rodent fossil record consists of jaws and teeth, we focused
12 on the dental characters. Following the nomenclatures of Cope-Osborn and Miller (detailed in
13 Figure 1), discrete characters were compared within the arboreal Murinae from Southeast
14 Asia, but also compared with those of their closest extant relatives based on our molecular
15 tree.
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20 21 *Molecular dating*

22 Divergence times among species were estimated from the combined supermatrix of nuclear
23 and mitochondrial sequences. A Bayesian relaxed molecular clock method was used to
24 estimate divergence dates whilst accounting for changes in evolutionary rates through time by
25 allowing for independent models of sequence evolution for each gene partition. The best
26 fitting substitution models for each partition were selected using JMODELTEST results. We
27 used BEAST v1.7.4 (Drummond & Rambaut, 2007) assuming a Yule model of speciation and
28 an uncorrelated log-normal distribution molecular clock as tree priors. Clock models were
29 unlinked across gene partitions in order to account for missing data (Lemmon *et al.*, 2009).
30 We ran MCMC chains for 200 million generations, with trees sampled every 5,000
31 generations. The program TRACER was used to assess algorithm convergence. We removed
32 the first 15% of trees before the algorithm had reached stability as a burn in. Trees from each
33 of the 4 independent runs were combined into a maximum clade credibility tree with mean
34 node heights calculated using TREEANNOTATOR.
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45 To calibrate the phylogeny, we selected five fossil constraints, as described from
46 previous studies (Jansa *et al.*, 2006; Lecompte *et al.*, 2008; Rowe *et al.*, 2011; Rowe *et al.*,
47 2008; Steppan *et al.*, 2004a). In order to take the uncertainty in the phylogenetic position of
48 these fossils into account, all constraints were set using hard minimum and soft upper
49 boundaries, using a lognormal prior, as suggested by recent paleontological studies (Benton &
50 Donoghue, 2007; Benton *et al.*, 2009; Parham *et al.*, 2012). We used the following
51 constraints:
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56 (I) We used the stem Apodemini fossils (11 Myr min) from the Early Vallesian (late
57 Miocene: 11.6-24.5 Myr; (Martin Suarez & Mein, 1998; Vangegeim *et al.*, 2006) to constrain
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3 the split between Apodemini / Millardini (MRCA of *Apodemus* / *Tokudaia*) and Praomyini /
4 Murini (MRCA of *Mus* / *Praomys* / *Mastomys* clade) (upper 95%: 8.91-21.8 Myr).

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6 (II) The MRCA of the *Apodemus mystacinus* and the *Sylvaemus* groups (affiliated
7 respectively to *A. flavicollis* and *A. sylvaticus*) were constrained using the *Apodemus* fossil
8 record (Aguilar & Michaux, 1996; Michaux *et al.*, 1997) from the Upper Miocene. We set a
9 median prior age at 7 Myr (upper 95%: 5.96-12.37 Myr).

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11 (III) We used the first fossil record of *Mus* (*Mus auctor*; Jacobs & Downs, 1994;
12 Jacobs *et al.*, 1990; Lundrigan *et al.*, 2002) to represent the minimum divergence at 5.7 Myr
13 (upper 95%: 4.66-11.07 Myr) between different *Mus* lineages (*Mus musculus* / *Mus pahari* /
14 *Mus setulosus*).

15
16 (IV) We used the African crown Arvicanthini lineage from the late Miocene (median
17 age 6 Myr; from the Tortonian) (Winkler, 2002) and a soft maximum prior extending to the
18 Serravalian (upper 95%: 3.91-16.81 Myr) as a constraint of the MRCA of Arvicanthini.

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20 (V) We set a minimum constraint for the MRCA of Hydromyini, using the first
21 Australian fossil evidence dated at 3.4 Myr (upper 95%: 1.3-14.21 Myr; Aplin, 2006; Rowe *et*
22 *al.*, 2008; Tedford *et al.*, 1992).

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24 Note that we did not use the oldest record of *Progonomys* for tree calibration, as the
25 interpretation of the early murine fossil record is part of our questions.

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Ancestral state reconstruction

We reconstructed ancestral states for the dental key character, previously used to define the *Micromys* and *Pithecheir* divisions: the cusp t7 (Figure 1). Based on Musser and Newcomb (1983) (see page 537, character 27), this trait was coded as ‘1’ if “a cusp t7 derived and if present, found on each first molar, usually on the second, and on the third” and as ‘0’ otherwise (“no cusp t7 (also called posterointernal or posterolabial cusp) on any upper molar”). Taxa with uncertain or unknown character state were coded as “missing”. The resulting classification of all species in our study dataset is available in the SI data (Figure S3).

The presence of an opposable first digit on the hindfoot (hallux) comprises another potential criteria for examining the morphological evolution of these arboreal rodents. An opposable hallux has been attributed to *Chiropodomys*, *Hapalomys*, *Vandeleuria*, *Vernaya*, *Pithecheir* and *Haeromys* representatives (Musser, 1979). However, because the hallux of some arboreal murids bears a nail instead of a claw, that hallux may be pseudo-opposable, rather than fully

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3 opposable (see “Other questions and speculations”, page 438 of Musser, 1979). We therefore
4 did not use this character for ancestral reconstruction.
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6 Ancestral character state reconstructions (ASR) was based on stochastic character
7 mapping as implemented in the *make.simmap* function in the R software package PHYTOOL
8 (Bollback, 2006; Revell, 2012). This SIMMAP approach reconstructs possible states at all
9 ancestral nodes, accounting for the uncertainty through MCMC sampling. We used the default
10 parameter settings and run 1,000 simulations. The *make.simmap* approach is similar to the
11 empirical Bayes approach for ASR introduced by Pagel & Meade (2004), in which character
12 rate models are set to ML estimates. The analyses were computed on the maximum clade
13 credibility tree and on 1,000 phylogenies randomly sampled from the BEAST posterior
14 distributions of trees (excluding the burn-in) in order to take into account the phylogenetic
15 uncertainty. The MCMC analyses were conducted twice, with an equal (1/k) and empirical
16 bias prior, respectively, to explore the impact of these two options on the results. Marginal
17 posterior probabilities for ancestral character states were calculated using the same 1,000 post
18 burn-in trees.
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29 **Results and Discussion**

30 *Polyphyly of Micromys and Pithecheir divisions: a re-examination of dental characters in the* 31 *light of molecular findings*

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33 As reported previously (Steppan et al., 2005; Rowe et al., 2008; Schenk et al., 2013), the 8
34 representatives of the *Micromys* division did not form a monophyletic group and were
35 distributed throughout the phylogeny of Murinae, confirming the polyphyletic status of the
36 division (Figure 2). As in other studies, we recovered a sister relationship of the genus
37 *Micromys* with the molecular tribe Rattini (Lecompte et al., 2008) that contains the
38 *Dacnomys*, *Maxomys* + *Crunomys*, *Melasmothrix* and *Rattus* divisions (PP=1, Bp=100%, see
39 Fabre et al., 2013; Pagès et al., 2010). We recovered a sister-relationship of *Chiropodomys*
40 with the Hydromyini (1, 100%) and an uncertain placement of *Vandeleuria* possibly with a
41 clade comprising the Malacomyini, Apodemini, Murini and Praomyini molecular tribes but
42 with weak support (0.81, 46%). Both of these results are congruent with previously published
43 molecular phylogenies (Rowe et al., 2008; Schenk et al., 2013). *Hapalomys* is placed as the
44 first lineage to diverge from other Murinae (monophyly of the other Murinae: 0.98/83) in
45 agreements with assumptions proposed by Badenhorst et al., 2012.
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3 Revising morphological traits of species in light of our novel molecular classification
4 appeared to result in an overall consistent picture. Indeed, *Chiropodomys* dental morphology
5 falls within the large range of dental morphological diversity displayed by Hydromyini
6 (including the basin-shaped molars of the carnivorous water rat *Hydromys* to the primitive and
7 *Progonomys*-like dental plan of the hopping mouse, *Notomys*) (Figure 3). *Chiropodomys*,
8 however, presents a stephanodont (paracone-metacone) connection (see character 1 (1) in
9 Figure 3), which is absent in all Hydromyini. This level of dental dissimilarity supports its
10 phylogenetic position outside this tribe. *Vandeleuria* displays a large, rounded t7
11 (posterostyle, (2)), a very weak metacone and a stephanodont (paracone-metacone)
12 connection ((1) in Figure 3), which fall within the range of dental variation of the Apodemini,
13 Murini, Malacomysini and Praomyini tribes. Murine dental morphology is characterized by the
14 “murine rasp”, a peculiar functional pattern corresponding to upper molars with three
15 longitudinal functional cusp rows interlocking with the two longitudinal functional cusp rows
16 of the lower molars ((3) in Figure 3) (e.g. Lazzari *et al.*, 2008). *Hapalomys* displays a more
17 complex “murine rasp” than any other Murinae, notably, with three longitudinal functional
18 cusp rows on lower molars and equally sized cusps in the three longitudinal cusp rows of the
19 upper molars ((4) in Figure 3). Considering this “murine rasp” as a highly derived dental trait
20 among Murinae probably explained why the basal divergence of *Hapalomys* from the
21 remaining Murinae has never been conceived based on morphological data alone. In
22 conclusion, the breakup of the former *Micromys* division based on our molecular tree appears
23 consistent with the highly different dental morphologies displayed by its representatives (*i.e.*
24 presence of large c1 and c3 labial cusps on lower m1-m2 in *Hapalomys* and *Chiropodomys*
25 (5) in Figure 3), which are totally absent in other genera; very reduced metacone on upper
26 M1-2 in *Micromys* and *Vandeleuria* whereas this cusp is very large in *Hapalomys* and
27 *Chiropodomys*; (6) in Figure 3).

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Representatives of the *Pithecheir* division are also dispersed through the murine
phylogeny (Figure 2). *Lenothrix* was placed as the sister taxon of *Margaretamys* (1, 95%) and
the two genera were phylogenetically nested within the *Dacnomys* division of the Rattini tribe
(here represented by the genera *Dacnomys*, *Chiromyscus*, *Leopoldamys*, *Niviventer*,
Saxatilomys and *Tonkinomys*) (1, 100%). This is consistent with the placement of
Margaretamys in a recent phylogenetic analysis (Schenk *et al.*, 2013). This result is congruent
with the strikingly similar dental morphology of these two genera, which both display a strong
t4bis associated with a distally-positioned t4 ((7) in Figure 4) (a character which is rare among
Murinae), a very massive mesostyle as large as the paracone and linked to this cusp on M1-2

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3 ((8) in Figure 4), and a well individualized posteroloph on M1-2 ((9) in Figure 4), which can
4 all be viewed as shared derived characters considering the ancestral morphology of the middle
5 Miocene Murinae (Lazzari *et al.*, 2010). They form currently the only cluster of two members
6 of the old *Pithecheir* division. We emphasize that the rodents of the *Dacnomys* division do not
7 display the derived characters mentioned above for the *Lenothrix-Margaretamys* group,
8 instead they are morphologically more similar to Murinae of the *Rattus* genus. The
9 *Tonkinomys* + *Saxatilomys* clade appears basal within *Dacnomys* division, *Lenothrix* +
10 *Margaretamys* representing a well-supported clade with remaining genera (*Leopoldamys*,
11 *Niviventer*, *Chiromyscus* and *Dacnomys*) (1, 99%).

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18 The genus *Pithecheir* was placed within a clade containing the molecular tribe Millardini with
19 moderate support (monophyly of *Pithecheir* + Millardini = 1, 81%). However, we could not
20 resolve the precise placement of *Pithecheir* within the Millardini. Our ML tree grouped
21 *Pithecheir* together with *Cremnomys* (41%) within Millardini, while our BI tree placed
22 *Pithecheir* as sister taxa to the Millardini tribe but with weak support for the monophyly of
23 Millardini (PP= 0.71). The dental morphology of *Pithecheir* is however very different from
24 the morphology displayed by species of the Millardini tribe such as *Millardia* and
25 *Cremnomys*. Upper molars of *Pithecheir* display massive, rounded posterostyles (t7, (10) in
26 Figure 4) which are completely absent in Millardini ; Millardini lower molars display an
27 accessory labial cusp which seems to be absent in *Pithecheir* ((11) in Figure 4).

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35 Given the strong support from our study to previous suggestions that the former
36 *Micromys* and *Pithecheir* divisions are polyphyletic, we propose to abandon this
37 nomenclature. Dental features shared by the lineages of these divisions (presence/absence of
38 cusp t1bis & t2bis, cusp t7 on the upper molar) should be considered as homoplastic characters
39 and can definitively not be used as informative characters to infer phylogenetic relationships.
40 It is important to note that *Chiropodomys*, *Hapalomys*, *Vandeleuria*, and potentially
41 *Pithecheir* are not nested within any of the currently well-accepted tribes of Murinae. Instead,
42 they are placed as a sister taxa of these tribes. In light of this observation, the former inclusion
43 of *Micromys minutus* within Rattini (Musser & Carleton, 2005) is puzzling. *Micromys* is
44 recognized as being the first lineage to diverge within the tribe (Lecompte *et al.*, 2008; Rowe
45 *et al.*, 2008) but it first appeared in the late Miocene in China (Horacek *et al.*, 2013), and its
46 recent distribution throughout Europe and northern Asia comprises a distinct biogeographical
47 region compared to the Rattini original diversification centre. Moreover, the dental
48 morphology of *Micromys* strongly differs from most other Rattini by its paracone-metacone
49 junction ((13) in Figure 3) and its large t7 on upper molars ((14) in Figure 3).

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3 Based on these results, we proposed to split the polyphyletic *Micromys* division into,
4 at least, 4 monotypic tribes: (i) Chiropodomysini, (ii) Hapalomyini, (iii) Micromyini, and (iv)
5 Vandeleuriani (Table 1). Additional data are needed to establish the status of the tribe
6 Vandeleuriani, given the large uncertainty in phylogenetic inference from all available
7 information.. We also proposed to split the *Pithecheir* division since *Lenothrix* and
8 *Margaretamys* should be recognized as representatives of *Dacnomys* division within the
9 Rattini tribe. However, because only moderate supports obtained in our study for any of the
10 possible phylogenetic relationships of *Pithecheir* (only *cytb* and *IRBP* fragments were
11 sequenced from museum specimens), further phylogenetic information will be required to
12 assess its affinities and its taxonomic rank. In the near future, changes in the nomenclature are
13 very likely to occur as additional molecular and morphological data will be available for the
14 remaining *incertae sedis* lineages of Sulawesi (*Eropelus*, *Haeromys*, *Lenomys*), Sunda
15 (*Haeromys*, *Pithecheirops*, *Kadarsonomys*), Flores (*Papagomys*, *Paulamys*), Southeast Asia
16 (*Vernaya*) and Philippines (*Abditomys*, *Anonymomys*), which include various rare species (see
17 also Aplin & Helgen, 2010).
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30 *Polyphyly of arboreal taxa: implication for interpreting the evolution of arboreal adaptation*
31 *within Murinae*

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33 Most of the lineages of the polyphyletic *Micromys* division appear as sister-lineage to major
34 tribes of Murinae (Figure 2). It holds true for some lineages of the *Pithecheir* polyphyletic
35 division if the placement of *Pithecheir* sister to Millardini (BI tree) is confirmed. Two
36 interpretations might be proposed in front of these results (i) *Micromys*, *Chiropodomys*,
37 *Vandeleuria* and *Hapalomys* tribes might be morphologically derived relics of early murine
38 diversifications that have survived extinction or (ii) these arboreal lineages might represent
39 plesiomorphic arboreal lineages and the Most Recent Common Ancestor (MRCA) of Murinae
40 would be arboreal. The examination of the locomotion of fossil ancestors of Murinae is
41 necessary to answer this question. The question "What is the ancestor of the true Murinae?"
42 asked by de Bruijn *et al.* (1996) and many others remains unanswered and a topic of ongoing
43 polemics (see Fabre *et al.*, 2013; Schenk *et al.*, 2013 for some recent discussion). Murinae are
44 defined by a unique set of external, cranial, postcranial, dental, reproductive, and arterial
45 features (Carleton & Musser, 1984). As the most abundant material of the rodent fossil record
46 consists of jaws and teeth, derived molar conditions form the primary basis for defining the
47 subfamily based on morphology alone. As mentioned earlier, the oldest extinct and recorded
48 taxon displaying both the derived dental plan and occlusal pattern characterizing all extant
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3 Murinae is the genus *Progonomys* Schaub, 1938, whose oldest representatives retrieved in
4 Pakistan are considered to be 12.3 Myr-old (Jacobs & Flynn, 2005). If the detailed and well-
5 calibrated fossil record from the Siwalik succession in Pakistan is an accurate depiction of
6 murine history, *Progonomys* should be either considered as the MRCA of extant murines or a
7 predecessor (Steppan *et al.*, 2004b). However, *Progonomys* is viewed by many authors as a
8 paraphyletic genus, since it houses species that have been brought together on the mere basis
9 of sharing plesiomorphic characters (Mein *et al.*, 1993). It is now viewed as the “basket case”
10 of all, or a part of extant Murinae. Interestingly, a close relationships between *P. debruijni* and
11 *Mus auctor*, the oldest representative of the genus *Mus*, has been proposed (*e.g.* Jacobs,
12 1978). Relationships between *P. cathalai* and the Apodemini, a tribe close to the Murini, have
13 also been proposed but remain controversial (see Aguilar & Michaux, 1996; Martin-Suarez &
14 Mein, 1998). Consequently, the extinct *Progonomys* is still considered by some authors as the
15 MRCA of the *Mus-Rattus* clade (a clade encompassing all the murine representatives with the
16 classical and typical murine dental pattern). If the paraphyletic genus *Progonomys*
17 corresponds to the *Mus-Rattus* dichotomy, the MRCA of Phloeomyini and *Hapalomys* should
18 be searched in genera such as the extinct *Potwarmus* and *Antemus* mainly from the middle
19 Miocene of South Asia, confirmed as stem Murinae by a recent cladistic analysis (Lopez-
20 Antonanzas, 2009), displaying an intermediary dental plan (Coillot *et al.*, 2013). Whichever is
21 the true ancestor of the Murinae, postcranial elements of *Progonomys*, *Antemus* and
22 *Potwarmus* have never been properly described, and the locomotion of these extinct taxa is
23 still unknown. However, in Europe, *Progonomys* species from the Iberian Peninsular are
24 thought to have been associated with open, dry habitats (*e.g.* Daams *et al.*, 1988), and are
25 usually regarded as terrestrial, mouse-like equivalents. Therefore, based on early murine fossil
26 records (Daams *et al.*, 1988; Jacobs & Downs, 1994; Jacobs *et al.*, 1990; Jacobs & Pilbeam,
27 1980; Jaeger *et al.*, 1986), the hypothesis considering *Micromys*, *Chiropodomys*, *Vandeleuria*,
28 *Hapalomys* and *Pithecheir* as morphologically derived relics of ancient murine
29 diversifications appears to have reasonable support. Our ASR analysis on the ancestral state
30 of the molar cusp t7 reinforces this assumption. Although our ASR analysis was confined to a
31 single morphological character, its most likely outcomes suggested multiple independent
32 emergence of the molar cusp t7 ~~the molar presence~~ in the murine phylogeny (Figure S3,
33 supplementary data). (Figure S3, supplementary data). Consequently, characters that were
34 formerly used to define the obsolete *Pithecheir* and *Micromys* divisions and that were
35 assumed to be associated with arboreal lifestyle (*e.g.* presence/absence of an opposable
36 hallux) are likely to be homoplastic too.
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3 Finally, if *Micromys*, *Chiropodomys*, *Hapalomys*, *Vandeleuria* and *Pithecheir* genera
4 represent morphologically derived relics of various distinct tribes, it raises questions about the
5 cause of extinction of their (unknown) closest relatives and whether survival of the extant
6 species occurred simply by chance or because of particular common adaptations that may
7 have enabled persistent species to bypass extinction events. The relatively high frequency of
8 fossil species records of the genus *Micromys* in the early Pliocene, opposed to rare records in
9 the early Pleistocene suggests a radiation of this genus during the early Pliocene and
10 effectively its demise during Pleistocene (Horacek *et al.*, 2013). However, although *Micromys*
11 is reported from a relatively large number of European fossil assemblages, in most instances
12 the material is restricted to just a few isolated teeth, often a single one (Horacek *et al.*, 2013).
13 Consequently, the limited amount of currently available information on morphological traits
14 of species having survived and gone extinct prevents conclusion on their specific adaption to
15 terrestrial and arboreal habitats and how extinction events were linked to possible changes and
16 constraints in available habitats. The evidence of polyphyletic relationships of arboreal
17 murine species provided in our study nevertheless opens interesting avenues for future
18 research to explore eco-evolutionary pathways of species adaptation and radiation into
19 terrestrial and arboreal habitats under geographically and temporally changing environmental
20 conditions.

21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 *Revisiting the early evolution of Murinae*

36 The unique molar morphology displayed by all the modern Murinae - three longitudinal rows
37 of cusps - is considered as the diagnostic character of Murinae subfamily. Murine upper
38 molars are characterized by three longitudinal rows of cusps due to the presence of
39 autapomorphic lingual cusps, while the plesiomorphic upper molars found in other Muroidea
40 display two longitudinal rows of cusps (Coillot *et al.*, 2013). With *Progonomys* being the
41 oldest fossil known to date displaying this complete murine dental plan, this 12.3 Mya old
42 fossil was consequently considered as the closest relative to the common ancestor of all the
43 modern Murinae. Conversely, representatives of the tribe Phloeomyini display a highly
44 derived murine pattern, with highly lophodont dental morphologies associated with the
45 presence of a posterostyle (t7) on upper molars at least in some genera (*e.g. Batomys*), and a
46 very large tma on first lower molars (Figure 3). Molecular data reveal that this tribe is
47 strongly anchored at the base of the murine tree (Steppan *et al.*, 2005). This finding raises
48 controversy about where to place *Progonomys* in the murine tree. Some authors considered
49 *Progonomys* to be either an ancestor, or a sister taxa of the *Mus-Rattus* clade. Alternatively,
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3 *Progonomys* was considered as the ancestor, or the sister taxa of all modern murines since
4 Phloeomyini corresponds to an insular lineage and because island evolution is known to
5 induce considerable morphological changes (e.g. Pagès *et al.*, 2011). Our study reveals a basal
6 divergence between the Southeast Asian *Hapalomys* division and the other Murinae.
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8 *Hapalomys* division regroups also fairly distinct taxa at the dental point of view compared to
9 other “classical” murines, displaying a more complex “murine rasp” with three longitudinal
10 functional cusp rows on lower molars and equally sized cusps in the three longitudinal cusp
11 rows of the upper molars (Misonne, 1969; Musser & Heaney, 1992).

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16 Consequently, our study opens once again the *Progonomys* Pandora’s box: where to place this
17 fossil constraint? It also raises questions about characters that are diagnostic of Murinae. Our
18 current molecular dating estimations could not help to solve these questions. Indeed, the
19 oldest 12.3 Myr-occurrence of *Progonomys* falls within the range of our estimates for both the
20 basal split of Hapalomyini from other Murinae (Hapalomyini/other Murinae: 11.60-15.89
21 Myr) and the divergence of the Phloeomyini from other Murinae (Phloeomyini/other
22 Murinae: 10.87-14.42 Myr). Due to the uncertainty of the sister lineages of *Progonomys* (see
23 also Rowe *et al.*, 2011; Rowe *et al.*, 2008; Schenk *et al.*, 2013; Steppan *et al.*, 2004b),
24 avoidance of this fossil constraints or its careful placement with use of multiple fossils seems
25 to be advocated. An independent evolution of the “murine rasp” has been suggested at least
26 for the Deomyinae (Chevret *et al.*, 1993; Lazzari *et al.*, 2008). Along with our findings of two
27 murine divisions with atypical murine dental plan diverging first, questions whether the
28 murine rasp is indeed a synapomorphy of the Murinae or whether it has evolved
29 independently within the Hapalomyini, Phloeomyini and other Murinae. A parsimonious
30 approach would suggest this feature to have evolved only once but in light of our findings,
31 parsimony explanation seems to poorly match Murine diversification for dental features (e.g.
32 cusp t7) and adaptations to arboreal versus terrestrial lifestyle alike.

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38 **Figure 1.** Occlusal views of upper and lower first molar teeth of Murinae. Nomenclature of
39 murine first molars, according to Cope-Osborn; correspondence with the nomenclature of
40 Miller indicated in brackets. Top: left upper molar. Bottom: right lower molar. Modified from
41 Lazzari *et al.*, 2010.
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47 **Figure 2.** Phylogenetic and molecular dating results for the Southeast Asian murine and
48 close-relative lineages. The tree is a chronogram (uncorrelated log-normal molecular clock)
49 based on a BEAST MCMC analysis of the combined data set. The green and blue colour
50 indicates the former *Micromys* and the *Pithecheir* divisions respectively. We proposed to split
51 the polyphyletic *Micromys* division into, at least, 4 monotypic tribes highlighted in green
52 capitals: (i) *Chiropodomys*, (ii) *Hapalomys*, (iii) *Micromys*, and (iv) *Vandeleurians*.
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Numbers at nodes represent branch supports (BP/PP). ‘*/’ stands for ‘BP=100%’, ‘/*’ for ‘PP=1.00’, ** for ‘BP=100% AND PP=1.00’, ‘-’ not supported by one out of the two analyses. When support information is lacking, it means that the branch is not supported.

Clocks indicate the fossil calibration points used for the molecular dating (see Fabre *et al.*, 2013); 95% credibility intervals of molecular estimates (median height) are given for each node. Abbreviations: PLIO. : Pliocene, Pi: Piacenzian, PLEIST.: Pleistocene, Myr: million years.

Figure 3. Dental characters of the arboreal Murinae from Southeast Asia compared with their sister-taxa in lights of the molecular phylogeny obtained in this study. Representatives of the paraphyletic *Micromys* division are highlighted in green, their sister-taxa in black. Plain and dotted arrow indicates respectively presence / absence of a character mentioned in the discussion.

Top: left upper molar. Bottom: right lower molar. Modified from Misonne, 1969; Musser, 1981.

Figure 4. Dental characters of the arboreal Murinae from Southeast Asia compared with their sister-taxa in lights of the molecular phylogeny obtained in this study. Representatives of the paraphyletic *Pithecheir* division in blue, sister-taxa in black. Plain and dotted arrow indicates respectively presence / absence of a character mentioned in the discussion.

Top: left upper molar. Bottom: right lower molar. Modified from Misonne, 1969; Musser, 1981.

Table 1. Higher level classification of extant Rodentia (see text for further details on references) largely inspired from state of the art molecular systematic and with explicit references to Wilson & Reeder, 2005. *: paraphyletic groups. Bold: members of the former *Micromys* and *Pithecheir* divisions. Several taxa are still classified as "*incertae sedis*" pending for molecular phylogenetic investigation.

Murinae	Tribes	Divisions	Putative members
<i>Hapalomys</i>	HAPALOMYINI	<i>Hapalomys</i> division	
<i>Batomys</i>	PHLOEOMYINI	<i>Phloeomys</i> division	
<i>Carpomys</i>			

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3	<i>Crateromys</i>			
4	<i>Musseromys</i>			
5	<i>Phloeomys</i>			
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7	<i>Chiropodomys</i>	CHIROPODOMYINI	<i>Chiropodomys</i> division	
8	<i>Apomys</i>	HYDROMYINI	<i>Chrotomys</i> division	
9	<i>Archboldomys</i>			
10	<i>Chrotomys</i>			
11	<i>Rhynchomys</i>			
12	<i>Soricomys</i>			
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14	<i>Conilurus</i>	HYDROMYINI	<i>Pseudomys</i> division*	
15	<i>Leggadina</i>			
16	<i>Leporillus</i>			
17	<i>Mastacomys</i>			
18	<i>Mesembriomys</i>			
19	<i>Notomys</i>			
20	<i>Pseudomys</i>			
21	<i>Zyomys</i>			
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23	<i>Crossomys</i>	HYDROMYINI	<i>Hydromys</i> division	<i>Baiyankamys</i>
24	<i>Hydromys</i>			
25	<i>Parahydromys</i>			
26				
27	<i>Leptomys</i>	HYDROMYINI	<i>Xeromys</i> division	<i>Paraleptomys</i>
28	<i>Microhydromys</i>			
29	<i>Pseudohydromys</i>			
30	<i>Xeromys</i>			
31				
32	<i>Melomys</i> *	HYDROMYINI	<i>Uromys</i> division	<i>Xenuromys</i>
33	<i>Paramelomys</i>			
34	<i>Protochromys</i>			
35	<i>Solomys</i>			
36	<i>Uromys</i>			
37				
38	<i>Abeomelomys</i>	HYDROMYINI	<i>Pogonomys</i> division	
39	<i>Anisomys</i>			
40	<i>Brassomys</i>			
41	<i>Chiruromys</i>			
42	<i>Coccymys</i>			
43	<i>Hyomys</i>			
44	<i>Lorentzimys</i>			
45	<i>Macruromys</i>			
46	<i>Mammelomys</i>			
47	<i>Mallomys</i>			
48	<i>Pogonomelomys</i>			
49	<i>Pogonomys</i>			
50				
51	<i>Micromys</i>	MICROMYINI	<i>Micromys</i> division	
52	<i>Maxomys</i>	RATTINI	<i>Maxomys</i> division	
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3	<i>Crunomys</i>			
4	<i>Chiromyscus</i>	RATTINI	<i>Dacnomys</i> division	<i>Anonymomys</i>
5	<i>Dacnomys</i>			
6	<i>Lenothrix</i>			
7	<i>Leopoldamys</i>			
8	<i>Margaretamys</i>			
9	<i>Niviventer</i>			
10	<i>Saxatilomys</i>			
11	<i>Tonkinomys</i>			
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14	<i>Bunomys</i>	RATTINI	<i>Rattus</i> division	
15	<i>Bandicota</i>			<i>Abditomys</i>
16	<i>Berylmys</i>			<i>Hadromys</i>
17	<i>Bullimus</i>			<i>Kadarsanomys</i>
18	<i>Diplothrix</i>			<i>Komodomys</i>
19	<i>Halmaheramys</i>			<i>Nesoromys</i>
20	<i>Limnomys</i>			<i>Palawanomys</i>
21	<i>Nesokia</i>			<i>Papagomys</i>
22	<i>Paruromys</i>			<i>Tryphomys</i>
23	<i>Paulamys</i>			
24	<i>Rattus*</i>			
25	<i>Srilankamys</i>			
26	<i>Sundamys</i>			
27	<i>Taeromys</i>			
28	<i>Tarsomys</i>			
29				
30	<i>Melasmothrix</i>	RATTINI	<i>Melasmothrix</i> division	
31	<i>Paucidentomys</i>			
32	<i>Sommeromys</i>			
33	<i>Tateomys</i>			
34	<i>Echiothrix</i>			
35	<i>Waiomys</i>			
36				
37	<i>Vandeleuria</i>	VANDELEURINI	<i>Vandeleuria</i> division	
38	<i>Mus</i>	MURINI	<i>Mus*</i> division	<i>Muriculus</i>
39	<i>Malpaisomys</i>			
40	<i>Colomys</i>	PRAOMYINI	<i>Stenocephalemys</i> division	<i>Nilopegamys</i>
41	<i>Zelotomys</i>			
42	<i>Heimyscus</i>			
43	<i>Hylomyscus</i>			
44	<i>Mastomys</i>			
45	<i>Myomyscus</i>			
46	<i>Praomys</i>			
47	<i>Stenocephalemys</i>			
48	<i>Myotomys</i>	OTOMYINI	<i>Otomys</i> division	
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1	<i>Parotomys</i>			
2	<i>Cretnomys</i>	MILLARDINI	<i>Millardia</i> division	<i>Diomys</i>
3	<i>Millardia</i>			<i>Madromys</i>
4	<i>Pithecheir</i>	MILLARDINI	<i>Pithecheir</i> division	<i>Pithecheirops</i>
5	<i>Apodemus</i>	APODEMINI		
6	<i>Tokudaia</i>			
7	<i>Aethomys</i>	ARVICANTHINI	<i>Aethomys</i> division	
8	<i>Micaelamys</i>			
9	<i>Arvicanthis</i>			
10	<i>Desmomys</i>			
11	<i>Lemniscomys</i>			
12	<i>Mylomys</i>			
13	<i>Pelomys</i>			
14	<i>Rhabdomys</i>			
15	<i>Dasymys</i>	ARVICANTHINI	<i>Dasymys</i> division	
16	<i>Golunda</i>	ARVICANTHINI	<i>Golunda</i> division	
17	<i>Dephomys</i>	ARVICANTHINI	<i>Hybomys</i> division	
18	<i>Hybomys</i>			
19	<i>Stochomys</i>			
20	<i>Grammomys</i>	ARVICANTHINI	<i>Oenomys</i> division	<i>Lamottemys</i>
21	<i>Oenomys</i>			
22	<i>Rhagamys</i>			
23	<i>Thamnomys</i>			
24	<i>Malacomys</i>	MALACOMYINI	<i>Malacomys</i> division	
25	<i>Vernaya</i>	Murinae <i>incertae sedis</i>		
26	<i>Haeromys</i>	Murinae <i>incertae sedis</i>		
27	<i>Eropeplus</i>	Murinae <i>incertae sedis</i>		
28	<i>Lenomys</i>	Murinae <i>incertae sedis</i>		
29	<i>Spelaeomys</i> +	Murinae <i>incertae sedis</i>		
30	<i>Coryphomys</i> +	Murinae <i>incertae sedis</i>		

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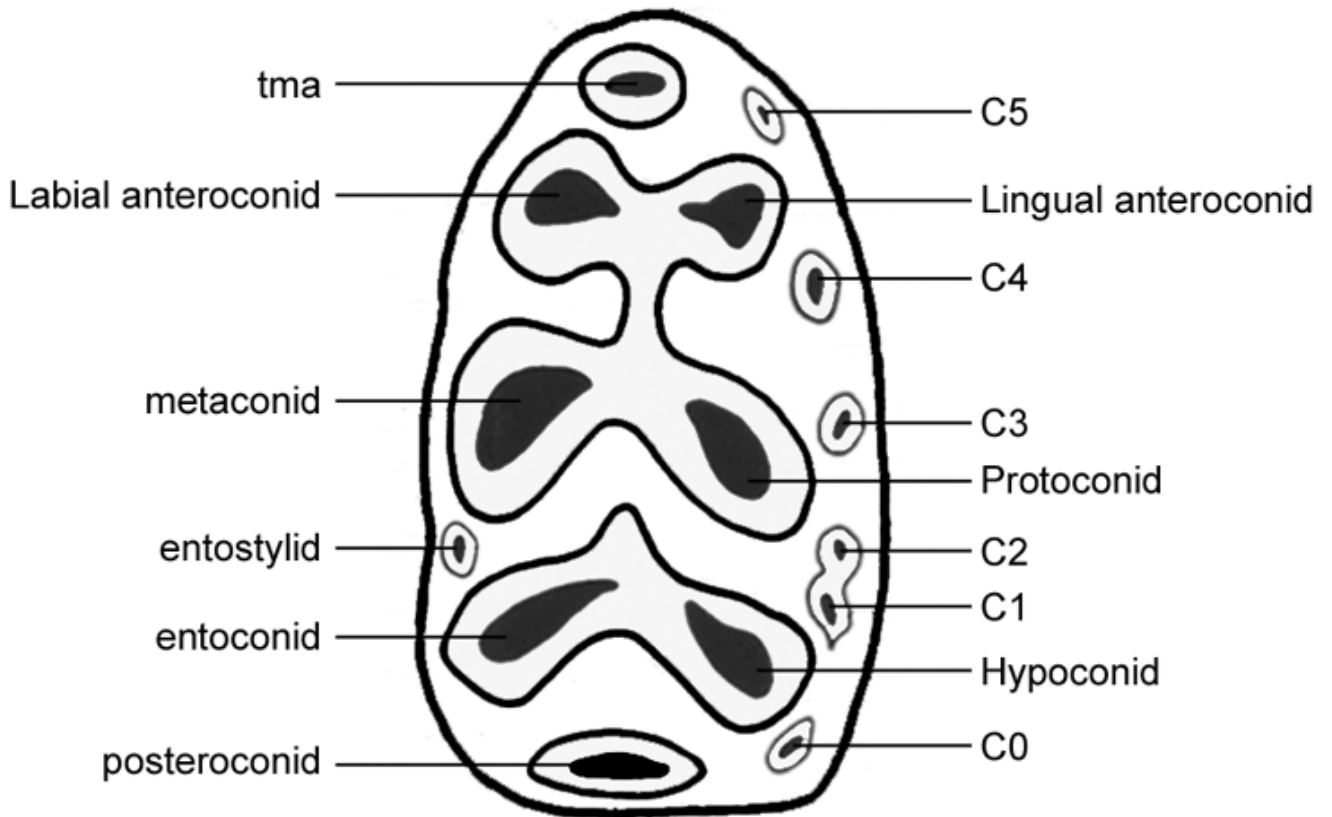
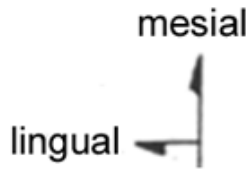
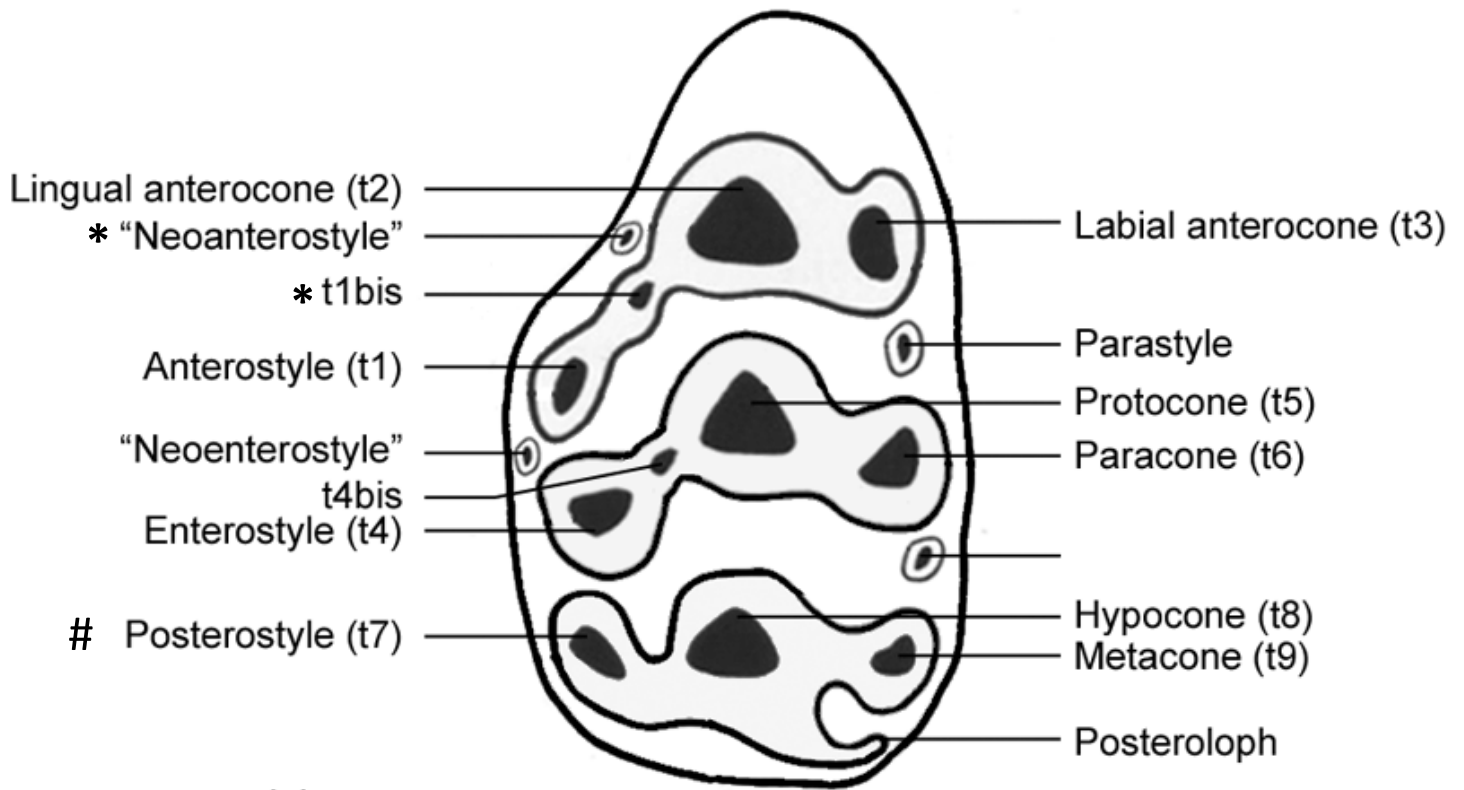
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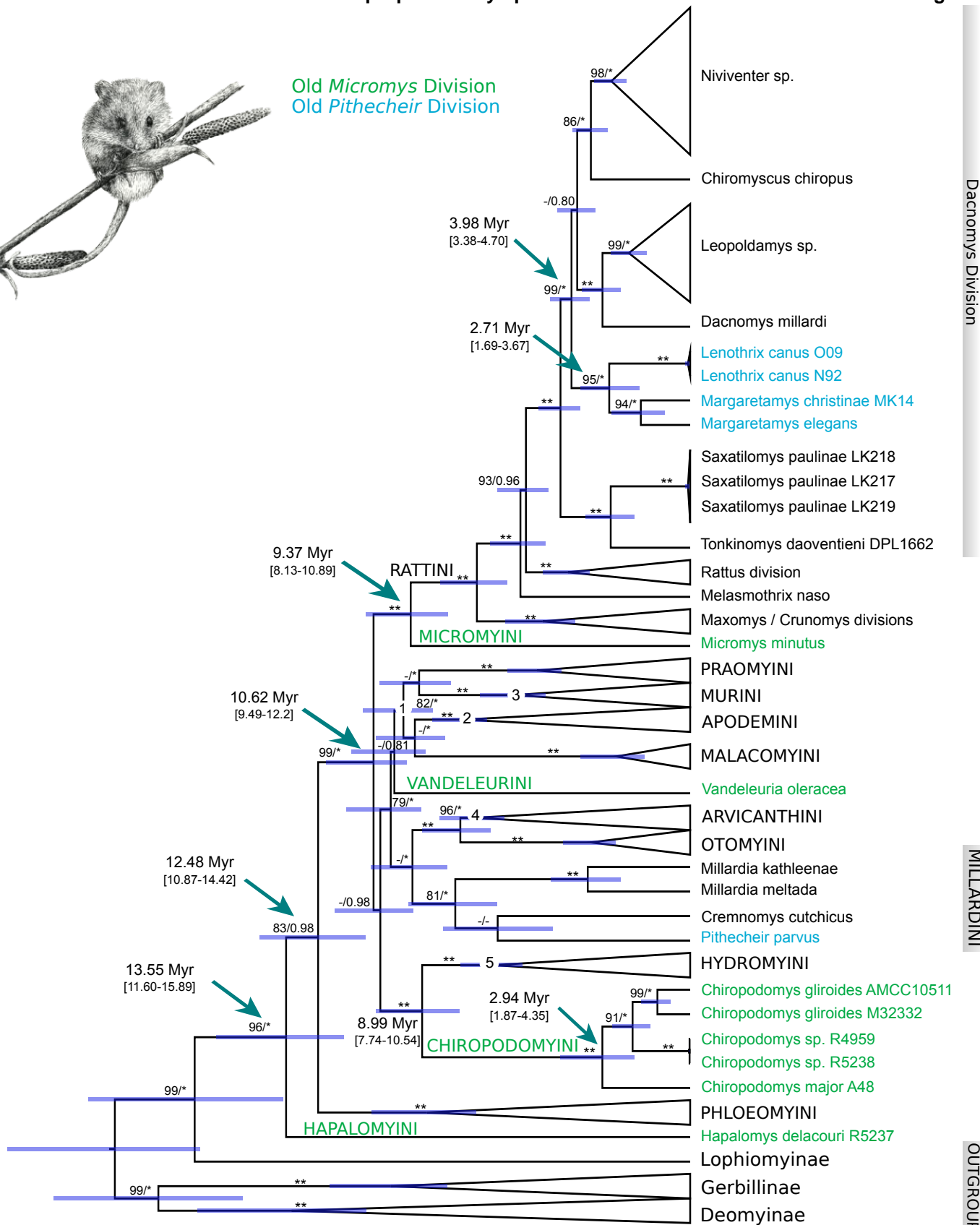
Two major teeth convergences in both *Micromys* and *Pithecheir* divisions:

*: presence of cusp t1bis and t2bis

#: presence of cusp t7



Old *Micromys* Division
Old *Pithecheir* Division



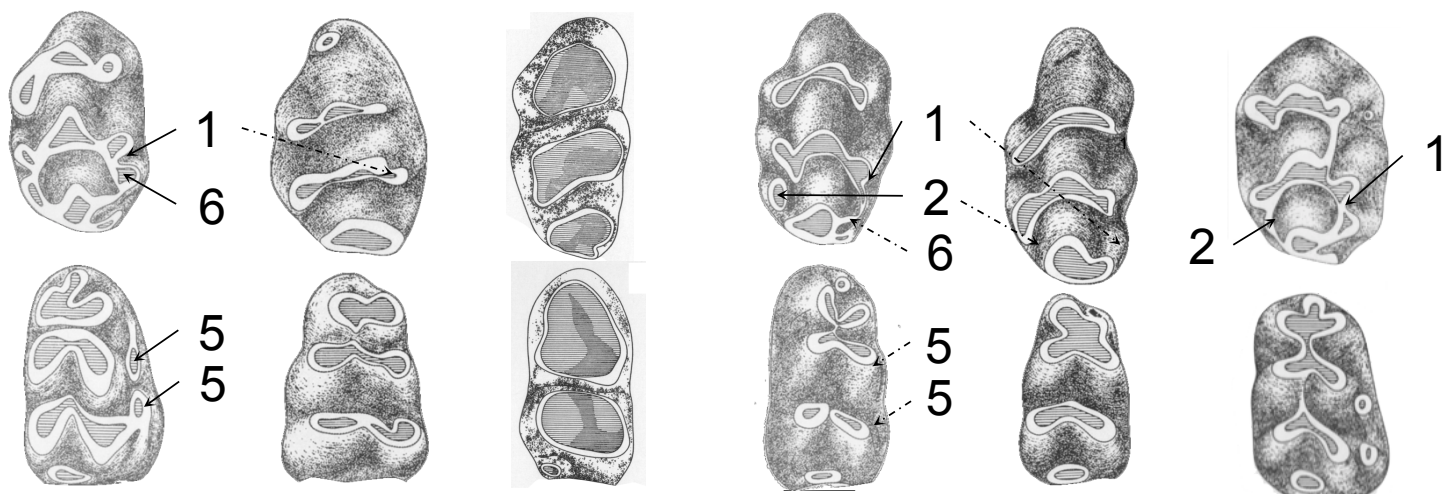
Dacnomys Division

MILLARDINI

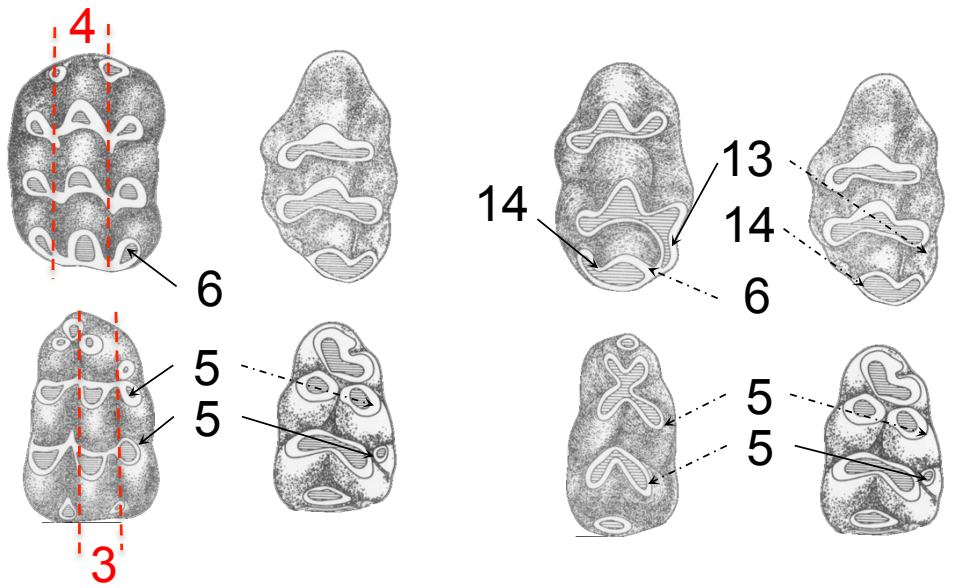
OUTGROUPS

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Paraphyletic *Micromys* division



Chiropodomys gliroides *Notomys alexis* *Hydromys chrysogaster* *Vandeleuria oleracea* *Mus booduga* *Apodemus sylvaticus*

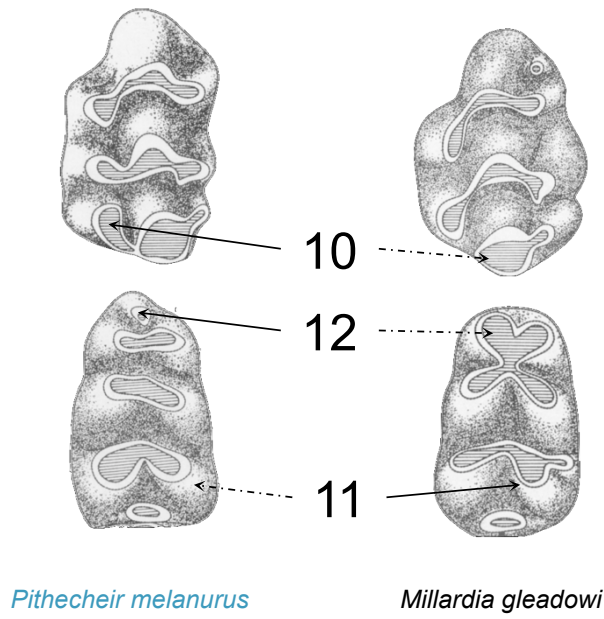
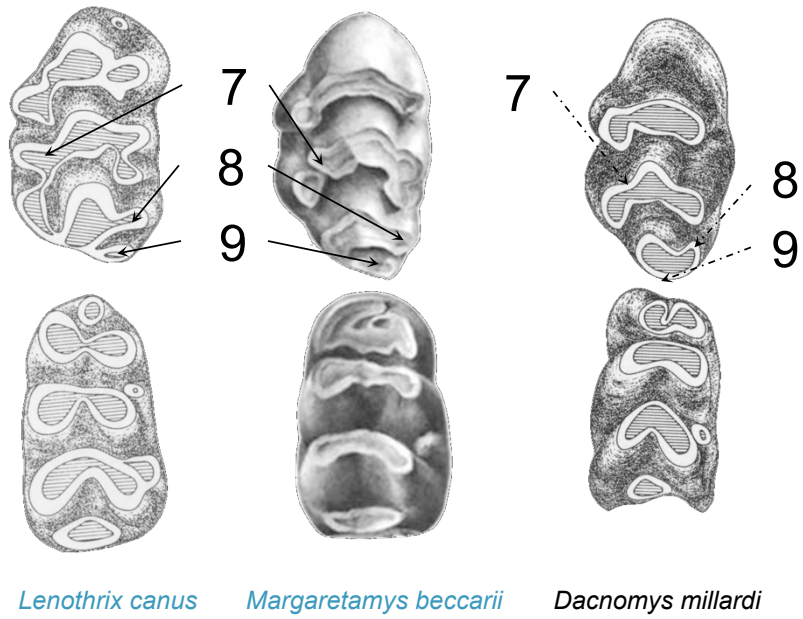


Hapalomys longicaudatus *Rattus rattus* *Micromys minutus* *Rattus rattus*

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Paraphyletic *Pithecheir* division



SUPPLEMENTARY INFORMATION

Figure S1: Maps of the Indo-Pacific area indicating

A) the contemporary major islands, seas, and biogeographic areas (map derived from (Fabre *et al.*, 2013)

B) the distribution of the genera of the *Micromys* and *Pithecheir* divisions respectively.

Maps were extracted and modified from R (Kiel, Germany).

A)



B)

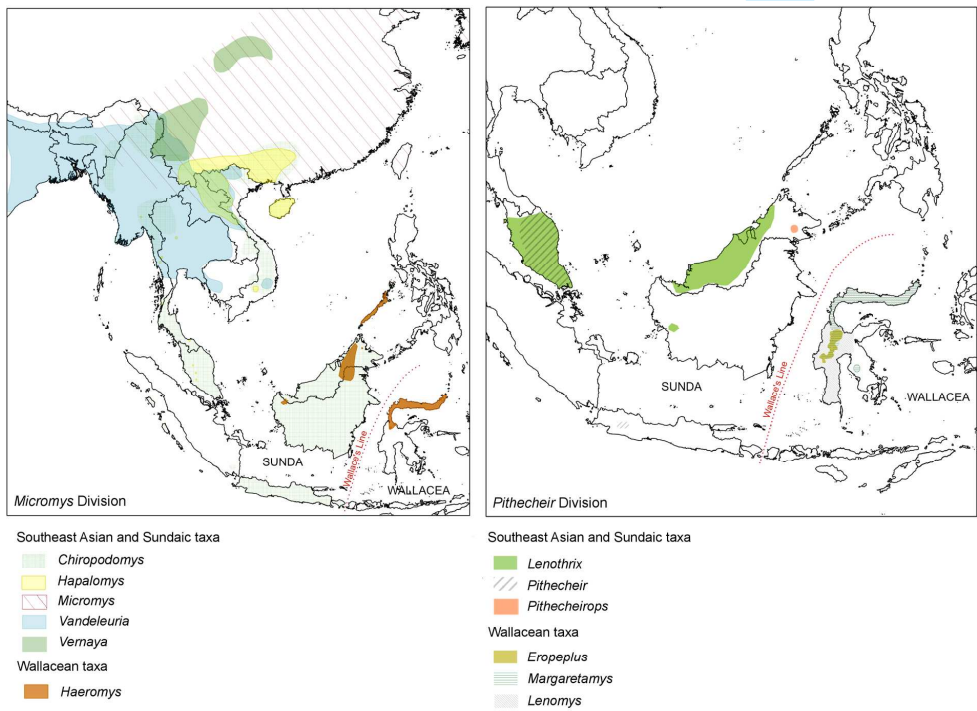


Table S1: List of the species considered in this study and GenBank accession numbers of sequences.

a) Information about samples handled in this study (new data)

Division	Genus	Species	Common Name	Voucher	Locality	Collection
<i>Rattus</i>	<i>Saxatylomys</i>	<i>paulinae</i>	Paulina's Limestone Rat	LK217	Khammouane, Laos	CERoPath
<i>Rattus</i>	<i>Saxatylomys</i>	<i>paulinae</i>	Paulina's Limestone Rat	LK218	Khammouane, Laos	CERoPath
<i>Rattus</i>	<i>Saxatylomys</i>	<i>paulinae</i>	Paulina's Limestone Rat	LK219	Khammouane, Laos	CERoPath
<i>Rattus</i>	<i>Tonkinomys</i>	<i>daoventieni</i>	Daovantien's Limestone Rat	DPL1662 (M-275575)	Huu Lien District, Lang Son Province, Vietnam	AMNH / AMCC
<i>Micromys</i>	<i>Micromys</i>	<i>minutus</i>	Eurasian Harvest Mouse	72 (MK0509 BZ02)	China	JP. Quéré
<i>Micromys</i>	<i>Micromys</i>	<i>minutus</i>	Eurasian Harvest Mouse	73 (MK0509 BZ07)	China	JP. Quéré
<i>Micromys</i>	<i>Vandeleuria</i>	<i>oleracea</i>	Asiatic Long-tailed Climbing Mouse	M30312*	Mt Popa, Popamyo Village	K. Aplin
<i>Micromys</i>	<i>Chiropodomys</i>	<i>gliroides</i>	Pencil-tailed Tree Mouse	M32332	Nampa Camp	K. Aplin
<i>Micromys</i>	<i>Chiropodomys</i>	<i>major</i>	Greater Pencil-tailed Tree Mouse	A48	Tawau Hills Park primary forest, Borneo	K. Wells
<i>Micromys</i>	<i>Chiropodomys</i>	<i>sp.</i>	-	R4959	Loei, Thailand	CERoPath
<i>Micromys</i>	<i>Chiropodomys</i>	<i>sp.</i>	-	R5238**	Loei, Thailand	CERoPath
<i>Micromys</i>	<i>Hapalomys</i>	<i>delacouri</i>	Lesser Marmoset Rat	R5237***	Loei, Thailand	CERoPath
<i>Pithecheir</i>	<i>Pithecheir</i>	<i>melanurus</i>	Javan Pithecheir	Pithecheir I (MNHN-ZM-MO 1900-580)	Java	MNHN
<i>Pithecheir</i>	<i>Pithecheir</i>	<i>melanurus</i>	Javan Pithecheir	Pithecheir II (MNHN-ZM-MO 1900-581)	Java	MNHN
<i>Pithecheir</i>	<i>Pithecheir</i>	<i>parvus</i>	Malay Peninsula Pithecheir	Pithecheir III (MNHN-ZM-MO 1977-251)	Simpang Pertang, Negri Sembilan, West Malaysia	MNHN
<i>Pithecheir</i>	<i>Pithecheir</i>	<i>parvus</i>	Malay Peninsula Pithecheir	Pithecheir IV (MNHN-ZM-MO 1977-252)	Selangor, Subang tima , West Malaysia	MNHN
<i>Pithecheir</i>	<i>Lenothrix</i>	<i>canus</i>	Sundaic Lenothrix	O09	Poring Hot Springs primary forest, Borneo	K. Wells
<i>Pithecheir</i>	<i>Lenothrix</i>	<i>canus</i>	Sundaic Lenothrix	N92	Poring Hot Springs primary forest, Borneo	K. Wells
<i>Pithecheir</i>	<i>Margaretamys</i>	<i>christinae</i>	Christine's Margareta Rat	RC1 / MK14	Pegunungan Mekongga, Southeast Sulawesi	R. Castiglia

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6 Most of these samples are vouchered and archived in accessible collections. Additional information
7 could be retrieved via the following database webpages:

8 <http://www.ceropath.org/>

9 <http://sci-web-001.amnh.org/db/emuwebamnh/>

10 <http://research.amnh.org/genomics/Facilities/AMCC/database/>

11 <https://science.mnhn.fr/institution/mnhn/collection/zm/item/search/form>

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13 Tissue samples provided by Dr. Ken Aplin and Dr. Jean-Pierre Quéré are housed at the Centre de
14 Biologie et de Gestion des Populations at Montpellier, France, with a part of the CeroPath
15 collection. Samples from Borneo (A48, O09 and N92) were collected from life captures with a
16 biopsy punch and have not been vouchered. Supplementary information on animal captures and
17 handling are detailed in Wells *et al.*, 2007. Sample of *Margaretamys christinae* (original field
18 number MK14) corresponds to the holotype specimen (Mortelliti *et al.*, 2012), deposited in the
19 Museum Zoologicum Bogoriense-LIPI, Cibinong, Java.

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26 * only *cytb* sequence was obtained from M30312. We combined this new *cytb* sequence with those
27 available in GenBank from another specimen of *Vandeleuria oleracea*.

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29 ** Six species of *Chiropodomys* are currently recognized (Musser & Carleton, 2005). Only one
30 species occurs in continental Southeast Asia, *C. gliroides*. According to Mammal Species of the
31 World, its distribution is extremely large and extends from W China to islands of the Sunda Shelf
32 (recorded in Burma, Thailand, Laos, Vietnam, Malay Peninsula, S Sumatra, Pulau Nias, Kepulauan
33 Tujuh, Kepulauan Natuna, Java, and Bali; probably also occurs on other small islands of the Sunda
34 Shelf and in Cambodia). Karyotype of a Thai specimen, R5238, was published by Badenhorst *et al.*,
35 2009 as having $2n=42$ and $NFa=40$. The authors reported that these results are in partial agreement
36 with previous data concerning this very poorly documented species. Indeed, Yong reported that
37 eight Malayan specimens were characterized by $2n=42$ and revealed differences in morphology of
38 autosomes and sex chromosomes (Yong, 1973, 1983). As a single specimen was available in
39 Badenhorst *et al.*, 2009 (*i.e.* R5238), the authors emphasized that it was impossible to distinguish
40 whether the differences correspond to intraspecific polymorphisms, or if they were indicative of
41 two cryptic species within *C. gliroides*. Recently, Yong and collaborators further investigated the
42 nucleolar organizer regions of *C. gliroides* from Peninsular Malaysia (Yong *et al.*, 2012). Here
43 again, they reported differences arguing for cryptic sibling species within *C. gliroides*. Currently, no
44 sequences of the Malaysian *Chiropodomys* are available to investigate this question with
45 phylogenetic tools. However, in our tree, 2 lineages within *C. gliroides* are retrieved: 1) a
46 Vietnamese lineage, AMCC 101511 from Vietnam (Vi Xuyen District, Ha Giang Province) (Rowe
47 *et al.*, 2008) and M32332 (Nampa Camp) (Bp = 99%, PP= 1.00); 2) a Thai lineage, R4959 and
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R5238 both from Loei (Bp = 100, PP= 1.00). These two lineages are clearly distinct from *Chiropodomys major* (A48 from Borneo).

*** Two species of *Hapalomys* are currently recognized (Musser & Carleton, 2005): *H. delacouri* in S China, N Laos and C Vietnam; and *H. longicaudatus* in SW China, SE Burma, SW and peninsular Thailand and Malay Peninsula. Karyotype of a Thai *H. delacouri* specimen, R5237, was described (Badenhorst *et al.*, 2012; Badenhorst *et al.*, 2009) as having $2n=48$ and $NFa=92$. A karyotype of a second specimen of *H. delacouri* from Southern Vietnam was reported as $2n=38$ and $NFa=48$ (Abramov *et al.*, 2012). These differences correspond to a range of variability that is too huge to be considered as intraspecific polymorphism (G. Dobigny, pers. comm.). Abramov and collaborators proposed to consider R5237 as another species of *Hapalomys*, *H. pasquieri*. *H. pasquieri* was previously described from Xieng Khouang in Northern Laos but is currently considered as a subspecies of *H. delacouri* by Musser ad Carleton (2005). No sequence has been published from the Vietnamese specimen, meaning that no molecular comparison could be achieved to disentangle these discrepancies.

Further investigations have to be carried out to refine the taxonomy of *Chiropodomys* and *Hapalomys*. However, these taxonomic uncertainties do not challenge our results concerning the relationships of these genera with the other murine representatives nor the polyphyly of the *Micromys* division.

b) Sequences extracted from GenBank:

Classification			cyt <i>b</i>	IRBP	GHR	BRCA1
Murinae						
Arvicanthini	<i>Aethomys</i> division	<i>Aethomys_chrysophilus</i>	AJ604515	AY326075	NA	NA
		<i>Micaelamys_namaquensis</i>	AF141215	AM408330	AY294914	EU349649
	<i>Arvicanthis</i> division	<i>Arvicanthis_niloticus</i>	AF004569	DQ022386	AM910944	NA
		<i>Arvicanthis_somalicus</i>	AF004573	NA	AY294918	NA
		<i>Arvicanthis_neumanni</i>	NA	KC953358	AY294918	EU349648
		<i>Desmomys_harringtoni</i>	AF141206	EU292144	NA	NA
		<i>Lemniscomys_barbarus</i>	NA	KC953387	DQ019062	KC953184
		<i>Lemniscomys_striatus</i>	AF141210	AM408321	AM910956	KC953184
		<i>Pelomys_fallax</i>	DQ022382	DQ022391	NA	NA
		<i>Rhabdomys_pumilio</i>	AF141214	AY326106	AY294913	EU349650
		<i>Mylomys_dybowski</i>	AF141212	EU292146	AM910965	NA
	<i>Dasymys</i> division	<i>Dasymys_incomtus</i>	AF141217	EU292143	AM910950	EU349653
		<i>Golunda_elliotti</i>	AM408338	AM408332	AM910951	NA
		<i>Hybomys_univittatus</i>	AF141219	DQ022388	DQ019059	KC953181
		<i>Stochomys_longicaudatus</i>	EU349786	EU349873	DQ019076	EU349652
		<i>Grammomys_dolichurus</i>	EU275252	EU349847	EU349800	NA
		<i>Grammomys_macmillani</i>	EU349746	EU349848	EU349802	KC953175

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6			<i>Grammomys surdaster</i>	EU349747	NA	EU349803	NA
7			<i>Grammomys ibeanus</i>	NA	KC953380	EU349801	KC953174
8			<i>Oenomys hypoxanthus</i>	EU349769	EU349865	DQ019069	EU349654
9	Otomyini	Subfamily Otomyinae	<i>Otomys anchietae</i>	AF492708	AY326101	GQ405388	NA
10			<i>Otomys angoniensis</i>	AM408343	AM408325	AM910971	EU349647
11			<i>Otomys denti</i>	NA	KC953428	KC953305	NA
12			<i>Parotomys brantsii</i>	EU349773	KC953432	AY294912	EU349646
13	Millardini	Millardia division	<i>Cremonomys cutchicus</i>	DQ022381	DQ022384	NA	NA
14			<i>Millardia kathleenae</i>	EU292148	EU292145	AM910963	NA
15			<i>Millardia meltada</i>	AF141221	AM408322	AM910962	NA
16	Apodemini	Apodemus division	<i>Apodemus agrarius</i>	EU349733	AB032858	DQ019054	EU349658
17			<i>Apodemus argenteus</i>	AB032848	AB032855	NA	NA
18			<i>Apodemus flavicollis</i>	AB032853	AB032860	AM910943	NA
19			<i>Apodemus mystacinus</i>	AF159394	AJ311158	AM910942	KC953157
20			<i>Apodemus semotus</i>	EU349734	AB032862	DQ019055	NA
21			<i>Apodemus speciosus</i>	AB032849	AB032856	AB491492	NA
22			<i>Apodemus sylvaticus</i>	AB033695	AB032863	NA	NA
23			<i>Tokudaia osimensis</i>	AB029429	AB033712	EU349828	EU349659
24	Malacomysini	Malacomys division	<i>Malacomys edwardsi</i>	DQ022379	DQ022392	AM910958	NA
25			<i>Malacomys longipes</i>	EU349757	DQ022393	DQ019064	EU349656
26	Praomyini	Colomys division	<i>Colomys goslingi</i>	AF518372	DQ022395	AM910948	NA
27			<i>Zelotomys hildegardeae</i>	EU349791	DQ022396	DQ019080	EU349661
28		Stenocephalemys division	<i>Heimyscus fumosus</i>	AF518333	DQ022397	AM910953	NA
29			<i>Hylomyscus parvus</i>	AF518330	DQ022399	DQ019060	NA
30			<i>Hylomyscus stella</i>	AF518331	AM408320	AM910955	NA
31			<i>Mastomys erythroleucis</i>	AF518338	AM408335	AM910959	KC953189
32			<i>Mastomys hildebrandti</i>	NA	KC953395	AY294916	AY295001
33			<i>Mastomys kollmannspergeri</i>	AF518345	DQ022402	AM910961	NA
34			<i>Mastomys natalensis</i>	AF518342	AY326093	EU349813	NA
35			<i>Mastomys pernanus</i>	AF518343	DQ022403	AM910960	NA
36			<i>Myomyscus brockmani</i>	AF518353	DQ022407	AM910966	NA
37			<i>Myomyscus verreauxii</i>	AF518355	DQ022408	AM910967	NA
38			<i>Myomyscus yemeni</i>	AF518357	DQ022409	AM910968	NA
39			<i>Praomys daltoni</i>	AF518349	DQ022406	AM910972	NA
40			<i>Praomys degraaffi</i>	AF518359	DQ022410	NA	NA
41			<i>Praomys jacksoni</i>	EU349778	DQ022411	DQ019071	EU349663
42			<i>Praomys misonnei</i>	AF518364	DQ022412	JF284232	NA
43			<i>Praomys tullbergi</i>	EU349779	AM408327	DQ019072	EU349662
44			<i>Praomys verschureni</i>	AF518373	DQ022394	NA	NA
45			<i>Stenocephalemys albipes</i>	AF518346	DQ022404	AM910977	NA
46			<i>Stenocephalemys albicaudata</i>	AF518369	DQ022414	AM910978	NA
47	Murini	Mus division	<i>Mus(Coelomys) crociduroides</i>	AJ698878	AJ698894	AM910964	NA
48			<i>Mus booduga</i>	AB125761	AB125796	NA	NA
49			<i>Mus cervicolor</i>	AB125766	AB125799	NA	NA
50			<i>Mus cookii</i>	AB125769	KC953404	KC953279	NA
51			<i>Mus terricolor</i>		AB125810	NA	NA
52			<i>Malpaisomys insularis</i>	JN418214	JN418213	NA	NA
53			<i>Mus pahari</i>	EU349767	EU349864	NA	NA
54			<i>Mus(Nannomys) minutoides</i>	AY057816	AJ875086	NA	NA
55			<i>Mus(Pyromys) platythrix</i>	AJ698880	AJ698895	NA	NA
56			<i>Mus musculus</i>	NA	NM015745	M33324	EU349657
57	Hydromyini	Micromys division	<i>Chiropodomys gliroides_M32332</i>	This_study	This_study	This_study	This_study
58			<i>Chiropodomys gliroides_AMCC10151</i>				
59			<i>Chiropodomys major_A48</i>	NA	EU349841	EU349797	EU349674
60			<i>Chiropodomys major_A48</i>	NA	This_study	This_study	This_study
			<i>Chiropodomys sp_R4959</i>	This_study	This_study	This_study	This_study
			<i>Chiropodomys sp_R5238</i>	This_study	This_study	This_study	This_study
		Chrotomys division	<i>Apomys datae</i>	AY324464	EU349836	KC878169	KC953158
			<i>Apomys hylcoetes</i>	EU349735	KC953357	AY294915	AY295000
			<i>Apomys insignis</i>	AY324470	DQ191492	NA	NA

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6		<i>Apomys microdon</i>	AY324480	DQ191493	GQ405366 NA
7		<i>Apomys musculus</i>	DQ191469	DQ191494	GQ405367 NA
8		<i>Archboldomys luzonensis</i>	AY687858	DQ191495	GQ405368 EU349675
9		<i>Archboldomys maximus</i>	JQ898033	JQ898078	NA NA
10		<i>Chrotomys gonzalesi</i>	AY687861	DQ191503	GQ405375 NA
11		<i>Chrotomys mindorensis</i>	JQ898037	JQ898073	NA NA
12		<i>Chrotomys sibuyanensis</i>	AY687862	DQ191504	GQ405376 NA
13		<i>Chrotomys silaceus</i>	JQ898040	DQ191502	GQ405377 NA
14		<i>Chrotomys whiteheadi</i>	JQ898045	JQ898074	NA NA
15		<i>Rhynchomys isarogensis</i>	JQ898050	AY326108	DQ019075 EU349677
16		<i>Soricomys leonardocoi</i>	JQ898062	JQ898077	NA NA
17		<i>Soricomys montanus</i>	JQ898066	JQ898076	NA NA
18		<i>Soricomys musseri</i>	JQ898071	JQ898075	NA NA
19	Hydromys division	<i>Hydromys chrysogaster</i>	AM408339	AM408319	AM910954 EU349699
20		<i>Parahydromys asper</i>	EU349771	EU349866	EU349820 EU349698
21	Pseudomys division	<i>Conilurus penicillatus</i>	EU349743	EU349844	DQ019057 EU349694
22		<i>Leggadina forresti</i>	EU349751	EU349850	DQ019061 EU349686
23		<i>Leporillus conditor</i>	EU349752	EU349851	EU349806 EU349692
24		<i>Mastacomys fuscus</i>	EU349760	EU349856	EU349812 EU349687
25		<i>Mesembriomys gouldii</i>	NA	EU349861	EU349817 EU349693
26		<i>Notomys fuscus</i>	EU349768	EU360811	NA NA
27		<i>Pseudomys australis</i>	EU349780	EU349870	DQ019073 EU349688
28		<i>Zyzomys argurus</i>	EU349792	EU349878	EU349831 EU349685
29		<i>Anisomys imitator</i>	EU349732	EU349833	DQ019052 NA
30		<i>Abeomelomys sevia</i>	EU349730	EU349832	EU349793 EU349682
31		<i>Chiruromys vates</i>	EU349741	EU349842	NA NA
32		<i>Hyomys goliath</i>	EU349750	KC953384	EU349805 EU349679
33		<i>Mallomys rothschildi</i>	EU349758	EU349854	EU349810 EU349681
34		<i>Mammelomys lanosus</i>	EU349759	EU349855	EU349811 KC953188
35		<i>Macruromys major</i>	EU349756	EU349853	EU349809 EU349678
36		<i>Pogonomys loriae</i>	EU349776	EU349868	EU349823 EU349683
37		<i>Pogonomys macrourus</i>	EU349777	EU349869	EU349824 EU349684
38		<i>Pogonomys sylvestris</i>	NA	GQ405365	GQ405389 NA
39	Uromys division	<i>Melomys rufescens</i>	EU349764	EU349860	EU349816 EU349690
40		<i>Melomys cervinipes</i>	NA	KC953399	
41		<i>Paramelomys levipes</i>	EU349772	EU349867	EU349821 EU349689
42		<i>Solomys salebrosus</i>	EU349785	EU349872	EU349827 EU349691
43		<i>Uromys caudimaculatus</i>	EU349789	EU349875	DQ019079 NA
44	Xeromys division	<i>Leptomys elegans</i>	EU349753	EU349852	EU349807 EU349697
45		<i>Pseudohydromys ellermani</i>	EU349763	EU349858	EU349814 EU349695
46		<i>Xeromys myoides</i>	EU349790	EU349877	EU349830 EU349696
47	Lorentzimys division	<i>Lorentzimys nouhuysi</i>	EU349755	GQ405363	GQ405383 EU349680
48	Rattini	Micromys division	<i>Micromys minutus</i>	EU349765	EU349862 EU349818 EU349664
49			<i>Micromys minutus_72_(MK0509_BZ02)</i>	HM217360	HM217598 This_study This_study
50			<i>Micromys minutus_73_(MK0509_BZ07)</i>	HM217361	HM217599 This_study This_study
51	Maxomys division	<i>Maxomys bartelsii</i>	EU349762	EU349857	DQ019066 EU349666
52		<i>Maxomys surifer</i>	HM217406	HM217644	DQ019065 KC953190
53		<i>Maxomys whiteheadi</i>	EU292150	AY326094	NA NA
54	Crunomys division	<i>Crunomys melanius</i>	DQ191477	DQ191506	GQ405379 NA
55		<i>Crunomys suncoides</i>	DQ191478	DQ191507	NA NA
56	Dacnomys division	<i>Chiromyscus chiropus</i>	EU349739	EU349840	EU349796 EU349665
57		<i>Dacnomys millardi</i>	JQ755896	JQ755960	DQ019058 KC953169
58		<i>Leopoldamys edwardsi</i>	AJ698881	AJ698897	NA NA
59		<i>Leopoldamys herberti</i>	JQ755848	JQ755958	NA NA
60		<i>Leopoldamys neilli</i>	HM217462	HM217699	NA NA
		<i>Leopoldamys revertens</i>	JQ173160	JX173169	NA NA
		<i>Leopoldamys sabanus</i>	HM217439	HM217676	DQ019063 KC953186
		<i>Niviventer cremoriventer</i>	EF053030	DQ019067	DQ019067 KC953198
		<i>Niviventer culteratus</i>	NA	KC953418	DQ019068 KC953199

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	<i>Niviventer confucianus</i>	NA	KC953416	KC953293	KC953540
	<i>Niviventer excelstor</i>	DQ191482	DQ191511	GQ405386	NA
	<i>Niviventer fulvescens</i>	HM217409	HM217647	JN009859	NA
	<i>Niviventer niviventer</i>	AM408344	AM408323	AM910969	NA
	<i>Niviventer rapit_UMMZ</i>	DQ191483	DQ191512	GQ405387	NA
	<i>Saxatilomys paulinae_LK217</i>	This_study	This_study	This_study	This_study
	<i>Saxatilomys paulinae_LK218</i>	This_study	This_study	This_study	This_study
	<i>Saxatilomys paulinae_LK219</i>	This_study	This_study	This_study	This_study
	<i>Saxatilomys paulinae</i>	JQ755859	JQ755941	NA	NA
	<i>Tonkinomys daoventieni_DPL1662</i>	This_study	This_study	This_study	This_study
Melasmothrix division	<i>Melasmothrix naso</i>	NA	KC953398	EU349815	NA
Rattus division	<i>Srilankamys ohiensis</i>	JN009856	JN009857	JN009860	NA
	<i>Berylmys berdmorei</i>	HM217401	HM217639	NA	NA
	<i>Berylmys bowersi</i>	HM217415	HM217653	AM910946	KC953160
	<i>Bullimus bagobus</i>	DQ191472	DQ191498	GQ405369	NA
	<i>Bullimus gamay</i>	DQ191473	DQ191499	GQ405370	NA
	<i>Bullimus luzonicus</i>	DQ191474	DQ191500	GQ405371	NA
	<i>Bunomys andrewsi_I8E1</i>	KF164214	KF164237	NA	NA
	<i>Bunomys chrysocomus_T1288</i>	AM910934	AM910937	AM910947	This study
	<i>Halmaheramys bokimekot</i>	KF164222	KF164255	NA	NA
	<i>Paruromys dominator</i>	EU349774	KC953433	EU349822	EU349669
	<i>Sundamys muelleri</i>	EU349787	AY326111	DQ019077	EU349668
	<i>Taeromys celebensis_I7F3</i>	KF164226	KF164249	KF164261	NA
	<i>Rattus andamanensis</i>	HM217403	HM217641	NA	NA
	<i>Rattus argentiventer</i>	HM217362	HM217600	NA	NA
	<i>Rattus exulans</i>	DQ191486	AY326105	GQ405391	NA
	<i>Rattus hoffmanni</i>	EF186441	NA	NA	NA
	<i>Rattus losea</i>	HM217454	HM217691	NA	NA
	<i>Rattus sakeratensis</i>	HM217454	HM217691	NA	NA
	<i>Rattus nitidus</i>	HM217478	HM217715	NA	NA
	<i>Rattus norvegicus</i>	EU349782	AJ429134	X16726	EU349671
	<i>Rattus rattus</i>	AB033702	AM408328	AM910976	NA
	<i>Rattus tanezumi</i>	DQ191488	DQ191515	GQ405393	NA
	<i>Rattus tiomanicus</i>	NA	KC953449	KC953320	NA
	<i>Rattus everetti</i>	DQ191485	DQ191513	GQ405390	NA
	<i>Limnomys bryophilus</i>	DQ191479	DQ191508	GQ405380	NA
	<i>Limnomys sibuanus</i>	DQ191480	DQ191509	GQ405381	NA
	<i>Tarsomys apoensis</i>	DQ191491	DQ191516	GQ405395	NA
	<i>Diplothrix legata</i>	AB033696	AB033706	EU349799	EU349670
	<i>Rattus colletti</i>	NA	HQ334598	NA	NA
	<i>Rattus fuscipes</i>	EF186436	HQ334623	NA	NA
	<i>Rattus giluwensis</i>	NA	HQ334606	NA	HQ334419
	<i>Rattus leucopus</i>	EU349781	HQ334615	EU349825	EU349672
	<i>Rattus lutreolus</i>	GU570661	HQ334613	NA	NA
	<i>Rattus morotaiensis_33228</i>	KF164232	KF164254	KF164272	NA
	<i>Rattus morotaiensis_33231</i>	KF164233	KF164257	KF164273	NA
	<i>Rattus novaeguineae</i>	NA	KC953447	KC953319	KC953210
	<i>Rattus niobe</i>	NA	HQ334580	NA	NA
	<i>Rattus praetor</i>	DQ191487	DQ191514	GQ405392	NA
	<i>Rattus sordidus</i>	NC014871	HQ334881	NA	HQ334411
	<i>Rattus steini</i>	NA	HQ334588	NA	NA
	<i>Rattus tunneyi</i>	EF186517	HQ334579	NA	NA
	<i>Rattus verecundus</i>	NA	HQ334589	NA	KC953211
	<i>Rattus villosissimus</i>	EU349783	HQ334576	EU349826	EU349673
	<i>Bandicota bengalensis</i>	AM408340	AM408331	AM910945	NA
	<i>Bandicota indica</i>	HM217408	HM217646	NA	NA
	<i>Bandicota savilei</i>	HM217387	HM217625	NA	NA
	<i>Nesokia indica</i>	AF160605	NA	NA	NA
Phloeomyini	<i>Batomys granti_USNM_458914</i>	AY324459	DQ191496	AY294917	AY295002
	<i>Batomys salomonseni</i>	DQ191471	DQ191497	NA	NA

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6			<i>Carpomys phaeurus_FMNH_175565</i>	DQ191475	DQ191501	GQ405373	NA
7			<i>Crateromys heaneyi_CIMNH_M628</i>	DQ191476	DQ191505	GQ405378	NA
8			<i>Musseromys gulantang_FMNH_178405</i>	NA	GQ405364	GQ405384	NA
9			<i>Phloeomys_sp</i>	DQ023480	KC8878237	DQ019070	EU349644
10			<i>Phloeomys_cumingi</i>	DQ191484	AY326103	NA	NA
11	<i>incertae sedis</i>	Micromys division	<i>Vandeleuria_oleracea_M30312</i>	this study	EU349876	EU349829	EU349655
12			<i>Hapalomys_delacouri_R5237</i>	This_study	This_study	This_study	This_study
13		Pithecheir division	<i>Margaretamys_elegans</i>	NA	KC953394	KC953274	NA
14			<i>Margaretamys_christinae_RCI_(MK14)</i>	This_study	This_study	This_study	This_study
15			<i>Pithecheir_melanurus_CG1900N580</i>	NA	NA	NA	NA
16			<i>Pithecheir_melanurus_CG1900N583</i>	NA	NA	NA	NA
17			<i>Pithecheir_parvus_CG1977N251</i>	This_study	This_study	This_study	This_study
18			<i>Pithecheir_parvus_CG1977N252</i>	This_study	This_study	This_study	This_study
19			<i>Lenothrix_canus_O09</i>	This_study	This_study	This_study	This_study
20			<i>Lenothrix_canus_N92</i>	This_study	This_study	This_study	This_study
21	OUTGROUP						
22	Gerbillinae		<i>Gerbillurus_paeba</i>	AJ430557	AM910941	AF332022	NA
23			<i>Gerbillus_gerbillus</i>	AF141226	FM162054	DQ019049	EU349700
24			<i>Gerbillus_nanus</i>	NA	KC953378	KC953262	NA
25			<i>Meriones_shawi</i>	AB381894	KC953400	AF332021	AF332048
26			<i>Meriones_unguiculatus</i>	NA	AY326095	AF247184	NA
27			<i>Desmodillus_auricularis</i>	AJ851272	KC953374	DQ019048	KC953171
28			<i>Gerbilliscus_(Tatera)_robusta</i>	NA	AY326113	AY294920	AY295005
29			<i>Gerbillurus_vallinus</i>	NA	KC953377	AF332022	EU349643
30			<i>Taterillus_emini</i>	NA	KC953461	DQ019050	KC953224
31	Deomyinae		<i>Deomys_ferrugineus</i>	EU349745	AY326084	AY294922	AY295007
32			<i>Lophuromys_flavopunctatus</i>	EU349754	AY326091	AY294921	AY295006
33			<i>Lophuromys_sikapusi</i>	AJ012023	KC953390	KC953271	NA
34			<i>Lophuromys_zena</i>	NA	KC953391	KC953272	NA
35			<i>Uranomys_ruddi</i>	EU349788	EU360812	DQ019051	EU349642
36			<i>Acomys_ignitus</i>	AJ233951	EU349846	DQ019049	AY295008
37			<i>Acomys_russatus</i>	NA	FM162053	FM162071	NA
38	Lophiomyinae		<i>Lophiomyis_inhausi</i>	NA	KC953389	NA	NA

*** During the reviewing process of this article, sequences of *Muriculus* as well as those of *Thallomys* and *Myotomys* were deposited in the public databank.

Unavailable in GenBank

incertae sedis

41		<i>Echiothrix</i> division	<i>Echiothrix</i>	NA	NA	NA	NA
42		<i>Hadromys</i> division	<i>Hadromys</i>	NA	NA	NA	NA
43		<i>Micromys</i> division	<i>Haeromys</i>	NA	NA	NA	NA
44			<i>Vernaya</i>	NA	NA	NA	NA
45		<i>Pithecheir</i> division	<i>Eropeplus</i>	NA	NA	NA	NA
46			<i>Lenomys</i>	NA	NA	NA	NA
47			<i>Pithecheirops</i>	NA	NA	NA	NA
48	Arvicanthini	<i>Dasymys</i> division	<i>Dephomys</i>	NA	NA	NA	NA
49			<i>Thallomys</i>	DQ381929**	*	NA	NA
50			<i>Thamnomys</i>	NA	NA	NA	NA
51			<i>Lamottemys</i>	NA	NA	NA	NA
52	Otomyini	Subfamily Otomyinae	<i>Myotomys</i>	JN574903***	NA	NA	NA
53	Millardini	<i>Millardia</i> division	<i>Diomys</i>	NA	NA	NA	NA
54			<i>Madromys</i>	NA	NA	NA	NA
55	Praomyini	<i>Colomys</i> division	<i>Nilopegamys</i>	NA	NA	NA	NA
56				KF928333**	KF928334**	NA	NA
57	Murini	<i>Mus</i> division	<i>Muriculus</i>	*	*	NA	NA

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Hydromyini	<i>Hydromys</i> division	<i>Baiyankamys</i>	NA	NA	NA	NA
		<i>Crossomys</i>	NA	NA	NA	NA
		<i>Microhydromys</i>	NA	NA	NA	NA
	<i>Pogonomys</i> division	<i>Paraleptomys</i>	NA	NA	NA	NA
		<i>Coccymys</i>	NA	NA	NA	NA
		<i>Pogonomelomys</i>	NA	NA	NA	NA
<i>Uromys</i> division		<i>Protochromys</i>	NA	NA	NA	NA
Rattini	<i>Melasmotherix</i> division	<i>Paucidentomys</i>	NA	NA	NA	NA
		<i>Tateomys</i>	NA	NA	NA	NA
	<i>Rattus</i> division	<i>Floresomys</i>	NA	NA	NA	NA
		<i>Kadarsonomys</i>	NA	NA	NA	NA
		<i>Nesoromys</i>	NA	NA	NA	NA
		<i>Palawanomys</i>	NA	NA	NA	NA
	<i>Tryphomys</i>	NA	NA	NA	NA	

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Table S2: Primer sets used in this study

Designation	Gene Name	Nucleotide sequence 5' --> 3'	Annealing Temperature	Fragment Length (bp)	Original Publication
cytb	cytochrome <i>b</i> apoenzyme				
L14723		ACCAATGACATGAAAAATCATCGTT	50°C	1213 (whole <i>cytb</i> gene and small parts of the flanking <i>rRNA</i>)	Irwin and Kocher, 1991
H15915		TCTCCATTCTGGTTACAAGAC			
IRBP1	interphotoreceptor retinoid binding protein exon 1 (fragment 1)				
I1-Rattus		ATTGAGCAGGCTATGAAGAG	58°C	785	Pagès <i>et al.</i> , 2010
J2-Rattus		TAGGGCTTGCTCYGCAGG			
IRBP2	interphotoreceptor retinoid binding protein exon 1 (fragment 2)				
I2		ATCCCCTATGTCATCTCCTACYTG	52°C	892	Poux and Douzery, 2004
J1		CGCAGGTCATGATGAGGTGCTCCGTGTCCTG			
GHR1	growth hormone receptor exon 10 (fragment 1)				
GHREXON10-fw	adkins	GGRAARTTRGAGGAGTGAACACMATCTT	58°C	~ 690 bp	Adkins <i>et al.</i> , 2001
GHR8-rev		TGGCATCTGACTCACAGAATAGG			Lecompte <i>et al.</i> , 2008
GHR2	growth hormone receptor exon 10 (fragment 2)				
GHR7-fw		AAGCTGATCTCTTGCCCTGACCAGAA	53°C	~ 600 bp	Lecompte <i>et al.</i> , 2008
GHR2-rev		GATTTGTTCAAGTTGGTCTGTGCTCAC			
BRCA1					
BRCA1-MP-fw		GRGACCMGCAGTTTATTGTTT	58°C	~ 1000 bp	this study
BRCA1-MP-rev		GGAAGAACACACCTGGTAG			
cytbI	cytochrome <i>b</i> apoenzyme - MUSEUM SPECIMENS, fragment I				
L14723		ACCAATGACATGAAAAATCATCGTT	60°C	472 bp	this study
cytbI-rev		TCAGAARGATATTTGCTCCTCATGG			
cytbII	cytochrome <i>b</i> apoenzyme - MUSEUM SPECIMENS, fragment II				
cytbII-fw		ATAGCAACYGCATTCATAGG	50°C	454 bp	this study

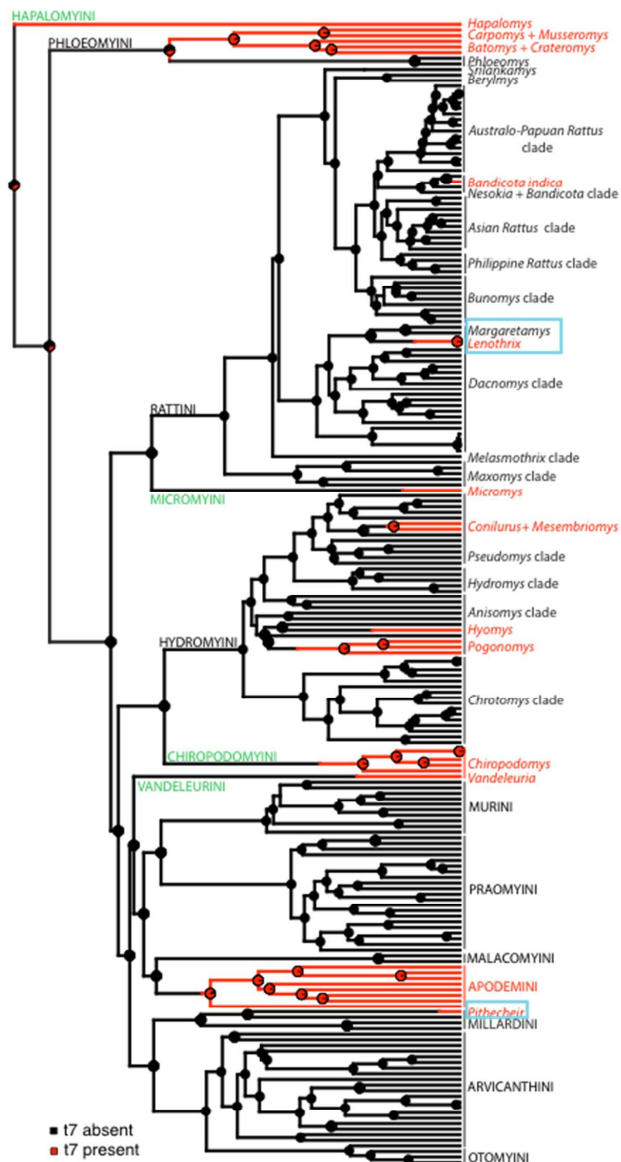
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cytbII-rev		AGRAARTATCATTCTGGTTT			
cytbIII	cytochrome <i>b</i> apoenzyme - MUSEUM SPECIMENS, fragment III				
cytbIII-fw		TTCCCAGACCTAYTAGGAGA	56°C	457 bp	this study
H15915		TCTCCATTCTGGTTTACAAGAC			
IRBPI	interphotoreceptor retinoid binding protein exon 1 - MUSEUM SPECIMENS, fragment I				
I1-Rattus		ATTGAGCAGGCTATGAAGAG	58°C	389 bp	this study
IRBPI-rev		GGGATCCCAGAGACRTGRCC			
IRBPII	interphotoreceptor retinoid binding protein exon 1 - MUSEUM SPECIMENS, fragment II				
IRBPII-fw		TCCTTGGTGCTAGATCTCCG	58°C	450 bp	this study
IRBPII-rev		TAGGGCTTGCTCTGCAGG			
IRBPIII	interphotoreceptor retinoid binding protein exon 1 - MUSEUM SPECIMENS, fragment III				
IRBPIII-fw		CAGACATGGGAAGGCAGTGG	62°C	441 bp	this study
IRBPIII-rev		GCAGGTAGCCCACATTGCC			
GHR1	growth hormone receptor exon 10 - MUSEUM SPECIMENS, fragment I				
GHREXON10-fw		GGRAARTTRGAGGAGGTGAACACMATCTT	62°C	460 bp	this study
GHR1-rev		GTTGGTGGGTTGAYTCAGTTTC			
GHR2	growth hormone receptor exon 10 - MUSEUM SPECIMENS, fragment II				
GHR2-fw		GATCTCTGTGCCTTGACCAG	58°C	436 bp	this study
GHR2-rev		TAAATGTCCTCTGGTTAAAG			
GHR3	growth hormone receptor exon 10 - MUSEUM SPECIMENS, fragment III				
GHR3-fw		CCTACTTCTGTGAGTCAGATGCC	62°C	310 bp	this study
GHR2-rev		GATTTGTTCAGTTGGTCTGTGCTCAC			

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6 Figure S2: Phylogenetic tree depicting relationships of the arboreal rodents based on the analysis of
7 the combined molecular dataset and reconstructed following Bayesian method.
8

9 The best-fit partitioning schemes (considering the three different codon positions of the four coding
10 genes) and models of molecular evolution were deeper investigated using PARTITIONFINDER
11 (Lanfear *et al.*, 2012). The best-fit partitioning scheme consisted in 3 subsets: 1) the first and the
12 second positions of the *Cyt b* codon were merged together, 2) the third position of the *Cyt b* codon
13 was treated separately, 3) all the positions of the nuclear genes were merged together. 56 different
14 substitution models for these three subsets were compared using the *greedy* algorithm. The best-fit
15 substitution models for these three subsets were compared using the *greedy* algorithm. The best-fit
16 substitution model was the GTR+I+G model for each subset according to cAIC values. MRBAYES
17 parameters were set accordingly (see supplementary information). All parameters except the
18 topology were unlinked across partitions, and two independent runs, each with 4 Markov chains
19 Monte Carlo (MCMC) samples comprising one cold and three heated chains, were computed
20 simultaneously. The MRBAYES analyses were run for 12×10^6 generations with trees sampled every
21 1,000 generations. The consensus tree was then computed subsequent to a burn-in of 10^6
22 generations (option “allcompat”). The node supports were estimated using posterior probabilities
23 (PP).
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Figure S3: Chronograms based on the maximum likelihood tree showing absence (black) and presence (red) of cusp t7 for Murinae species. The pie charts represent the probability of the ancestral dental trait characters. The green and blue colour indicates the former *Micromys* and the *Pithecheir* divisions respectively. Highlighted in green capitals are the 4 monotypic tribes we proposed based on the new phylogenetic results: (i) Chiropodomysini, (ii) Hapalomyini, (iii) Micromyini, and (iv) Vandeleuriani. See material and method for details.



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Text S1: Molecular results

Samples preserved in ethanol - *Cytb* sequences obtained from tissue of *Margaretamys christinae* were not considered in the analyses because *Numt* sequences or heteroplasmy were suspected. Chromatograms with at least 10 double pics were obtained, but translation into amino acid sequence did not reveal any stop codon (as it could be observed in case of a recent *Numt* insertion or heteroplasmy). Contamination by exogenous DNA was ruled out as numerous nuclear sequences produced for another ongoing analysis revealed to be perfectly clean.

Museum samples - As museum samples contain tiny amounts of poorly preserved DNA, additional primer sets were designed to target the 3 markers into 3 overlapping fragments (see Table S2). Ancient DNA work was performed in an independent room dedicated to ancient DNA analysis (degraded DNA platform, Labex CeMEB), following the standard procedures and using specific equipment and personal protections (e.g. Pääbo *et al.*, 2004). DNA of the four *Pithecheir* samples was extracted at the same time than those of nine *Gerbillus* samples from museum. For each PCR attempts, all the three PCR blanks remained negative indicating that no contamination and no carrier-effect occurred during extraction and pre-amplification steps. Independent PCRs were performed and furnished the same conclusions (see below for further details).

Cytochrome *b* marker

Fragment 1: 3 successful PCR attempts for MNHN-ZM-MO 1977-251 and 2 for MNHN-ZM-MO 1977-252. Sequences were 100% identical for a same sample but differed at one position between the two samples. This difference occurs at the third codon position and was considered as intraspecific polymorphism (coded Y for C or T in the consensus sequence of *Pithecheir parvus*). At this position all the murid species of our dataset harbour a C or a T.

Fragment 2: a single successful PCR attempt for MNHN-ZM-MO 1977-251. Because of failure to reproduce this sequence, this fragment was not considered in the subsequent analyses.

Fragment 3: 3 successful PCR attempts for MNHN-ZM-MO 1977-251 and 2 for MNHN-ZM-MO 1977-252. Sequences were 100% identical for a same sample and between samples.

IRBP marker

Fragment 1: PCR failures for all the 4 samples

Fragment 2: a single successful PCR attempt for MNHN-ZM-MO 1977-251. Because of failure to reproduce this sequence, this fragment was not considered in the subsequent analyses.

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6 Fragment 3: 3 successful PCR attempts for MNHN-ZM-MO 1977-251 and 2 for MNHN-ZM-MO
7 1977-252. Sequences were 100% identical for a same sample and between samples.
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10 11 GHR marker

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13 Fragment 1: 3 successful PCR attempts for MNHN-ZM-MO 1977-251 and 1 for MNHN-ZM-MO
14 1977-252. Sequences were 100% identical between samples.
15

16 Fragment 2: PCR failures for all the 4 samples

17 Fragment 3: 3 successful PCR attempts for MNHN-ZM-MO 1977-251 and 2 for MNHN-ZM-MO
18 1977-252. Sequences were 100% identical for a same sample and between samples.
19

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