Evolution / Évolution

Cytochrome b-based phylogeny of the *Praomys* group (Rodentia, Murinae): a new African radiation?

Émilie Lecompte[a]*, Laurent Granjon[a,b], Julian Kerbis Peterhans[c], Christiane Denys[a]

[a] *Laboratoire « Zoologie, Mammifères et Oiseaux », Muséum national d'histoire naturelle, 55, rue Buffon, 75005 Paris, France*
[b] *Laboratoire de mammalogie (CBGP, UMR R022), IRD, BP 2528, Bamako, Mali*
[c] *Field Museum of Natural History, Chicago, Illinois 60605-2496, USA*

Abstract – Complete cytochrome b gene sequences allows, for the first time, establishing a nearly complete phylogeny among the *Praomys* group sensu lato. The genera *Praomys*, *Mastomys* and *Stenocephalemys* appear paraphyletic. *Myomys* is polyphyletic and this genus name probably needs to be restricted to its type species, *M. verreauxii*. The genera *Zelotomys* and *Colomys* appear as sister groups. *Mastomys pernanus* and *Malacomys verschureni* nest within the *Praomys* group, but their generic assignation must be further clarified. The genus *Heimyscus* appears closest to *Praomys* than to *Hylomyscus*. The different lineages probably result from an adaptive radiation at the end of the Miocene. *To cite this article: É. Lecompte et al., C. R. Biologies 325 (2002) 827–840.* © 2002 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS

evolution / *Praomys* group / adaptative radiation / divergence times

Résumé – **Phylogénie du groupe *Praomys* (Rodentia, Murinae) basée sur le cytochrome b : une nouvelle radiation africaine ?** Des séquences complètes du cytochrome b permettent pour la première fois d'établir une phylogénie presque complète du groupe *Praomys* sensu lato. Les genres *Praomys, Mastomys* et *Stenocephalemys* y apparaissent paraphylétiques. *Myomys* est polyphylétique et semble devoir être réduit à son espèce type, *M. verreauxii*. Les genres *Zelotomys* et *Colomys* apparaissent comme groupes frères. *Mastomys pernanus* et *Malacomys verschureni* appartiennent aussi au groupe *Praomys*, mais leur assignation générique doit être revue. Le genre *Heimyscus* apparaît plus proche du genre *Praomys* que du genre *Hylomyscus*. Les différentes lignées semblent résulter d'une radiation adaptative à la fin du Miocène. *Pour citer cet article : É. Lecompte et al., C. R. Biologies 325 (2002) 827–840.* © 2002 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS

évolution / groupe *Praomys* / radiation adaptative / temps de divergence

Version abrégée

Le groupe *Praomys* représente un ensemble de genres de rongeurs murinés, essentiellement africains, dont le contenu exact ainsi que les relations phylogénétiques inter et intra-génériques sont jusqu'à présent débattus. Alors que les genres *Heimyscus, Hylomyscus, Mastomys, Myomys, Praomys* et *Stenocephalemys* sont des

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Correspondence and reprints.
E-mail address: lecompte@mnhn.fr (E. Lecompte).

représentants indiscutables de ce groupe, certains auteurs ont proposé qu'y soient également ajoutés *Zelotomys*, *Colomys* et l'espèce *Malacomys verschureni*. Par ailleurs, la monophylie de genres tels que *Myomys* et *Praomys* a été plusieurs fois mise en cause, de même que la position de certaines espèces dans ces genres ou dans d'autres du groupe (par exemple, *Mastomys pernanus*). Afin de tenter de résoudre certaines de ces incertitudes, nous avons réalisé une reconstitution phylogénétique de ce groupe à partir des séquences complètes du gène mitochondrial du cytochrome b d'un échantillon représentatif des espèces de l'ensemble des genres concernés, à savoir : *Praomys tullbergi*, *P. misonnei*, *P. sp. nov.*, *P. hartwigi obscurus*, *P. jacksoni* et *P. degraaffi* ; *Mastomys natalensis*, *M. erythroleucus*, *M. coucha*, *M. huberti*, *M. verheyeni* et *M. pernanus* ; *Myomys albipes*, *M. daltoni*, *M. derooi*, *M. fumatus*, *M. verreauxii* et *M. yemeni* ; *Hylomyscus stella*, *H. parvus* et *H. alleni* ; *Heimyscus fumosus* ; *Stenocephalemys albocaudata* et *S. griseicauda* ; *Colomys goslingi* ; *Zelotomys hildegardeae* et *Malacomys verschureni*. Par ailleurs, à partir d'estimations des principales dates de divergence dans ce groupe, calées sur la date supposée de divergence entre *Mus* et *Rattus*, nous discutons de la chronologie des événements et des modalités d'émergence de sa diversité, aujourd'hui importante.

Les séquences de 48 spécimens ont été obtenues selon une procédure standard, et traitées avec dix autres issues de Genbank. Une analyse de saturation a été réalisée, montrant que les transitions en première et troisième position de codon étaient saturées. Ces dernières n'ont de ce fait pas été prises en compte dans les analyses. Une analyse de parcimonie (MP) ainsi qu'une analyse de maximum de vraisemblance (ML) et un traitement de la matrice des distances (NJ) ont été effectués sur les séquences nucléotidiques ainsi que sur les séquences d'acides aminés déduites. Le modèle de substitution qui correspond le mieux au jeu de données a été choisi grâce au programme Modeltest ; ce modèle a été utilisé pour les analyses ML et NJ. La solidité des branchements obtenus a été testée grâce à la méthode du ré-échantillonnage et par l'indice de Bremer.

Les séquences obtenues ont montré les caractéristiques classiques du gène du cytochrome b des Mammifères, et une composition en bases nucléotidiques comparable à celle observée chez d'autres rongeurs muroïdés (peu de G – 12,2% – fréquences similaires de A, T et C – 26,7 à 32,1%). Sur l'ensemble du jeu de données, 563 sites ont été trouvés variables (140 en première, 62 en deuxième et 361 en troisième position de codon), dont 423 informatifs pour l'analyse de parcimonie. Les distances génétiques ont varié de 5,3% entre *Myomys albipes* et *Stenocephalemys* et de 17,9%

entre *Mastomys verheyeni* et *M. pernanus*. L'analyse de parcimonie sur les séquences nucléotidiques a abouti à l'obtention de 24 arbres de 1033 pas. Les analyses de maximum de vraisemblance et de distance ont donné un arbre de topologie largement congruente avec celle du cladogramme consensuel. Les analyses basées sur les séquences protéiques ont conduit à des arbres beaucoup moins bien résolus. Les arbres obtenus par MP, ML ou NJ sur les séquences nucléotidiques montrent le groupe *Praomys* monophylétique lorsqu'il inclut *M. verschureni*, *Colomys* et *Zelotomys*. Parmi les résultats congruents dans les trois types d'analyse, il faut noter la paraphylie de *Praomys*, qui se trouve séparé en deux groupes d'espèces, le groupe *jacksoni* (incluant ici *P. jacksoni* et *P. degraaffi*) et le groupe *tullbergi* (incluant ici *P. tullbergi*, *P. misonnei*, *P. hartwigi obscurus* et *Praomys sp. nov.*). *Myomys* apparaît quant à lui polyphylétique, avec *M. daltoni* et *M. derooi* associés à *Praomys*, *M. albipes* à *Stenocephalemys*, *M. fumatus* et *M. yemeni* montrant des affinités moins bien soutenues (le premier avec *Mastomys*, le second avec le groupe *Stenocephalemys–M. albipes*). Un clade « éthiopien », réunissant les deux espèces de *Stenocephalemys* et *M. albipes*, est très robuste, de même que *Zelotomys hildegardeae* apparaît comme groupe frère de *Colomys goslingi*. Le genre *Mastomys* est paraphylétique, du fait de la divergence marquée de *M. pernanus* par rapport aux autres espèces du genre considérées ici. Parmi ces dernières, *M. coucha*, *M. huberti*, *M. erythroleucus* et *M. natalensis* apparaissent s'être différenciées dans cet ordre, *M. verheyeni* étant le groupe frère de cet ensemble de quatre espèces.

Ces résultats confirment pour certains des données acquises dans d'autres domaines. La monophylie de *Praomys* et de *Myomys* avait déjà été mise en cause, et l'ensemble des résultats maintenant accumulés doit aboutir à des révisions nomenclaturales dans ces genres. Ainsi *Praomys* doit-il, soit inclure *M. daltoni* et *M. derooi*, soit être divisé en deux genres (l'un incluant *M. daltoni* et *M. derooi*). Par ailleurs, les espèces actuellement rattachées à *Myomys* doivent être distribuées dans différents autres genres, *Myomys verreauxii*, l'espèce type du genre, restant éventuellement la seule dans ce genre. *Mastomys pernanus* doit sans doute être considéré comme appartenant à un autre genre, alors que les cinq autres espèces considérées ici sont assez fortement associées. Toutefois, l'ordre de branchement des différentes espèces demande encore à être confirmé, puisqu'il n'est pas en total accord avec celui déduit d'analyses d'hybridation ADN–ADN, d'électrophorèse des protéines ou chromosomiques déjà réalisées sur ce groupe. La distinction entre *Heimyscus* et *Hylomyscus* est clairement confirmée ici, de même que l'inclusion

de *Zelotomys*, *Colomys* et *Malacomys verschureni* dans le groupe *Praomys*. *Zelotomys* et *Colomys* apparaissent même relativement étroitement apparentés, alors que la position de *M. verschureni* est moins claire. Enfin, le seul taxon non africain de l'échantillon, à savoir *M. yemeni*, originaire de la péninsule Arabique, appartient sans ambiguïté au groupe *Praomys*, et semble plus précisément être apparenté aux espèces du « clade éthiopien », géographiquement proches. Ceci suggère un passage relativement récent de *M. yemeni* dans la péninsule Arabique, à partir de l'Afrique de l'Est.

En partant d'une date de divergence entre *Mus* et *Rattus* estimée à 12 millions d'années (Ma), et sachant qu'il y a 70 transversions en troisième position de codon entre les séquences du cytochrome b de ces deux taxons, nous avons appliqué un taux de transversion de 1,53% par Ma aux divergences inter-taxons de notre jeu de données. À partir de là, il ressort que le groupe *Praomys*, tel qu'il est défini dans nos analyses, aurait émergé il y a environ 11,4 Ma. Ensuite, la majorité des groupes (assimilables à des genres) se seraient différenciés entre 8,5 et 7,3 Ma, soit en un laps de temps assez court, à la fin du Miocène. Cette diversification à partir d'ancêtres provenant probablement d'Asie s'appa-rente par sa rapidité à une radiation adaptative, comme celle qui aurait présidé à l'émergence de la diversité dans la tribu des Arvicanthini, un autre groupe de rongeurs murinés africains. On peut penser que des facteurs éco-climatiques particuliers ont favorisé à cette époque l'entrée de ces immigrants en Afrique, et leur rapide colonisation du continent, accompagnée d'une évolution explosive. À partir de là, en effet, la multi-plication du nombre des espèces a été rapide, les espèces actuelles ayant pour la plupart émergé entre 2 et 3 Ma. Il est intéressant de noter que, selon les groupes, cette évolution s'est ou non accompagnée de changements morpho-anatomiques visibles : dans le « clade éthiopien », les différences morphologiques sont telles entre *M. albipes* et *Stenocephalemys* spp. que ces taxons ont été érigés en genres différents ; dans le genre *Mastomys*, comme entre plusieurs espèces du genre *Praomys*, la différenciation morphologique est restée négligeable, au point que la plupart de ces espèces doivent être considérées comme des espèces jumelles. Des hypothèses quant aux causes de ces différences entre les taux d'évolution moléculaire et morphologique ont été avancées, qui mériteraient d'être testées sur ces rongeurs africains.

1. Introduction

From various perspectives, the *Praomys* group is one of the most successful groups of Old World rodents. Taxonomically, their diversification is important, and one may conservatively include in it, as a starting point, six genera (*Heimyscus*, *Hylomyscus*, *Mastomys*, *Myomys*, *Praomys* and *Stenocephalemys*), comprising 34 currently recognised species [1, and references hereunder]. Ecologically, they have colonised various biotopes, ranging from the equatorial rain forest to Sahelian savannas. At the community level, many of them can build abundant populations. Finally, their interactions with human populations can have important conse-quences with regard to agriculture and human health. The systematics of the whole group, as well as its constituent taxa, has been very unstable, experiencing many changes according to taxonomic treatments and authors [2–10]. At various times, different authors have either included the current genera as sub-genera within *Praomys*, or have suggested linkages between them. For example, *Hylomyscus*, *Mastomys* and *Myomys* were considered as sub-genera within *Rattus/Epimys* or *Praomys* [2, 11, 12]. *Heimyscus fumosus* was originally considered to be a member of *Hylomyscus* [13], while Van der Straeten and Dieterlen [14] originally described *Myomys ruppi* as a species of *Praomys*, sharing features with *Myomys albipes* and *Stenocephalemys*. Moreover, different authors have included additional genera (*Zelo-tomys* [10, 15], *Stenocephalemys* [14, 16, 17], *Colomys* [16], *Heimyscus* [4, 13]) or species (*Malacomys vers-chureni* [18]), within the *Praomys* group. Here, we refer to the '*Praomys* group' as this extended suite of genera and species. However, the relationships between and within these taxa are still not well understood. This is mainly due to the low level of morphological differen-tiation among the species as well as between the genera, making it difficult to find phylogenetically informative characters. Further, the monophyly of the genera *Praomys*, *Myomys*, and *Stenocephalemys* has been questioned by several studies [16, 17, 19, 20]. Up to now, the majority of studies on the systematics of the *Praomys* group have been based on phenetic analyses (morphological, biometrical or molecular) and have involved relatively few of the relevant taxa. Only one study, based on a cladistic analysis of morphological characters on most of the African members of the *Praomys* group is available to date [20].

Here we present the first cytochrome b-based phy-logeny of the *Praomys* group as represented by a significant sample of species from all currently recog-nised genera. More precisely, this study is the first where almost all the *Myomys* species are considered, as well as the species *Mastomys verheyeni* and *Mastomys*

pernanus. It also includes many species from the other genera comprising the *Praomys* group, including the poorly known *Zelotomys hildegardeae*, *Colomys goslingi* and *Malacomys verschureni*. The monophyly of these genera will be tested as well as the various hypotheses concerning their relationships. Taxonomical and nomenclatural implications will be proposed and discussed. These results provide insights into the chronological succession of divergence events in this group. Based on divergence time estimates, we discuss some of the possible patterns of evolution among the *Praomys* group.

2. Material and methods

2.1. Species sampling

A total of 58 specimens of murine rodents representing 36 different taxa were included in the phylogenetic analyses. In the *Praomys* group, the genus *Praomys* was represented by *P. tullbergi*, *P. misonnei*, *P. sp nov* [21], *P. hartwigi obscurus*, *P. jacksoni* and *P. degraaffi*; *Mastomys* by *M. natalensis*, *M. erythroleucus*, *M. coucha*, *M. huberti*, *M. verheyeni* and *M. pernanus*; *Myomys* by *M. albipes*, *M. daltoni*, *M. derooi*, *M. fumatus*, *M. verreauxii* and *M. yemeni*; *Hylomyscus* by *H. stella*, *H. parvus* and *H. alleni*; *Heimyscus* by *H. fumosus; Stenocephalemys* by *S. albocaudata* and *S. griseicauda. Colomys goslingi*, *Zelotomys hildegardeae* and *Malacomys verschureni* were also studied. For the list of material see Table 1 . Some taxa were included from Genbank: *Mastomys huberti* (AF141220) and the outgroup taxa *Arvicanthis niloticus* (AF004572), *Hybomys univittatus* (AF141219), *Lemniscomys bellieri* (AF004586), *Dasymys incomtus* (AF141217), *Aethomys sp* (AF004587), *Rattus norvegicus* (AB033713), *Mus musculus* (AB033699), *Apodemus flavicollis* (AB032853) and *Apodemus sylvaticus* (AB033695), which were chosen following the results of previous molecular analyses [6, 22].

2.2. DNA extraction, amplification and sequencing

Total genomic DNA was extracted from liver, heart or muscles preserved in 70% ethanol using a CTAB protocol [23]. Mitochondrial sequences containing the cytochrome b gene were isolated via the polymerase chain reaction (PCR). The entire cytochrome b gene was amplified using the primers L14723 (5' ACC AAT GAC ATG AAA AAT CAT CGT T 3') and H15915 (5' TCT CCA TTT CTG GTT TAC AAG AC 3') in the flanking region of the cytochrome b gene. Additional internal primers, used when the DNA was too fragmented and for the sequencing, were H15553 (5' TAG GCA AAT AGG AAA TAT CAT TCT GGT 3'), L15408 (5' ATA GAC AAA ATC CCA TTC CA 3'), L15146 (5' CAT GAG GAC AAA TAT CAT CTT GAG 3'), H15149 (5' CTC AGA ATG ATA TTT GTC CTC 3'), L15513 (5' CTA GGA GAC CCA GAC AAC TA 3'). Primers name indicates the DNA strand (H, heavy or L light) and the position of the 3' end of the oligonucleotide.

Double-stranded PCR amplifications were performed in 50 µl reaction volumes using primers L14723 and H15915. Each reaction included 0.6 µl primers (50 pM µl^{-1}), 2.5 µl of DMSO, 2 µl of desoxynucleoside–triphosphate mixture, 5 µl of reaction buffer (10X) (Appligen) and 0.3 µl of taq DNA polymerase (Appligen). All PCRs used the following thermal cycling parameters: 4 min at 94 °C, 36 cycles (40 s at 94 °C, 45 s at 50 °C, 40 s at 72 °C). Double-stranded PCR products were purified from agarose gel using the MinElute purification kit (Qiagen). Taxa were sequenced directly from purified PCR products using primers mentioned above. Approximately 100 pmol ml^{-1} of double-stranded PCR product was used in an automatic sequencer CEQ2000 (Beckman). The sequences were entered and manually aligned using the Bioedit software [24]. All the sequences are available in Genbank under accession numbers AF518328–AF518375.

2.3. Saturation analyses

Mutational saturation was studied for each codon position, for transitions and transversions separately, by plotting the pairwise observed number of sequence differences (in percentage) against the pairwise number of substitutions in the maximum parsimony tree as inferred by PAUP 3.1.1. [25].

2.4. Phylogenetic analyses

Phylogenetic relationships were analysed by maximum-parsimony (MP), neighbour-joining (NJ) and maximum-likelihood (ML) methods. The phylogenetic analyses were conducted using PAUP 4.0b4a [26]. Critical values of skewness (g1 statistics) of the tree length distribution were used to access overall phylogenetic signal in the data set. The critical values were computed from a distribution of 10 000 randomly generated trees using PAUP.

The MP analysis was done with a heuristic search using stepwise addition. Robustness of trees was assessed by the bootstrap method [27] performed by PAUP (1000 replicates) and by the Decay Index (DI) [28] using the Autodecay software [29]. The program Modeltest 3.04 [30] was used to select the substitution model that best fitted the data according to hierarchical

Table 1. List of the specimens examined with geographic origin, collector and collection number. MNHN: Muséum national d'histoire naturelle, Paris; CM: Carnegie Museum, Pittsburgh; FNS: Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt; RUCA: Department of Biology of the University of Antwerp; FMNH: Field Museum of Natural History, Chicago; SMNS: Staatliches Museum für Naturkunde, Stuttgart; ZFMK: Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn; T numbers refer to the catalogue of mammalian tissues curated at the University of Montpellier.

Specimens	Geographic origin	Collectors	Museum number
Hylomyscus alleni	Gabon, province estuaire	LW. Robbins	CM - TK 21550
Hylomyscus parvus	Cameroon, Ikenge	DA. Schlitter	CM - SP 10502
Hylomyscus parvus	Cameroon, Ikenge	DA. Schlitter	CM - SP 10514
Hylomyscus stella	Kenya, Kakamega	DA. Schlitter	CM - SP 5032
Heimyscus fumosus	Gabon, R. de la Moukalaba	V. Nicolas/E. Lecompte	MNHN - 2001-064
Heimyscus fumosus	Gabon, R. de la Moukalaba	V. Nicolas/E. Lecompte	MNHN - 2001-076
Mastomys coucha	South Africa, Bloemfontein	P. Taylor	MNHN - 1999-104
Mastomys coucha	South Africa, Bloemfontein	P. Taylor	MNHN - 1999-106
Mastomys erythroleucus	Mali, Kangaba	B. Sicard	MNHN - 1999-322
Mastomys erythroleucus	Ethiopia, Mizzan-Tefferi	L. Lavrenchenko	MNHN - 1999-551
Mastomys erythroleucus	Chad, Tinga	C. Denys/L. Granjon	4123
Mastomys huberti	Mali, Emnal'here	B. Sicard	SK 317
Mastomys natalensis	Senegal, Kédougou	K. Bâ	MNHN - 1999-349
Mastomys natalensis	South Africa, Badplaas	P. Taylor	MNHN - 1999-099
Mastomys natalensis	Zimbabwe	P. Taylor	MNHN - 1999-110
Mastomys pernanus	Tanzania, Dakawa	H. Leirs	RUCA - 1624
Mastomys verheyeni	Nigeria, Dugumne	W. Brei	SM - 54752
Mastomys verheyeni	Nigeria, Dugumne	W. Brei	SM - 54755
Myomys albipes	Ethiopia, Mizan-Tefferi	L. Lavrenchenko	MNHN - 1999-561
Myomys albipes	Ethiopia, Entoto	M. Corti	T-1581
Myomys daltoni	Mali, Gao	B. Sicard	MNHN - 1999-392
Myomys daltoni	Benin, Deroubanou	W. Brei	SMNS - 39353
Myomys derooi	Ghana, Yendi	DA. Schlitter	CM - SP 10190
Myomys derooi	Benin, Partago	W. Brei	SMNS - 39394
Myomys fumatus	Kenya, Naivasha	DA. Schlitter	CM - TK 33059
Myomys fumatus	Kenya, Naivasha	DA. Schlitter	CM - TK 33060
Myomys verreauxii	South Africa, Paarl Moutains	P. Taylor	MNHN - 1999-102
Myomys verreauxii	South Africa, Cape	P. Taylor	MNHN - 1999-112
Myomys yemeni	Saudi Arabia, 20 km Abha, Taïf road	P. Gaucher	MNHN - 1994-079
Myomys yemeni	Saudi Arabia, Alba	P. Gaucher	T-1457
Praomys degraaffi	Burundi, Kibira National Park	JC. Kerbis	FMNH - 138046
Praomys degraaffi	Uganda, Gahinga gorilla NP	JC. Kerbis	FMNH - 157790
Praomys jacksoni	Gabon, Mayibout	C. Fournier-Chambrillon	MNHN - 1999-402
Praomys jacksoni	Uganda, Kalanga	JC. Kerbis	FMNH - 138095
Praomys misonnei	Uganda, Budongo	JM. Chupasko	FMNH - 165317
Praomys misonnei	Kenya, Kakamega	DA. Schlitter	CM - SP 5018
Praomys misonnei	Democratic Republic of Congo, Epulu	JC. Kerbis	FMNH - 149594
Praomys tullbergi	Ghana, Katamanso	DA. Schlitter	CM - SP 10188
Praomys hartwigi obscurus	Nigeria, Gangirwal	G. Nikolaus	SMNS - 41313
Praomys hartwigi obscurus	Nigeria	G. Nikolaus	ZFMK - 88-130
Praomys sp. nov.	Congo, Tchissanga	L. Granjon	T-795
Stenocephalemys albocaudata	Ethiopia, Sanetti	M. Corti	T-1590
Stenocephalemys albocaudata	Ethiopia, Sanetti	M. Corti	T-1589
Stenocephalemys griseicauda	Ethiopia, Mt Chilalo	H. Rupp	SMNS - 35945
Colomys goslingi	Sudan, Gilo	G. Nikolaus	SMNS - 30124
Malacomys verschureni	Democratic Republic of Congo, Irangi	F. Dieterlen	SMNS - 131
Zelotomys hildegardeae	Uganda, Queen Elizabeth Park	A. Hoffman	3190
Zelotomys hildegardeae	Uganda, Queen Elizabeth Park	A. Hoffman	3191

likelihood ratio tests. The NJ tree was performed from the distance matrix calculated under the selected model, and the robustness of inferences was assessed through bootstrap resampling (1000 replicates). The ML analyses was performed with ten random additions of taxa under the selected model, the robustness of inferences was assessed through bootstrap resampling (100 replicates) using PAUP [26]. Analyses were also performed on the amino acid (AA) sequences, both with NJ and MP methods.

2.5. Relative-rate test

Relative-rate tests were conducted both with RRTree, version 1.0 [31], by taking into account the taxonomic representativeness and its phylogenetic relationships, and with the Mega program [32]. Quantifications of the rate differences were performed either on the proportions of synonymous (Ks) and non-synonymous (Ka) substitutions with RRTree, or on all three codon positions with Mega. Relative-rate tests were performed among the *Praomys* group species; *Arvicanthis*, *Mus* and *Apodemus* were chosen as outgroups.

3. Results

3.1. Cytochrome b gene sequences, base composition, saturation and sequence variation

Complete cytochrome b gene sequences were obtained for 48 specimens and analysed together with additional available Murinae sequences (cf. Table 1). In order to check for the mitochondrial origin of the cytochrome b gene sequences, the corresponding amino acid sequences were checked for the presence of aberrant amino acids (as stop codon), deletions or insertions. The sequence was 1140 bp long in all examined specimens, coding for 380 amino acids. The gene began in all studied specimens with the first three conserved codons (ATG, ACA and AAC) and there was no complete stop codon at the end of the gene, only a single T or C.

Base composition of the cytochrome b gene in the examined Murinae was quite similar to that of previously reported mammalian sequences [33] and comparable to values found in some muroid rodents [34]: the abundance of Gs was low (12.2%), whereas the percentages of A, T and C were quite similar (26.7–32.1%). As expected, the first and second positions showed less variability than the third codon positions [33].

The saturation curves are presented in Fig. 1. Transitions at the second codon position and transversions at the three codon positions were not saturated, while transitions at the first and third were saturated (Fig. 1). Consequently, the weighting scheme used has consisted in the elimination of transitions at the first and third position. Within the *Mastomys* species *M. erythroleucus*, *M. natalensis*, *M. huberti* and *M. coucha*, no saturation was found at any position (Fig. 1); so an independent analysis was conducted without any weighting for this group in MP and a ML analysis was conducted with a model selected by Modeltest 3.04 [30] on the *Mastomys* dataset.

For the phylogenetic analyses, a data set of 58 specimens and 1140 nucleotides was used. These sequences could be unambiguously aligned. Of these sites, 563 were variable and 423 were parsimony informative; 140 (24.9%) of the variable nucleotides were at the first, 62 (11.0%) at the second and 361 (64.1%) at the third codon position. Of the phylogenetically informative sites, 84 (19.9%) were at the first, 30 (7.1%) at the second and 323 309 (73.0%) at the third codon position.

3.2. Genetic distances

Within the *Praomys* group, the inter-genera genetic distances ranged from 5.3% (between *Myomys albipes* and *Stenocephalemys*) to 17.9% (between *Mastomys verheyeni* and *Mastomys pernanus*). Within the genera, the range of divergence values was of the same order, going from 6.8% (within *Stenocephalemys*) to 17.9% (within *Mastomys*).

3.3. Phylogenetic analyses

The MP analysis on nucleotide data yielded 24 trees of 1033 steps, the strict consensus of which is presented in Fig. 2. The g1 statistics is significantly different (g1 = − 0.55, P < 0.01) from what would be expected from random phylogenetic noise. The NJ analysis on nucleotide data is presented in Fig. 3. The models selected were GTR + I + G for the whole *Praomys* group and TVM + I + G for the *Mastomys* data set. The ML analysis data yielded a tree highest-likelihood (ln L = 15 006.786), presented in Fig. 4. The MP analysis on amino acid data yielded 1886 trees of 436 steps (CI = 0.552); the MP and the NJ trees drawn from protein sequences (not shown) only display some groups already identified in the others analyses.

3.4. Phylogenetic relationships

With a few exceptions, MP, ML and NJ results are quite consistent with each other. Terminal clades are consistently confirmed in the different analyses and are typically well-supported in analyses based on DNA sequences. Some taxa or clades branching at the base of the *Praomys* group have an unstable position among the trees. The three ML, MP and NJ trees indicate that the *Praomys* group is monophyletic when it includes *Malacomys verschureni*, *Colomys* and *Zelotomys* (Figs. 2–4). This is supported, however, by quite a low bootstrap value of 76% in MP but with a high Decay Index value of 8 and a bootstrap value of 87% in ML and 93% in NJ. The sister group is the genus *Apodemus* (73% BP in MP, DI = 4; 88% in NJ and 79% in ML), both in analyses based on nucleotides and amino acids sequences.

The phylogenetic relationships among the genera within the *Praomys* group are not always clearly
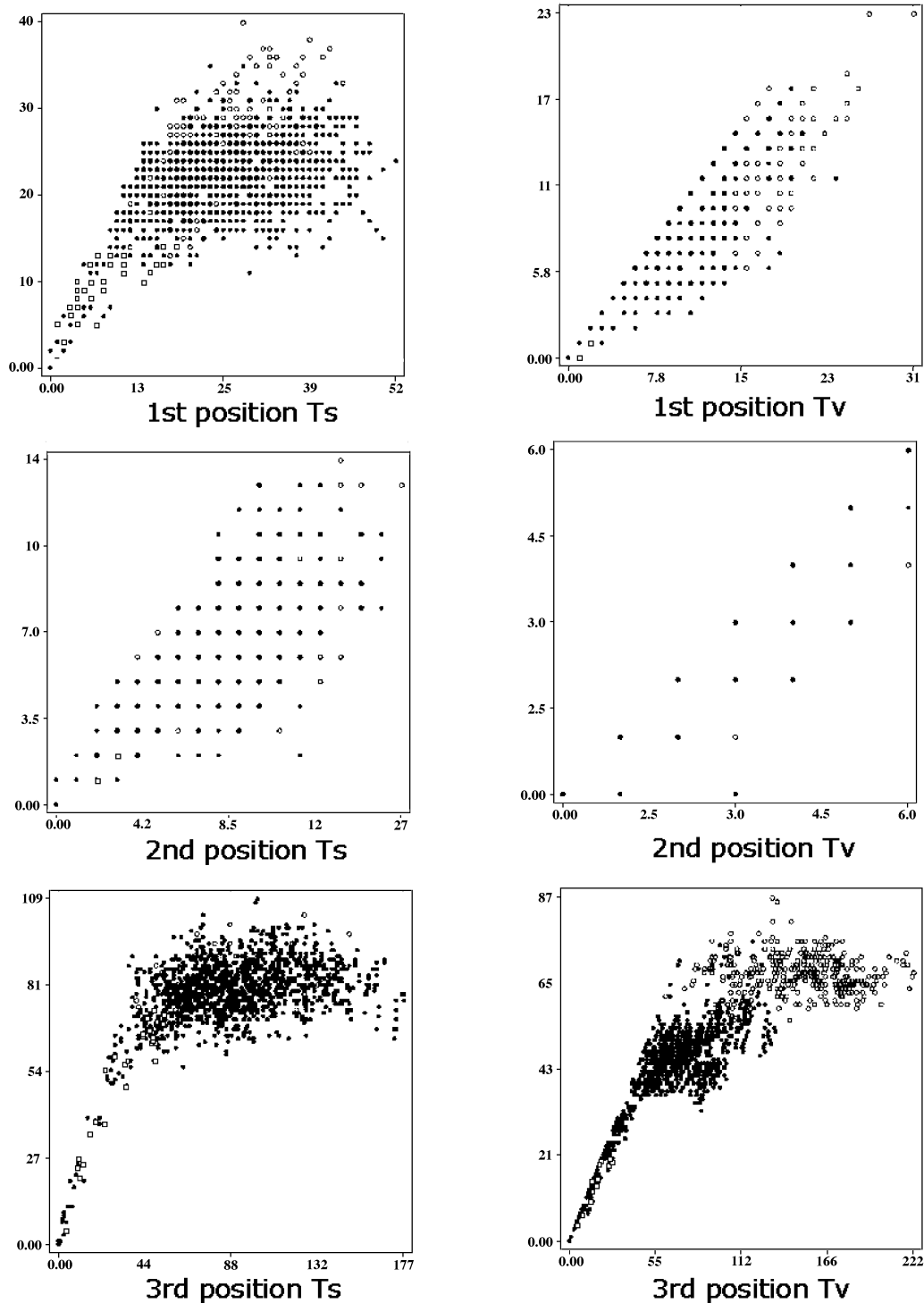
Fig. 1. Graphs illustrating the levels of saturation in the complete 1140 pb data set at each codon position, for transitions (Ts) and transversions (Tv). Numbers of pairwise observed sequence differences (as a percentage, *Y* axis) are plotted against the corresponding numbers of pairwise inferred substitutions occurring along branches joining two species in the maximum parsimony tree of PAUP (*X* axis). The following symbols are used in all saturation graphs: full circles, comparisons within the *Praomys* group; open circles, comparisons of outgroup taxa with *Praomys* group; open squares, comparisons between *Mastomys coucha*, *M. erythroleucus*, *M. huberti* and *M. natalensis*.

resolved, but some clades are strongly supported. For example, within the genus *Praomys* (which appears paraphyletic) two clades (*jacksoni* and *tullbergi* groups) are well supported (94% and 83% BP in MP; DI = 6;
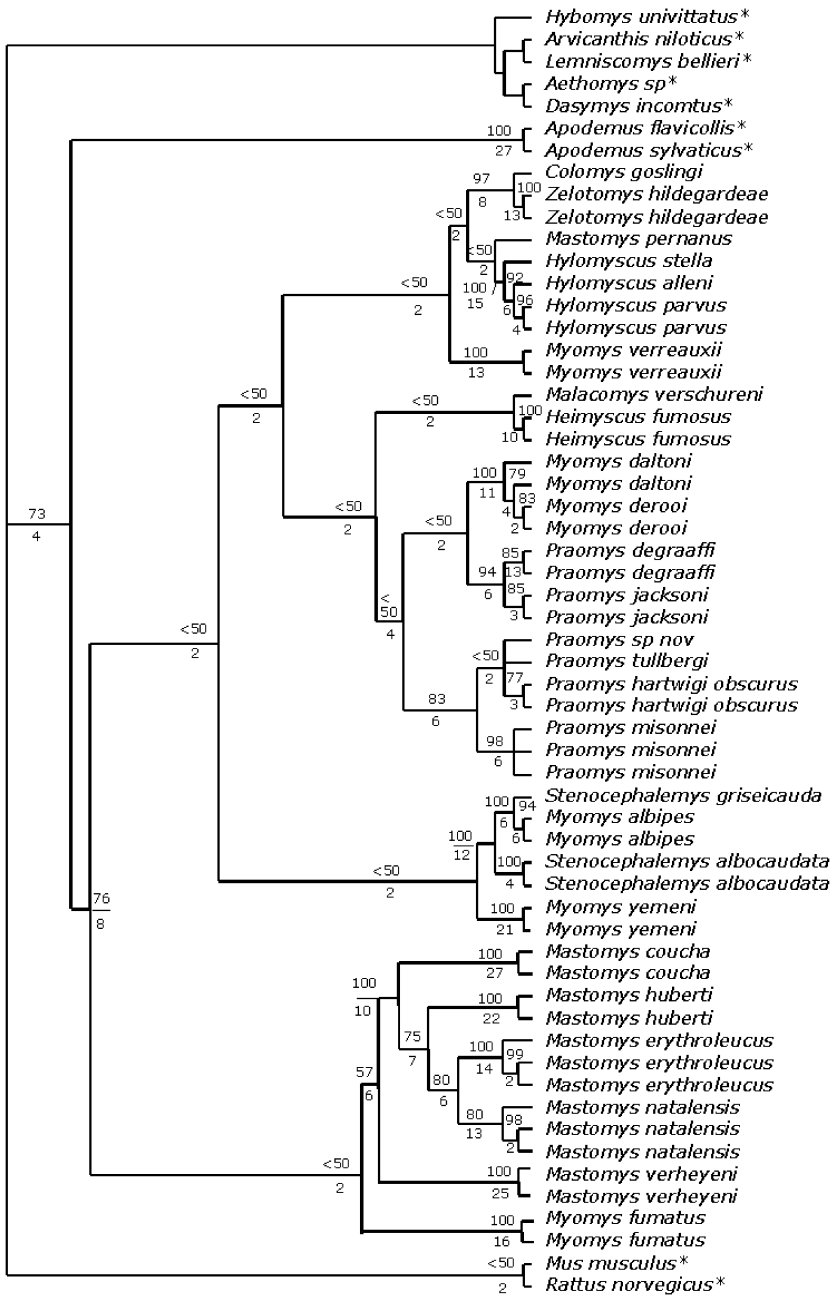
Fig. 2. Phylogenetic relationships among nucleotide sequences of the complete cytochrome b gene (1140 pb) of 49 specimens of the *Praomys* group using maximum parsimony. The murid rodents used as outgroup are indicated with an asterisk. Trees are generated with a heuristic search (PAUP 4.0b4a) on non-saturated substitution (first and third position transitions removed). The numbers above branches are % bootstrap values (1000 replicates) and the number below represent the Bremer support Index. Strict consensus of 24 trees of 1033 steps, CI = 0.339, RI = 0.667, RC = 0.226.

93% and 92% in ML, respectively, Figs. 2 and 4). These two groups maintain their integrity in the NJ AA trees. The genus *Myomys* appears polyphyletic: *Myomys fumatus* clusters with *Mastomys*, while *Myomys daltoni* and *Myomys derooi* cluster with the genus *Praomys*. However, none of these phylogenetic relationships involving the *Myomys* species is strongly supported. The genus *Stenocephalemys* also appears to be paraphyletic. Along with *Myomys albipes, Stenocephalemys*, forms a strongly supported (100% BP in both MP and ML; DI = 12; Figs. 2 and 4) Ethiopian clade. This clade is also evident in the analyses based

on amino acids. The monophyly of the genus *Hylomyscus*, represented here by three species, is strongly supported (100% BP in both MP and ML; DI = 15, Figs. 2 and 4) and is also recovered in the AA-based trees. *Zelotomys hildegardeae* appears as the sister group of *Colomys goslingi* with a high support (97% BP in MP; DI = 8; 98% BP in ML, Figs. 2 and 4), a relationship also found in the two AA-based analyses. *Myomys verreauxii* is found aligned to *Colomys* and *Zelotomys*, albeit with quite low bootstrap value (61% BP in ML; 63% BP in NJ, Fig. 4). The genus *Mastomys* is paraphyletic due to the species *Mastomys pernanus*
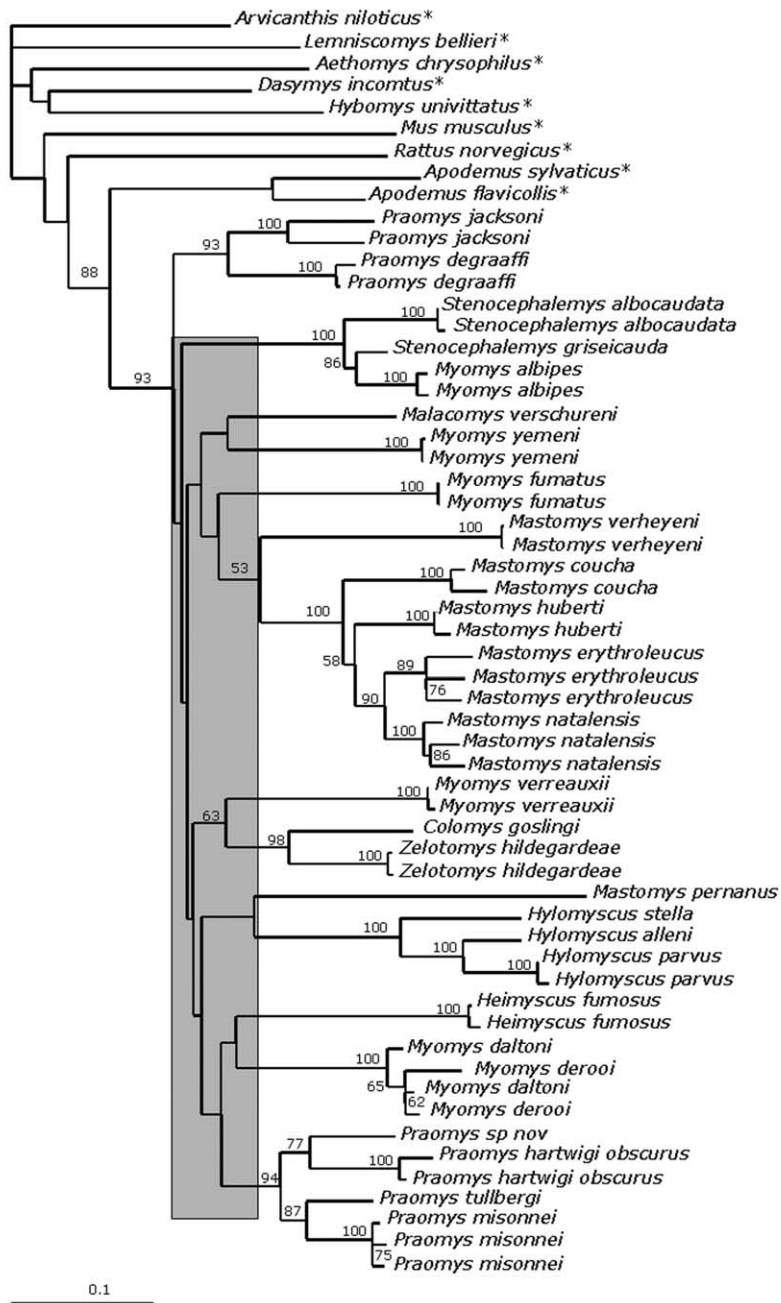
Fig. 3. Phylogenetic relationships among nucleotide sequences of the complete cytochrome b gene (1140 pb) of 49 specimens of the *Praomys* group using the Neighbour-Joining method. The murid rodents used as outgroup are indicated with an asterisk. Tree was generated on distance matrix calculated under the model selected by Modeltest 3.04. The numbers above branches are bootstrap values above 50% (1000 replicates). Scale bar indicates 10% divergence. The grey area indicates the period of emergence of most of the major lineages.

that appears quite divergent from the others. The other four species (*M. erythroleucus*, *M. natalensis*, *M. huberti* and *M. coucha)* form a highly supported clade (100% BP, DI = 10) of closely related species (sequences diverge by 10% at the most), a finding consistent with the MP and NJ analyses based on amino acids. The sister group of this clade is represented by *Mastomys verheyeni* with a Decay Index of 6, but with very low bootstrap support (57% in MP; 53% in NJ, Figs. 2–4). The relationships within the four closest species were not clearly resolved with the global analyses (polytomy between *M. coucha*, *M. huberti* and the grouping *M. natalensis/M. erythroleucus*), while

they were using all the substitutions: the tree obtained was integrated in the global phylogeny. In ML (global model), the relationships are incongruent with those recovered in MP analysis but when using the model for the *Mastomys* data set, the relationships are the same that in MP analysis, i.e. *Mastomys coucha* is the first species to diverge, then *M. huberti*, whereas *M. natalensis* and *M. erythroleucus* are sister groups.

3.5. Relative-rate tests

Synonymous (Ks) changes did not show significant differences between the species within the *Praomys* group. However, Ka comparisons showed that only
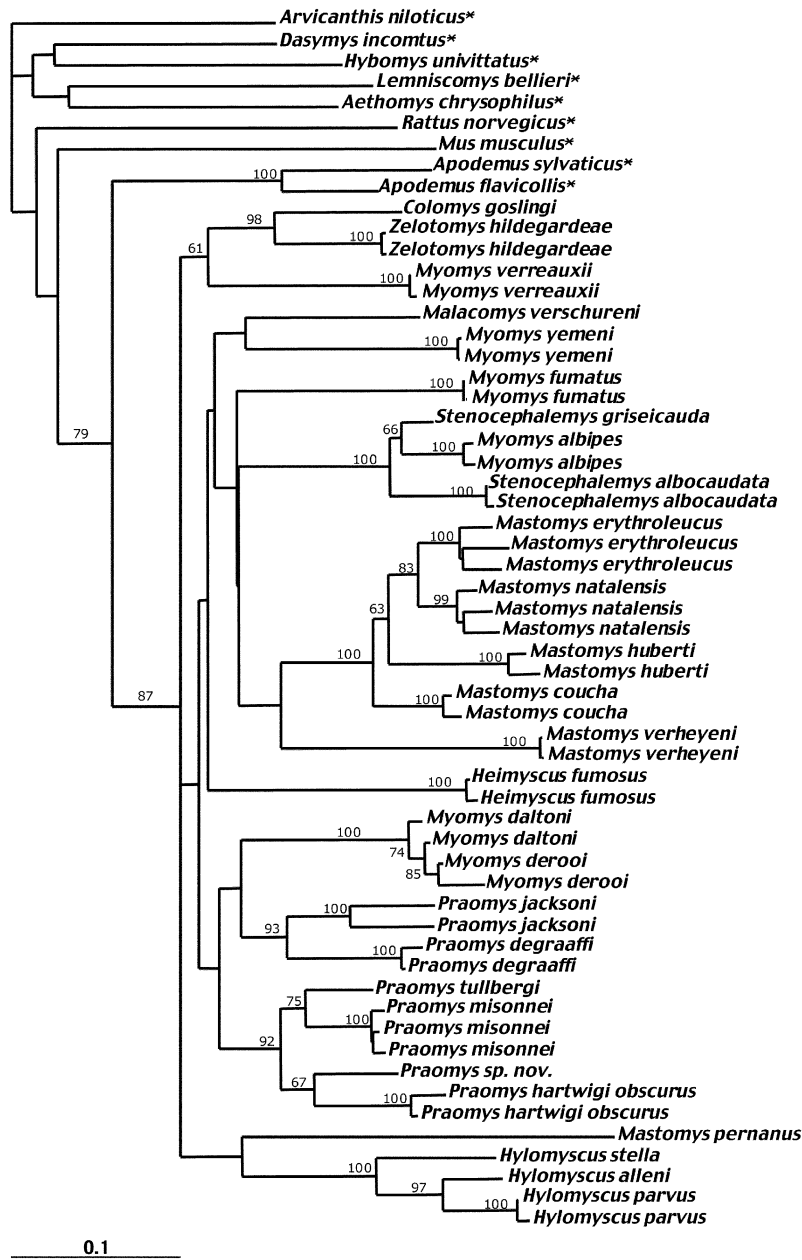
Fig. 4. Phylogenetic relationships among nucleotide sequences of the complete cytochrome b gene (1140 pb) of 49 specimens of the *Praomys* group using maximum-likelihood method. The murid rodents used as outgroup are indicated with an asterisk. Trees are generated with an heuristic search (PAUP 4.0b4a), under the model GTR+I+G, selected by Modeltest 3.04. The numbers above branches are bootstrap values above 50% (100 replicates). Highest-likelihood tree (ln *L*=15 006.786). Scale bar indicates 10% divergence.

Mastomys pernanus was quickly evolving ($P < 0.05$). As the RRTree test is rather sensitive to the rate of species used as outgroups [31], we also applied the test using Mega [32]. These results obtained confirm the RRTree test when *Apodemus* or *Rattus* are used as outgroups; however, when using *Mus* as outgroup, no taxon show significant difference of evolution rate. Consequently, when applying a molecular clock to estimate the separation dates between the species and

genera within the *Praomys* group, *M. pernanus* was not taken into account.

4. Discussion

4.1. Genetic distances

The genetic distances observed within the *Praomys* group are similar to those known between other rodent

genera, which were found to span a wide range. For example, between 9 and 20% sequence divergence has been reported among some caviomorph genera [35], while between 6 and 15% sequence divergence has been found among European muroids [34].

4.2. Phylogenetic analyses

The results of our phylogenetic analyses are consistent with expectations based on previous studies. Although its dental structure has been reviewed [10, 15], the affinities of *Zelotomys* have not been discussed on the basis of biochemical techniques. Jaeger and Davis concluded that it was close to the *Praomys* group [10, 15], a proposal confirmed in our study. Similarly, *Colomys* was proposed for inclusion within the *Praomys* group in a recent molecular study [16], while, on the basis of its long feet, and because of its semi-aquatic habits, it has often been compared with *Malacomys* [36, 37]. *Zelotomys* and *Colomys* appear closely related here, as proposed by Misonne on the basis of dental characters [4], but their sister group was not unambiguously identified, although the species *M. verreauxii* could represent a good candidate. *Heimyscus fumosus* was considered a member of the genus *Hylomyscus*, before Misonne [4] created a new genus for this species. Our study confirms that *Heimyscus* is quite divergent from *Hylomyscus* and that it is probably more closely related to *Praomys*. Moreover, the genus *Myomys* was already proposed to be paraphyletic [14, 16, 17, 19]. The close affinity of *Myomys albipes* with *Stenocephalemys* was demonstrated by morphometrical, chromosomal, morphological and molecular analyses [14, 16, 17]. *Myomys fumatus* was found to be closely related to *Mastomys* [38] on the basis of chromosomal and protein data. Other *Myomys* species have been proposed to be related to *Praomys* (e.g. *Myomys daltoni* and *Myomys derooi*), or to *Mastomys* (*Myomys verreauxii*) [19]. Were these relationships confirmed, this polyphyly of *Myomys* should lead to nomenclatural revision of the genus. For instance, *Myomys fumatus* would join *Mastomys* [38], *Myomys daltoni* and *Myomys derooi* would have to be placed within *Praomys*, while *Myomys yemeni* and *Myomys albipes* would join *Stenocephalemys*. The species *Myomys yemeni,* which lives on the Arabian Peninsula, also clusters within the *Praomys* group. Its apparently weak divergence from purely African species such as *Myomys albipes* and *Stenocephalemys* spp. suggests that *M. yemeni* only recently established in the Arabian Peninsula. *Myomys verreauxii*, the only South African species, is the type species of the genus and would retain the name '*Myomys*'.

In our study, the genus *Praomys* is found paraphyletic. In earlier studies based on DNA/DNA hybridisation and morphometrics, the monophyly of this genus was questioned, based on the high divergence between the *P. jacksoni* and *P. tullbergi* groups [6, 18]. The two well-supported groups (*P. jacksoni*/*P. tullbergi*) distinguished here, have been identified in other analyses, using chromosomal [39, 40], palatal ridges [41], and craniodental characters [18, 20, 42]. Here the *P. jacksoni* group includes the species *P. jacksoni* and *P. degraaffi*, which is congruent with morphometrical and morphological studies [20, 43]. According to morphological characters [20], the sister taxon to the *P. jacksoni* group is *Myomys daltoni*. The *P. tullbergi* group includes *P. tullbergi*, *P. misonnei*, *P. hartwigi obscurus* and *P. sp. nov.* [21], which is also congruent with analyses based on morphological and morphometrical data [20, 42].

Although *Mastomys*, as currently recognised [1], appears to be paraphyletic, four of the *Mastomys* species (*M. erythroleucus*, *M. natalensis*, *M. huberti* and *M. coucha*) form a strongly supported clade. These species have often been found to be closely related [6–8, 44]. Based on chromosomal and DNA/DNA hybridisation data, *M. coucha* was the first species to diverge [6, 7] while *M. natalensis* and *M. huberti* were found to be the most closely related ones [7]. However, using protein electrophoresis data on specimens from Senegal, *M. huberti* appeared closer to *M. erythroleucus* than to *M. natalensis* [44], but this pattern of relationships may have been obscured by the much reduced genetic variability of *M. natalensis* at the edge of its distribution area. Our analysis confirms that *M. coucha* is the sister group of the three other species. However, *M. erythroleucus* is placed here as the sister taxon of *M. natalensis*. *Mastomys verheyeni* seems to be the sister group of these four species. It is easily distinguishable morphologically from the other species [5], but its phylogenetic position has never been discussed. Finally, the rare *Mastomys pernanus* was included for the first time in a phylogenetic analysis. Van der Straeten [45] first mentioned its high morphometrical divergence from *Mastomys* and questioned its affinities. Our study confirms that this species should no longer be considered a member of *Mastomys*.

Malacomys verschureni was thought to show affinities with *Praomys* [18, 46], and indeed has been often labelled as *Praomys* within museum collections [46], but had not been included in any phylogenetic study so far. Here we confirm that this species belongs to the *Praomys* group, with an especially close relationship to *Heimyscus*.

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Table 2. Estimates of divergence times using third position transversion changes numbers for the complete cytochrome b gene dataset, and based on a *Mus–Rattus* split at 12 and 23 Myr (cf. text), using a rate of third position transversion change of 1.53% per Myr and 0.80% per Myr, respectively. Events are listed as they appear in Fig. 2.

	Number of third position transversion differences (mean)	Divergence time estimates (Myr) according to the *Mus–Rattus* split at:	
		12 Myr	23 Myr
Apodemus / Praomys group	66.1	11.4	21.7
1st divergence within *Praomys* group	49.6	8.5	16.3
2nd divergence (Ethiopian clade / *Praomys, Myomys, Hylomyscus*)	46.9	8.1	15.4
P. tullbergi group / *M. daltoni, P. jacksoni* group	30.5	5.2	10
Myomys daltoni / Praomys jacksoni group	28.5	4.9	9.4
Within *Praomys tullbergi* group	12.5	2.2	4.1
Within *Praomys jacksoni* group	20.5	3.5	6.7
M. yemeni / Ethiopian clade	44.9	7.7	14.8
Within Ethiopian clade (*M. albipes-Stenocephalemys*)	13.4	2.3	4.4
M. verreauxii / Colomys + Zelotomys	38.7	6.6	12.7
Colomys / Zelotomys	23	3.9	7.6
M. fumatus / four *Mastomys* species group	42.6	7.3	14.0
M. verheyeni / four *Mastomys* species group	41.2	7.1	13.5
M. coucha / M. erythroleucus, M. huberti, M. natalensis	17.3	3.0	5.7

The incongruences between the MP, ML and NJ trees and between the nucleotide-based and amino acid-based analyses concerning the basal nodes suggest a telescoping in time of the cladogenetic events, which may have resulted from an adaptive radiation (see below).

4.3. Divergence times

Using the available fossil record, a molecular clock has been calibrated in murid rodents for cytochrome b [47], based on the divergence date between *Mus* and *Rattus* and the transversion rate at third codon position. Palaeontological data suggest that this split occurred around 10–14 Myr [48–50]. There are 70 transversions at the third codon position between *Mus musculus* and *Rattus norvegicus*. Taking a mean divergence time of 12 Myr, the rate of third position transversion change is 1.53% per Myr. Using this transversion rate among the taxa under consideration, estimates of divergence times for the cladogenetic events are provided (Table 2). However, a recent molecular study proposed that the *Mus–Rattus* split may have occurred 23 Myr ago [51]. Thus, divergence dates are also proposed for a split of *Mus–Rattus* at 23 Myr (Table 2); nevertheless, only the divergence dates based on the split at 12 Myr will be discussed further in order to compare with previous studies based on this dating.

The divergence time separating the *Praomys* group from *Apodemus* is estimated here at 11.4 Myr. This date is older than the estimate of 8 Myr for the emergence of the *Praomys* group from the *Mus* lineage based on DNA/DNA hybridisation data [6]. The same concerns the estimation of divergence between the genera of the

Praomys group (8.5 here vs 4 Myr via DNA/DNA hybridisation data [6]). Among the *Praomys* group, the resolution is weak above the species level while the node suggesting that *Apodemus* is the sister taxon of this group is quite well supported, although much older. One explanation would be a deficit of information due to saturation, but the saturated substitutions were removed and the tree length distributions were significantly skewed, indicating a phylogenetic signal in the dataset. Another possible explanation to this apparent telescoping of events is that a phase of extensive diversification did occur in the group, leading to a number of lineages. All the basal splits within the *Praomys* group are estimated around 7.3 and 8.5 Myr (see Fig. 3). This period of time is rather short and could be an indication that the emergence of the different lineages occurred during an adaptive radiation that took place during Late Miocene. This period was also the one proposed for the split of the Arvicanthini from the rest of Murinae [22] and for the first appearance of an Antilopinae bovid in Africa as well as migration of endemic Reduncini of genus *Kobus* in Eurasia [52]. This suggests that some eco-climatic event did favour the radiations and immigrations in Africa. The emergences of Arvicanthini and the *Praomys* group, calibrated in the same manner, are contemporaneous, and using a molecular clock calibrated on 23 Myr for the *Mus–Rattus* split would maintain this contemporaneity.

The fossil record is rather scarce in the *Praomys* group: the earliest records are from Laetoli (Tanzania) dated at 3.7 Myr [53] for a species of *Mastomys*, 3.3 Myr for a species of *Praomys* in Hadar (Ethiopia)

[54] and around 3 Myr for *Zelotomys* in Gcwihaba (Botswana) [55]. The emergence of the genus *Mastomys* is estimated here (Table 2) at 7.1 Myr, a date that is compatible with the age of the Laetoli fossil. The estimate of 3 Myr for the emergence of the four *Mastomys* species (*erythroleucus, natalensis, huberti* and *coucha*) is much older than the one of 1 Myr calculated from DNA/DNA hybridisation data [6]. This date of separation may appear remote in comparison with the great morphological similarity between these four *Mastomys* species [8, 56, 57], but is more in agreement with their karyotypic differentiation [7, 8, 56]. The divergence date of the two *Praomys* groups is estimated at 5.2 Myr, while the divergence between the species within each groups is much more recent (i.e. 2.2 Myr and 3.5 Myr for the *tullbergi* and the *jacksoni* groups, respectively). The divergence within the Ethiopian clade *Stenocephalemys–Myomys albipes* is estimated around 2.3 Myr. Within this clade, Fadda et al. [16], in a molecular analysis based on 16S sequences, found quite similar divergence times (with a time scale calibrated on 12 Myr for the *Mus–Rattus* split): 1.3 Myr between *M. albipes* and *Stenocephalemys griseicauda* against 1.9 Myr in our analysis and 2.24 for the clade versus 2.4 Myr here. Also, Fadda et al. [16] found between 5.9 and 6.4 Myr for the split of *Myomys*

daltoni from the Ethiopian group, which is less than the 8 Myr value found here.

The date of divergence of this Ethiopian clade (*Myomys albipes–Stenocephalemys*) is approximately the same as the one estimated for the diversification between *Mastomys* species or within the *tullbergi* group, comprising sibling species; however, the species of the Ethiopian clade are so distinguishable from each others that they were not included in the same genus. This is an additional example where rates of morphological evolution do not correlate with rates of molecular evolution. This observation was early highlighted by Wilson and his co-workers [58–60], and subsequent molecular studies in species groups that have undergone recent adaptive radiations, such as African rift lake cichlids [61], columbines [62], and the Hawaiian silversword alliance [63], have documented marked incongruities in rates of morphological and molecular evolution. A proposed resolution to this paradox has been the conjecture that morphological evolution proceeds via diversification in regulatory loci, and so that phenotypic evolution may correlate better with regulatory gene divergence [64]. Such hypotheses would worth be tested on African rodents in which the patterns and processes of evolution appear highly diversified.

References

[1] G.G. Musser, M.D. Carleton, Family Muridae, in: D.E. Wilson, D.M. Reeder (Eds.), Mammals species of the world: a taxonomic and geographic reference, Smithsonian Institution Press, Washington & London, 1993, pp. 1206.

[2] J.R. Ellerman, T.C.S. Morrison-Scott, R.W. Hayman, Southern African mammals 1758 to 1951: a reclassification, British Museum (Natural History), London, 1953.

[3] D.R. Rosevear, The Rodents of West Africa, London, 1969.

[4] X. Misonne, African and Indo-Australian muridae evolutionary trends, Annales du Musée royal d'Afrique centrale, Tervuren, Belgique, 172, 1969, pp. 1–219.

[5] L.W. Robbins, E. Van der Straeten, Comments on the systematics of *Mastomys* Thomas, 1915 with description of a new west African species, Senckenb. Biol. 69 (1989) 1–14.

[6] P. Chevret, L. Granjon, J.-M. Duplantier, C. Denys, F.M. Catzeflis, Molecular phylogeny of the *Praomys* complex (Rodentia: Murinae): a study based on DNA/DNA hybridization experiments, Zool. J. Linn. Soc. 112 (1994) 425–442.

[7] J. Britton-Davidian, J. Catalan, L. Granjon, J.-M. Duplantier, Chromosomal phylogeny and evolution in the genus *Mastomys* (Mammalia, Rodentia), J. Mammal. 76 (1995) 248–262.

[8] L. Granjon, J.-M. Duplantier, J. Catalan, J. Britton-Davidian, Systematics of the genus *Mastomys* (Thomas, 1915) (Rodentia: Muridae): a review, Belg. J. Zool. 127 (1997) 7–18.

[9] O. Thomas, The generic position of certain African Muridae, hitherto referred to *Aethomys* and *Praomys*, Ann. Mag. Nat. Hist., Ser. 9 17 (1926) 174.

[10] D.H.S. Davis, Classification problems of African Muridae, Zool. Afr. I (1) (1965) 121–145.

[11] O. Thomas, List of Mammals collected on the upper Congo by Christy for the Congo Museum, Tervueren, Ann. Mag. Nat. Hist. Ser. 8 16 (1915) 465–481.

[12] X. Misonne, Order Rodentia. Part 6, in: J. Meester, H.X. Setzer (Eds.), The mammals of Africa, an identification manual, Smithsonian Institution Press, Washington, DC, 1974.

[13] A. Brosset, G. Dubost, H. Heim de Balsac, Mammifères inédits récoltés au Gabon, Biol. Gabonica 1 (1965) 148–175.

[14] E. Van der Straeten, F. Dieterlen, Description de *Praomys ruppi*, une nouvelle espèce de Muridae d'Éthiopie, Proceedings of the 3rd international colloquium on the Ecology and Taxinomy of African Small Mammals, 1983, pp. 121–127.

[15] J.-J. Jaeger, Les rongeurs (Mammalia, Rodentia) du Pléistocène inférieur d'Olduvai Bed I (Tanzanie). 1re partie : Les Muridés, in: R.J.G. Savage, S.C. Coryndon (Eds.), Fossil Vertebrates, Academic Press, New York & London, 1976, pp. 57–120.

[16] C. Fadda, M. Corti, E. Verheyen, Molecular phylogeny of *Myomys/Stenocephalemys* complex and its relationships with related African genera, Biochem. Syst. Ecol. 29 (2001) 585–596.

[17] L.A. Lavrenchenko, A.N. Milishnikov, V.M. Aniskin, A.A. Warshavsky, Systematics and phylogeny of the genus *Stenocephalemys* Frick, 1914, (Rodentia, Muridae): a multidisciplinary approach, Mammalia 63 (1999) 475–494.

[18] E. Van der Straeten, A.M. Dudu, Systematics and distribution of *Praomys* from the Masako Forest Reserve (Zaire), with the description of a new, in: G. Peters, R. Hutterer (Eds.), Vertebrates in the Tropics, Museum Alexander Koenig, Bonn, 1990, pp. 73–83.

[19] E. Van der Straeten, Biometrical relationships between *Praomys–Myomys–Mastomys* and *Myomyscus* (= *Praomys* complex) (Mammalia, Muridae), Afr. Small Mammals Newslett. 3 (1979) 27–30.

[20] E. Lecompte, L. Granjon, C. Denys, The phylogeny of the *Praomys* complex (Rodentia:Muridae) and its phylogeographic implications, J. Zool. Syst. Evol. Res. 40 (2002) 8–25.

[21] E. Van der Straeten, E. Lecompte, C. Denys, Une nouvelle espèce de Muridae africain (Mammalia, Rodentia), Bonn. Zool. Beitr. (in press).

[22] J.-F. Ducroz, V. Volobouev, L. Granjon, An assessment of the systematics of arvicanthine rodents using mitochondrial DNA sequences: evolutionary and biogeographical implications, J. Mammal Evol. 8 (2001) 173–206.

[23] B. Winnepenninckx, T. Backeljau, R. De Wachter, Extraction of high molecular weight DNA from molluscs, Trends Genet. 9 (1993) 407.

[24] T.A. Hall, BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT, Nucl. Acids Symp. Ser. 41 (1999) 95–98.

[25] D.L. Swofford, PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1.1. Program and documentation, Illinois Natural History Survey, Champaign, 1993.

[26] D.L. Swofford, PAUP: Phylogenetic Analysis Using Parsimony, version 4.0b4a, Illinois Natural History Survey, Champaign, 1998.

[27] J. Felsenstein, Confidence limits on phylogenies: an approach using the bootstrap, Evolution 39 (1985) 783–791.

[28] K. Bremer, Branch support and tree stability, Cladistics 10 (1994) 295–304.

[29] T. Eriksson, AutoDecay ver. 4.0, Department of Botany, Stockholm University. Stockholm, Sweden, 1998.

[30] D. Posada, K.A. Crandall, Modeltest: testing the model of DNA substitution, Bioinformatics 19 (9) (1998) 817–818.

[31] M. Robinson, M. Gouy, C. Gautier, D. Mouchiroud, Sensitivity of the relative-rate test to taxonomic sampling, Mol. Biol. Evol. 15 (9) (1998) 1091–1098.

[32] S. Kumar, K. Tamura, B. Jakobsen I, M. Nei, MEGA2: Molecular Evolutionary Genetics Analysis software, Arizona State University, Tempe, Arizona, USA, 2001.

[33] D.M. Irwin, T.D. Kocher, A.C. Wilson, Evolution of the cytochrome b gene of mammals, J. Mol. Evol. 32 (1991) 128–144.

[34] Y. Martin, G. Gerlach, C. Schlötterer, A. Meyer, Molecular phylogeny of European muroid rodents based on complete cytochrome b sequences, Mol. Phylogenet. Evol. 16 (2000) 37–47.

[35] M.C. Lara, J.L. Patton, M. Nazareth, F. Da Silva, The simultaneous diversification of South American Echimyid Rodents (Hystricognathi) based on complete cytochrome b sequences, Mol. Phyl. Evol. 5 (1996) 403–413.

[36] F. Dieterlen, B. Statzner, The African rodent *Colomys goslingi* Thomas & Wroughton 1907 (Rodentia: Muridae): a predator in limnetic ecosystems, Z. Saugetierkd. 46 (1981) 369–383.

[37] J.C. Kerbis Peterhans, B.D. Patterson, The Ethiopian water mouse *Nilopegamys* Osgood, with comments on semi-aquatic adaptations in African Muridae, Zool. J. Linn. Soc. 113 (1995) 329–349.

[38] M.B. Qumsiyeh, S.W. King, J. Arroyo-Cabrales, I.R. Aggundey, D.A. Schlitter, R.J. Baker, K.J. Morrow, Chromosomal and protein evolution in morphologically similar species of *Praomys sensu lato* (Rodentia, Muridae), J. Hered. 81 (1990) 58–65.

[39] R. Matthey, La formule chromosomique chez sept espèces et sous-espèces de Murinae Africains, Mammalia 27 (1963) 157–176.

[40] R. Matthey, Études de cytogénétique sur les Murinae africains appartenant aux genres *Arvicanthis*, *Praomys*, *Acomys* et *Mastomys* (Rodentia), Mammalia 29 (1965) 228–249.

[41] M. Eisentraut, Das Gaumenfaltenmuster bei westafrikanischen Muriden, Zool. Jb. Syst. Bd. 96 (1969) 478–490.

[42] E. Van der Straeten, F. Dieterlen, *Praomys misonnei*, a new species of Muridae from Eastern Zaïre (Mammalia), Stuttgarter Beiträge zur Naturkunde, Ser. A (Biol.) 402 (1987) 1–11.

[43] E. Van der Straeten, J.C. Kerbis Peterhans, *Praomys degraaffi*, a new species of Muridae (Mammalia) from central Africa, S. Afr. J. Zool. 34 (1999) 80–90.

[44] J.-M. Duplantier, L. Granjon, E. Mathieu, F. Bonhomme, Structures génétiques comparées de trois espèces de rongeurs africains du genre *Mastomys* au Sénégal, Genetica 81 (1990) 179–192.

[45] E. Van der Straeten, Notes on *Mastomys pernanus* (Kershaw, 1921), Bonn. Zool. Beitr. 48 (1999) (1921) 225–230.

[46] F. Dieterlen, E. Van der Straeten, New specimens of *Malacomys verschureni* from Eastern Zaïre, Rev. Zool. Afr. 98 (1984) 861–868.

[47] M.F. Smith, J.L. Patton, The diversification of South American murid rodents: evidence from mitochondrial DNA sequence data for the akodontine tribe, Biol. J. Linn. Soc. 50 (1993) 149–177.

[48] J.-J. Jaeger, H. Tong, C. Denys, Âge de la divergence *Mus–Rattus*: Comparaison des données paléontologiques et moléculaires, C. R. Acad. Sci. Paris, Ser. III 302 (1986) 917–922.

[49] L.L. Jacobs, L.J. Flynn, W.R. Downs, Neogene rodents of southern Asia, in: C.C. Black, M.R. Dawson (Eds.), Papers on Fossil Rodents in Honor of Albert Elmer Wood, Nat. Hist. Mus. Sci., Los Angeles, 1989, pp. 157–177.

[50] L.L. Jacobs, L.J. Flynn, W.R. Downs, J.C. Barry, *Quo vadis, Antemus?* The Siwalik muroid record, in: E.H. Lindsay, V. Fahlbush, P. Mein (Eds.), European Neogene Mammal Chronology, Plenum, New York, 1990, pp. 573–586.

[51] R.M. Adkins, E.L. Gelke, D. Rowe, R.L. Honneycutt, Molecular phylogeny and divergence time estimates for major rodent groups: evidence from multiple genes, Mol. Biol. Evol. 18 (2001) 777–791.

[52] H. Thomas, Les Bovidae (Artiodactyla: Mammalia) du Miocène du sous-continent indien, de la péninsule Arabique et de l'Afrique: biostratigraphie, biogéographie et écologie, Palaeogeogr. Palaeoclimatol. Palaeoecol. 45 (1984) 251–299.

[53] C. Denys, J.-J. Jaeger, A biostratigraphic problem: the case of the East African Plio-Pleistocene rodent faunas, Mod. Geol. 10 (1986) 215–233.

[54] M. Sabatier, Les rongeurs du site Pliocène à Hominidés de Hadar (Éthiopie), Palaeovertebrata 12 (1982) 1–56.

[55] M. Pickford, P. Mein, The discovery of fossiliferous Plio-Pleistocene cave fillings in Ngamiland, Botswana, C. R. Acad. Sci. Paris, Ser. III 307 (1988) 1681–1686.

[56] J.-M. Duplantier, J. Britton-Davidian, L. Granjon, Chromosomal characterization of three species of the genus *Mastomys* in Senegal, Z. Zool. Syst. Evol. 28 (1990) 289–298.

[57] N.J. Dippenaar, P. Swanepoel, D.H. Gordon, Diagnostic morphometrics of two medically important southern African rodents, *Mastomys natalensis* and *M. coucha* (Rodentia: Muridae), S. Afr. J. Sci. 89 (1993) 300–303.

[58] M.C. King, A.C. Wilson, Evolution at two levels in humans and chimpanzees, Science 188 (1975) 107–116.

[59] L.M. Cherty, S.M. Case, A.C. Wilson, Frog perspective on the morphological difference between humans and chimpanzees, Science 200 (1978) 209–211.

[60] A.C. Wilson, in: F.J. Ayala (Ed.), Molecular Evolution, Sinauer, Sunderland, MA, 1977, pp. 225.

[61] A. Meyer, T.D. Kocher, P. Basasibwaki, A.C. Wilson, Monophyletic origin of Lake Victoria cichlid fishes suggested by mitochondrial DNA sequences, Nature 347 (1990) 550–553.

[62] S.A. Hodges, M. Arnold, Columbines: a geographically widespread species flock, Proc. Natl Acad. Sci. USA 91 (1994) 5129–5132.

[63] B.G. Baldwin, R.H. Robichaux, in: W.L. Wagner, V.A. Funk (Eds.), Hawaiian biogeography: evolution on a hot spot archipelago, Smithsonian Press, Washington DC, 1995, pp. 259–287.

[64] M. Barrier, R.H. Robichaux, M.D. Purugganan, Accelerated regulatory gene evolution in an adaptive radiation, Proc. Natl Acad. Sci. USA 98 (2001) 10208–10213.

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