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Molecular phylogeny of the *Praomys* complex (Rodentia: Murinae): a study based on DNA/DNA hybridization experiments.

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Within the Murinae (Muridae: Rodentia), the African rats of the *Praomys* group, whose systematics has been studied through different approaches, have raised numerous taxonomic problems. Different taxa related to *Praomys* have successively been described, among which *Mastomys*, *Myomys* and *Hylomyscus* were considered either as separate genera or subgenera of *Praomys*. In order to clarify the relationships within the *Praomys* group, we conducted a series of DNA/DNA hybridization experiments involving different species of *Praomys*, *Mastomys*, *Myomys* and *Hylomyscus* plus other Murinae and a Cricetomyinae. This study indicates that the *Praomys* complex is a monophyletic entity clearly separated from the other African and Asian Murinae. If *Mastomys* and *Hylomyscus* appeared to be independent genera, the taxonomic situation of *Praomys* and *Myomys* is more difficult to ascertain. Indeed, *Praomys tullbergi* appears more closely related to *Myomys daltoni* than to another species of *Praomys*, namely *P. jacksoni*, suggesting paraphyly for *Praomys*. Furthermore, *P. jacksoni* is as distant from *P. tullbergi* as from any species of *Mastomys*. Additional species of *Praomys* and, especially, of *Myomys*, are needed for reaching a definitive conclusion on these latter taxa. The *Praomys* group is more related to *Mus* than to *Rattus*. To calibrate our molecular distances with geological time, we used a dating of 10 Myr for the *Mus/Rattus* dichotomy. The inferred rate of molecular evolution suggests a dating of *c.* 8 Myr for the separation of the *Praomys* group from the *Mus* lineage.

ADDITIONAL KEY WORDS:—evolution – *Mastomys* – divergence timing – DNA/DNA hybridization.

CONTENTS

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INTRODUCTION

Among African murine rodents, the *Praomys* group comprises five taxa: *Praomys*, *Mastomys* (multimammate rats), *Myomys*, *Myomyscus* and *Hylomyscus* (climbing wood mice), which have been treated either as related genera (Rosevear, 1969; Carleton & Musser, 1984; Nowak, 1991) or subgenera within *Praomys* (Misonne, 1974; Nowak & Paradiso, 1983). All living members of *Praomys sensu lato* are found almost exclusively in Africa and are mouse-like rodents; most of them are primarily terrestrial (*Mastomys*, *Praomys*) while others are arboreal and scansorial (*Myomys*, *Hylomyscus*)—for general accounts on the biology of these genera, see Nowak, (1991). The relationships between these genera/subgenera and their species are not well understood, in part due to the low level of morphological differentiation between the numerous species so far described (see Rosevear, 1969, for details). The aim of this paper is to examine the relationships of these taxa using a comparative molecular approach.

After first being placed in the genus *Mus*, *Praomys*, as well as *Mastomys* and *Myomys*, were later considered as members of the genus *Epimys* by Thomas (1915), who distinguished *Hylomyscus* as a separate genus. Ellerman (1941) classified all of them in the genus *Rattus* with most of the other African Murinae. Shortridge (1942) considered *Myomys* as a distinct genus and introduced *Myomyscus* as a subgenus of *Myomys* (but Musser & Carleton (1993) suggest that both names are synonyms for nomenclatural reasons). Davis (1962) elevated *Praomys* to generic rank and relegated the other taxa as subgenera; this opinion was followed by several authors, for example Misonne (1969), Kingdon (1974), Honacki, Kinman & Koeppl (1982), Happold (1987) and Nowak & Paradiso (1983). But Misonne (1969) considered only *Mastomys*, *Hylomyscus* and *Myomyscus* as subgenera. For others, such as Rosevear (1969), Carleton & Musser (1984), Robbins, Choate & Robbins (1980), and Nowak (1991), all these taxa were ranked as full genera. The systematic conclusions of all these previous studies were based on body, skull and tooth morphology.

In addition to these morphological characters, biometrical studies were also used to decipher the relationships among *Praomys sensu lato*. For Van der Straeten (1979), *Mastomys*, *Praomys* and *Myomyscus* were biometrically well differentiated, whereas *Myomys* could not be considered as a genus separate from *Praomys*. However, these results were contradicted by a subsequent study, using phenetics on biometrical data, where *Myomys* appeared closer to *Mastomys* than to any other related genus (Van der Straeten & Dieterlen, 1983).

From a karyological point of view, a detailed chromosomal study of 10 murine genera (Viegas-Péquignot *et al.*, 1983) grouped *Mastomys huberti*, *Myomys daltoni* and *Hylomyscus stella* with the genera *Arvicanthis* and *Thamnomys*, and this monophyletic group was clearly separated from five other murine genera. In a further study, Viegas-Péquignot *et al.* (1986) showed that *Mastomys* (represented by *M. erythroleucus* and *M. huberti*), *Praomys* (*P. jacksoni*) and *Myomys* (*M. daltoni*)

formed a 'chromosomal cluster', to which *Hylomyscus* (*H. stella*) was the closest among 15 other murine (mainly African) rodents studied. Viegas-Péquignot *et al.* (1983, 1986) analysed chromosomal rearrangements and banding patterns in order to determine shared characters defining their chromosomal groups of species, but without taking into account the primitive or derived nature of these characters (Qumsiyeh & Baker, 1988). Qumsiyeh *et al.* (1990), in a comparative study based on protein variations and chromosomal characters, considered that *Mastomys* and *Myomys* were subgenera of *Praomys*. On the contrary, Britton-Davidian *et al.* (1995), also using chromosomal and protein data, favoured the monophyly of the genus *Mastomys*, whose sister-group was *Praomys* and *Myomys*.

Finally, electrophoretic data confirmed the relatedness of *Praomys* and *Myomys*, with *Mastomys* as their sister group and, more distantly related, *Hylomyscus* (Iskandar & Bonhomme, 1984; Bonhomme *et al.*, 1986).

The oldest palaeontological data pertaining to *Praomys sensu lato* are dated 3.6 Myr in the Laetoli Beds deposits of East Africa (Denys & Jaeger, 1986), and they have been attributed to the genus *Mastomys* (*M. cinereus*); as a whole, African available fossils represent only *Mastomys sensu stricto* and *Praomys sensu lato* (Jaeger, 1976; Black & Krishtalka, 1986; C. Denys, unpublished data).

In their thorough review of murid taxonomy and systematics, Musser & Carleton (1993: 642) emphasized that "not only the contents of *Praomys* require careful systematic revision, but its phylogenetic relationships relative to *Mastomys*, *Myomys* and *Hylomyscus* also need resolution through revisionary studies". To understand the place of *Praomys sensu lato* among the Murinae, we performed DNA/DNA hybridization experiments involving *Praomys tullbergi*, *P. lukolelae*, *Mastomys coucha*, *M. natalensis*, *M. huberti*, *M. erythroleucus*, *Myomys daltoni*, *Hylomyscus stella*, *H. fumosus*, and several other murine genera. A Cricetomyinae—*Cricetomys*—another murine subfamily *sensu* Carleton & Musser (1984), was taken as the outgroup.

MATERIAL AND METHODS

DNA samples were extracted from 95% ethanol preserved tissues housed in the collection of Preserved Mammalian Tissues of the Institut des Sciences de l'Evolution, Montpellier (Catzeflis, 1991). Table 1 lists all the taxa involved in this study, their geographic origins and collectors' names.

DNA/DNA hybridization

DNA of each species, 1–3 samples per species, was purified and sheared into fragments of *c.* 500 base pairs (bp) length (range 200–1000 bp). The non-repeated nuclear DNA fractions were isolated by removing onto hydroxyapatite columns (BIO-GEL HTP, Biorad Laboratories) the highly repeated sequences which have reassociated at Cot 1000 (Cot: product of the DNA concentration by the time of reassociation) in 0.48 M phosphate buffer at 55°C. These non-repeated DNA fractions were chemically labelled with ^{125}I, and their average fragment size ranged from *c.* 300 to *c.* 700 pb, based on sizing gels following the procedures of Hunt, Hall & Britten (1981) and Werman, Springer & Britten (1990).

TABLE 1. List of 19 taxa (and DNA samples) involved in DNA/DNA hybridization experiments, with their geographical origin and name of collectors.

Taxa and DNA sample	Geographic origin	Collector
Praomys tullbergi (4099, 4633)	Gabon	V. Nancé
Praomys lukolelae[a] (4592, 4639)	Congo	L. Granjon
Praomys jacksoni (4540, 4575)	Burundi	T. Maddalena
Myomys daltoni (4026, 4634)	Senegal	J.-M. Duplantier
Mastomys huberti (4021, 4101, 4432)	Senegal	J.-M. Duplantier
Mastomys erythroleucus (4491)	Congo	L. Granjon
Mastomys natalensis (4494, 4593)	Senegal	J.-M. Duplantier
Mastomys coucha (4587, 4644)	South Africa: Breeding colony (J. Britton-Davidian)	
Hylomyscus stella (4590, 4690)	Burundi	T. Maddalena
Hylomyscus fumosus (4665)	Congo	L. Granjon
Mus cervicolor (4105, 4106)	Thailand: breeding colony (F. Bonhomme)	
Mus musculus (57, 3761b)	Austria: breeding colony (F. Bonhomme)	
Mus saxicola (4485, 4486)	India	F. Catzeflis
Mus caroli (4108)	Thailand: breeding colony (F. Bonhomme)	
Nannomys cf *setulosus* (4591)	Gabon	V. Nancé
Nannomys sp. (4116, 4117)	Togo	F. Petter
Rattus tiomanicus (4294)	Borneo	R. Stuebing
Rattus rattus (4260)	France	P. Perret
Cricetomys gambianus (4240, 4433)	Senegal	J.-M. Duplantier

[a]: *Praomys lukolelae* sensu Petter 1975 (based on original specimen described by Hatts, 1934)

DNA/DNA hybrids, formed by one part of labelled DNA (tracer) and 1000 parts of non-labelled total DNA (driver), were allowed to reassociate after heat denaturation to a Cot of 16 000 at 60°C in 0.48 M phosphate buffer. The thermal elutions were begun at 55°C with 2.5°C increments up to 95°C, and the raw data are the radioactive counts eluted at each of the 17 temperatures in the 55–95°C range. The procedures are the same as those published in Brownell (1983), Werman *et al.* (1990) and Sibley & Ahlquist (1991).

Several statistics can be calculated to estimate the differences between the thermal elution curves of homoduplex (tracer and driver of the same species) and heteroduplex (tracer and driver of different species) hybrids. These statistics are Tm, Mode, NPH and T50H, and they have been described in detail by Sheldon & Bledsoe (1989), Catzeflis (1990) and Werman *et al.* (1990). In this paper we used Tm and Mode, which are less variable than the other statistics for the muroid rodents (Catzeflis, 1990), and which are much less prone to experimental conditions than T50H or NPH, as Sarich *et al.* (1989) have shown. Tm is the temperature at which 50% of the hybrid DNA has been dissociated between 62.5 and 95°C, and Mode is the highest point of the melting curve of radioactive counts versus temperature.

Phylogeny reconstruction

The basic results (Mode, delta-Mode; Tm, delta-Tm) are treated by two different approaches:

(1) A complete distance matrix was analysed, which involves eight taxa: one species of each of the four genera *Praomys*, *Mastomys*, *Hylomyscus* and *Myomys*, three other Murinae (*Mus*, *Nannomys* and *Rattus*), and *Cricetomys* (as an outgroup). By building a complete matrix of distances with replicates in each cell, an

examination of the extent of non-reciprocity and of the variability in rates of DNA change as advocated by Farris (1985, 1986) becomes feasible. To this complete 8×8 distance matrix a bootstrap procedure was applied as described by Krajewski & Dickerman (1990) and Sheldon *et al.* (1992). The bootstrap, which is realized on uncorrected values, samples with replacement the replicate measures in each cell of a complete matrix. This original matrix either contains distances, i.e. delta-values, or else absolute temperatures, i.e. Tm or Mode values. For each bootstrapping procedure, a pseudo-replicate matrix is constructed by recalculating the average distance for each cell, and correcting for non-reciprocity by the symmetrization procedure described in Sarich & Cronin (1976) (which produces a corrective factor for each column, i.e. for each tracer). This symmetrized pseudo-replicate matrix is treated by the FITCH program (from PHYLIP package: Felsenstein, 1990), which estimates the best-fit tree. This cycle is repeated 1500 times for each of the four matrices of data (delta-Tm, Tm, delta-Mode and Mode), and the resulting topologies are recorded. Next, a majority-rule consensus tree is derived from the replicate bootstrap topologies by the CONSENSE program in PHYLIP (Felsenstein, 1990). Each node of the resulting consensus tree is characterized by the frequency at which the dichotomy of interest has been found among the 1500 pseudoreplicate trees.

(2) We used a simple clustering procedure to build a tree including all 19 taxa involved in DNA/DNA hybridization experiments. For this enlarged set of taxa, the raw delta-Tm values were also corrected for non-reciprocity, following Sarich & Cronin (1976). The symmetrized delta-Tm values were then transformed into percent base pair mismatch (bpm) estimates by the relation of 1°C delta-Tm = 1.18% bpm (Springer, Davidson & Britten, 1992). These estimates were finally transformed into percent nucleotide substitutions (% nucl. subst.) by the Jukes & Cantor (1969) formula, which corrects for multiple substitutions. The % nucl. subst. values are calibrated against the geological time provided by the fossil record, in our case the *Mus-Rattus* dichotomy estimated at *c.* 10 Myr (Jacobs & Pilbeam, 1980; Jaeger, Tong & Denys, 1986). [The *Mus-Rattus* split might well be of a slightly older age, such as 12–13 Myr, as recently proposed by Flynn *et al.* (1990) and Jacobs *et al.* (1989); in this case, our molecular time scale should be corrected by a factor of 1.2 to 1.3, thus yielding slightly older estimates.] This correlation can only be applied up to *c.* delta-Tm = 15°C, because of a compression effect affecting large Tm values (Sheldon & Bledsoe, 1989).

This approach assumes a near-equality of rates along the different lineages under scrutiny. The departure from rate uniformity can be estimated by the relative-rate test, by measuring the [(AC−BC)]/(AC+BC) percentage value in three-taxon (A, B, C) groups, where C is the outgroup for A and B (such as *Hylomyscus* as an outgroup for *Praomys* and *Mastomys*).

RESULTS

Eight taxa were radioactively labelled (tracers): *Praomys tullbergi, Mastomys huberti, Hylomyscus stella, Myomys daltoni, Mus cervicolor, Nannomys* cf *setulosus, Rattus tiomanicus* and *Cricetomys gambianus.*

Figures 1 and 2 illustrate a few melting curves obtained for some of the hybridized taxa: cumulative data for calculating Tm based on tracer *Mastomys*

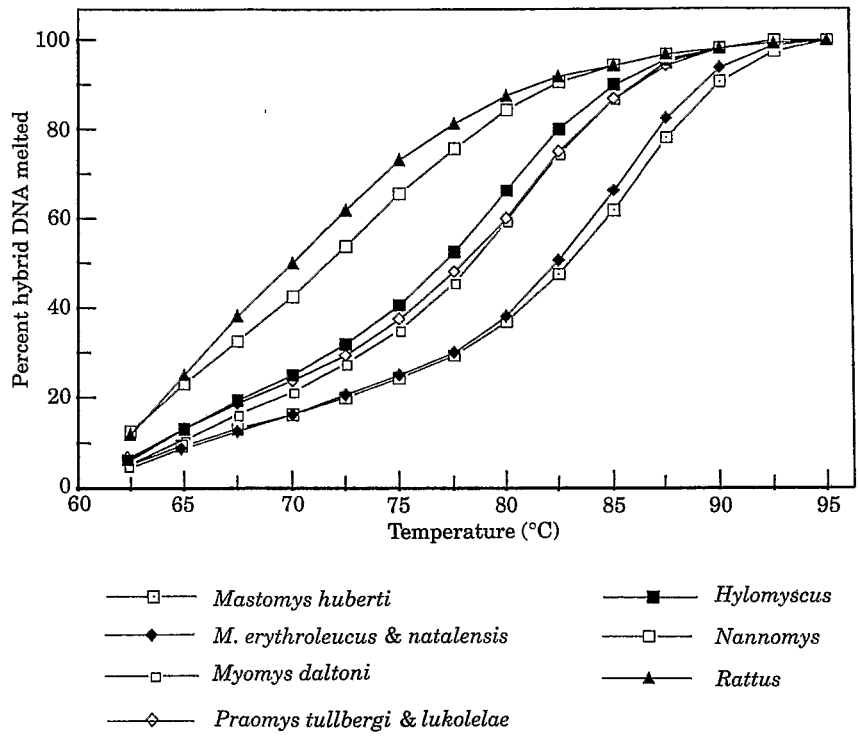

Figure 1. Melting curves for the determination of Tm. Each curve is the average of N hybrids. Homolog **Mastomys huberti/Mastomys huberti* ($n=6$); **Mastomys huberti/Mastomys erythroleucus* and *M. natalensis* ($n=5$); **Mastomys huberti/Myomys daltoni* ($n=3$); **Mastomys huberti/Praomys jacksoni* ($n=2$); **Mastomys huberti/Praomys tullbergi* and *P. lukolelae* ($n=4$); **Mastomys huberti/Hylomyscus stella* ($n=3$); **Mastomys huberti/Nannomys* cf *setulosus* ($n=2$); **Mastomys huberti/Rattus tiomanicus* and *R. rattus* ($n=2$)

huberti on Figure 1, and modal data for calculating Mode based on the tracer *Praomys tullbergi* on Figure 2. The different taxa of the *Praomys* group are clearly narrowly related to each other, and well separated from *Mus* and *Rattus*. On Figures 2, *Myomys* appears to be more closely related to *Praomys* than to *Mastomys*, and *Praomys jacksoni* is as distant from *Praomys tullbergi* as *Mastomys*. On both Figures 1 and 2, *Hylomyscus* is the most divergent taxon within the *Praomys sensu lato* assemblage.

The average amount of non-reciprocity before any symmetrization procedure was 2.33% and 3.44% for delta-Tm and delta-Mode matrices, respectively. After correcting the 8×8 matrices for non-reciprocity, this average value amounts to 0.95% for delta-Tm and to 2.45% for delta-Mode. These results indicate that, as far as reciprocity is concerned, delta-Tm values give a better result than delta-Mode, and this may be due to the difficulty of properly calculating the real mode in the cases of a double-peak which interferes with the true modal peak in the 62.5–67.5°C range (Catzeflis, 1990: fig. 5).

Bootstrapping on eight taxa

The first treatments applied to our data deal with a complete 8×8 matrix, in order to focus on the inter-generic relationships. Consequently, the DNA/DNA

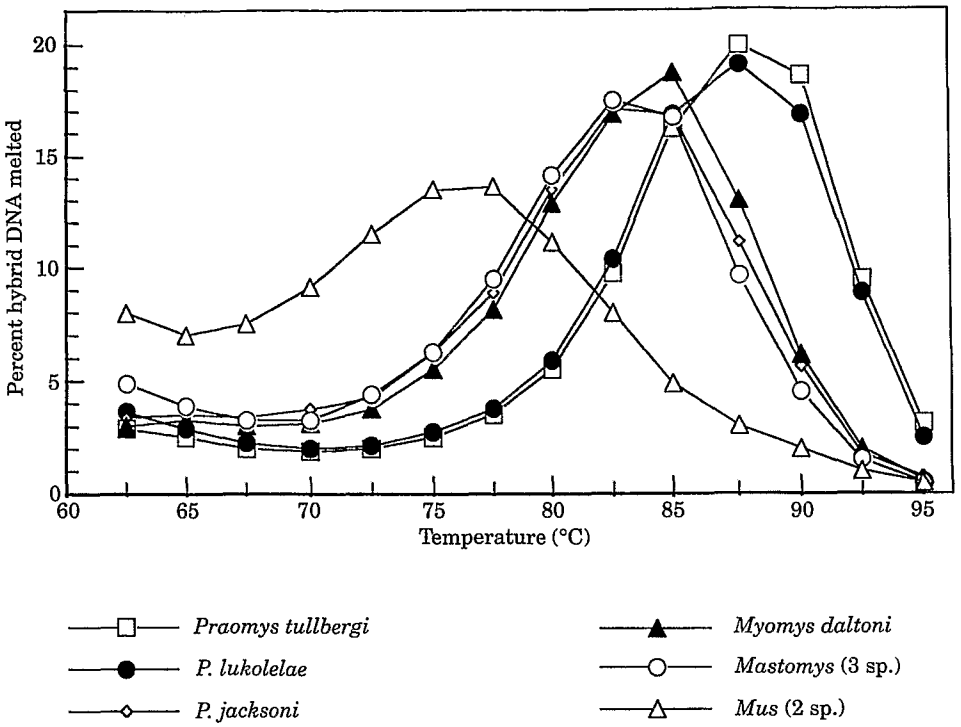

Figure 2. Melting curves for the determination of Mode. Each curve represents the average of N hybrids. Homolog **Praomys tullbergi/Praomys tullbergi* ($n=5$); **Praomys tullbergi/Praomys lukolelae* ($n=3$); **Praomys tullbergi/Myomys daltoni* ($n=3$); **Praomys tullbergi/Praomys jacksoni* ($n=3$); **Praomys tullbergi/Mastomys huberti* ($n=4$); **Praomys tullbergi/Mus musculus* and *M. saxicola* ($n=3$)

hybridization results of the different species within each genus are pooled, as they give the same information (distance) with regard to another genus (see Table 2 for examples of near-equality of rates within each genus). For *Praomys*, we pooled the data from the species *P. lukolelae* and *P. tullbergi* only, as it appeared (see below) that the third species—*P. jacksoni*—might well be paraphyletic. Even with this reduced 8×8 taxa matrix, some data (four cells out of 64) were not available. In place of the missing value corresponding to the **Mus/Myomys* hybrid, we used the average value based upon the different **Mus/Praomys* and **Mus/Mastomys* hybrids, because these taxa (*Mastomys* and *Praomys*) are more related to *Myomys* than to any other genus. We also note from Table 2 that hybrids made with **Nannomys*, which is closely related to *Mus* (Catzeflis & Denys, 1992), yield the same values (delta-Tm) with regard to *Mastomys, Praomys, Myomys* or else *Hylomyscus*. The same procedure was applied for filling the missing cells concerning **Mus/Hylomyscus*, **Rattus/Myomys* and **Rattus/Hylomyscus*. To test for the possible influence of these four missing original values, we first applied a bootstrap procedure to a complete 6×6 matrix, dropping *Rattus* and *Mus*; this gave the same results as those derived from the 8×8 matrix for the branching order of the taxa within the *Praomys* complex. But, as *Mus* and *Rattus* are important taxa defining the Murinae, and for understanding their relationships with regard to the *Praomys* complex, we completed the four missing values of the 8×8 matrix as described above.

TABLE 2. Uncorrected delta-Tm values (in °C) for all tracer/driver reactions. The correcting factor for each tracer indicated at the bottom of each column is used to decrease the non-reciprocity (Sarich & Cronin, 1976). These corrected delta-Tm values are averaged for each dichotomy in Table 3 and used to reconstruct the tree of Figure 4. Four different species have been used as drivers for representing *Mus: M. musculus, M. saxicola, M. cervicolor* and *M. caroli.*

	Delta-Tm (Tm)							
*Tracers Drivers	*Mastomys huberti*	*Praomys tullbergi*	*Hylomyscus stella*	*Myomys daltoni*	*Mus cervicolor*	*Nannomys* cf *setulosus*	*Rattus tiomanicus*	*Cricetomys gambianus*
Mastomys huberti	0.0	5.2, 5.1	5.9, 5.8	4.8, 4.1	—	—	—	—
Mastomys erythroleucus	0.7, 0.4	5.2, 5.3	6.2	4.9	11.4, 11.3	11.5, 11.4	12.6, 12.7	16.4, 16.5
Mastomys natalensis	0.4±0.1 (n=4)	—	6.5	5.7, 5.2	—	—	12.7	—
Mastomys coucha	1.4, 1.4	5.4, 5.4	6.0	4.8	—	11.9	—	16.3
Praomys tullbergi	4.8, 4.4	0.0	6.0, 6.0	4.0, 4.3	—	11.2, 11.8	12.3	16.0
Praomys lukolelae	4.7, 5.0	0.6±0.2 (n=3)	5.8	4.0	11.0±0.4 (n=3)	11.5	13.2, 13.1	16.5, 16.6
Praomys jacksoni	4.8, 5.3	4.7±0.3 (n=3)	6.2, 6.2	4.4±0.3	—	—	—	—
Hylomyscus stella	5.9±0.1 (n=3)	5.9±0.1 (n=3)	0.0	5.7±0.1 (n=3)	—	11.5±0.1 (n=4)	—	16.2±0.2 (n=3)
Hylomyscus fumosus	—	—	4.8, 4.8	—	—	—	—	—
Myomys daltoni	4.5±0.3 (n=3)	4.1±0.0 (n=3)	5.8±0.1 (n=3)	0.0	—	11.2±0.1 (n=3)	—	15.8±0.1 (n=3)
Mus	10.4±0.7 (n=3)	11.3±0.4 (n=3)	11.2±0.1 (n=3)	10.7±0.4 (n=4)	0.0	7.1±0.2 (n=19)	12.7±0.5 (n=3)	16.4±0.2 (n=3)
Nannomys	10.9±0.2 (n=4)	11.6±0.1 (n=4)	11.6±0.2 (n=3)	11.4±0.2 (n=6)	7.3±0.2 (n=5)	0.0	13.2, 13.3	16.8, 16.2
Nannomys sp	—	—	—	—	—	4.0±0.3 (n=3)	—	—
Rattus	12.9, 13.0	13.8±0.1 (n=3)	13.9±0.3 (n=4)	13.6±0.3 (n=4)	13.8±0.2 (n=3)	13.8±0.2 (n=4)	0.0	16.2±0.2 (n=3)
Cricetomys	16.3, 16.3	17.9, 17.9	16.8, 17.6	16.8, 18.0	16.1, 16.3	17.5±0.2 (n=3)	15.4+0.2 (n=3)	0.0
Correcting factors:	1.06	0.97	0.99	0.98	0.99	1.00	1.07	1.04

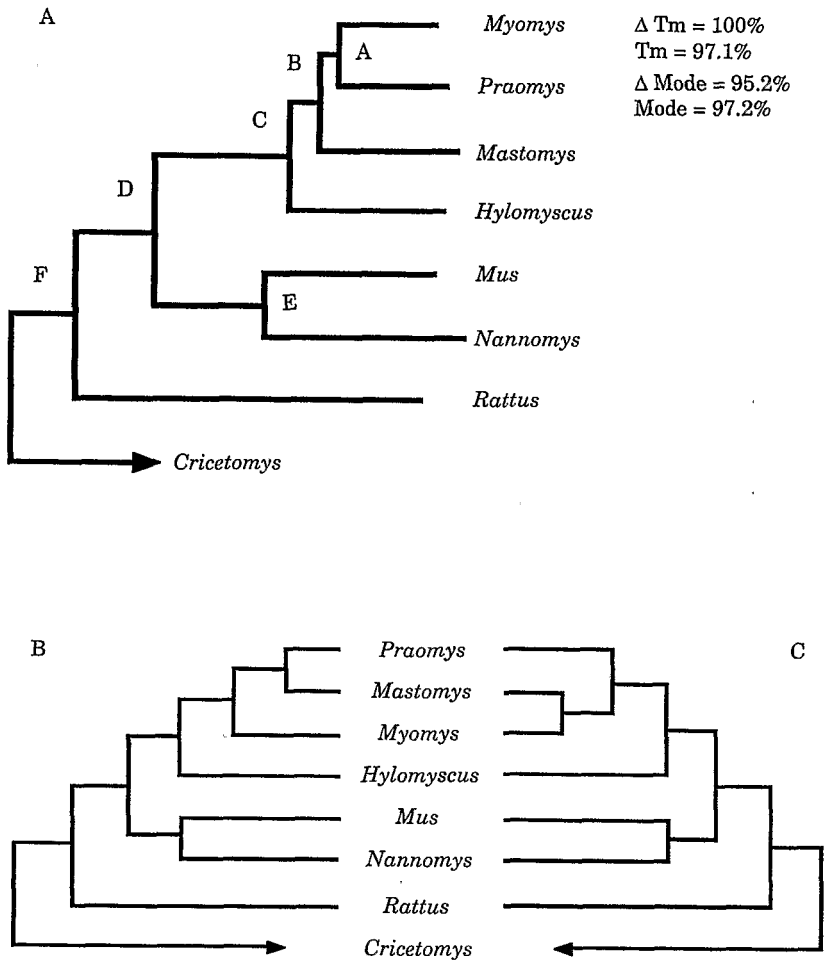

Figure 3 Three different trees obtained by the bootstrapping procedures on the 8×8 matrices of Tm, delta-Tm, Mode, and delta-Mode values. The majority consensus tree is on the top (A), and the two minority trees are in the bottom (B & C). Indicated are the observed frequences, among 1500 replicates, of each branching pattern for each kind of index of dissimilarity. In panel A, the branch lengths (in °C) between the different nodes (lettered A to F) and terminal taxa are based on the average values derived from 50 bootstrap replicates of delta-Tm values: A-*Myomys* = 1.86±0.04, A-*Praomys* = 2.11±0.05, A–B = 0.35±0.04, B-*Mastomys* = 2.56±0.05, B–C = 0.47±0.05, C-*Hylomyscus* = 2.91±0.03, C–D = 2.58±0.03, D–E = 2.03±0.04, E-*Mus* = 3.3±0.05, E-*Nannomys* = 3.8±0.04, D–F = 1.41±0.09, F-*Rattus* = 6.55±0.05.

TABLE 3. Raw, uncorrected, Tm values (in °C) for the 8*8 complete matrix subjected to the bootstrap procedure.

	Tracer: *Nannomys setulosus*						
Nannomys	85.17	85.11	84.94	85.13	85.22		
Mus	78.15	78.15	78.29				
Cricetomys	67.43	67.69	67.58				
Mastomys	73.70	73.75	73.10				
Praomys	73.64	73.89	73.36				
Hylomyscus	73.64	73.46	73.31	73.54			
Myomys	73.90	73.69	74.06				
Rattus	71.10	71.26	71.52				
	Tracer: *Mus cervicolor*						
Nannomys	77.66	77.62	77.92	77.98	77.85	77.97	
Mus	85.21	85.13	85.33	85.05	85.16	85.11	85.22
	85.20						
Cricetomys	69.07	68.94					
Mastomys	73.89	73.88					
Praomys	73.88	73.89	74.64				
Hylomyscus	74.04[a]						
Myomys	74.04[a]						
Rattus	71.33	71.60	71.54				
	Tracer: *Cricetomys gambianus*						
Nannomys	66.62	66.21					
Mus	66.61	66.81	66.55				
Cricetomys	82.87	83.97	83.01	82.66			
Mastomys	66.59	66.54	66.57				
Praomys	66.54	66.45	66.87				
Hylomyscus	66.73	66.37	66.75				
Myomys	66.72	66.93	67.00				
Rattus	66.65	66.72	66.65				
	Tracer: *Mastomys huberti*						
Nannomys	71.73	71.66	71.75	71.88			
Mus	72.94	72.77	71.61				
Cricetomys	65.99	66.28					
Mastomys	82.90	83.09	83.27	82.73	82.91	82.87	82.77
	82.62						
Praomys	77.86	78.31	77.91	78.03			
Hylomyscus	76.96	76.94	77.04				
Myomys	78.35	78.52	78.08				
Rattus	70.05	69.88					

The complete bootstrap procedure was done on delta-Tm values (Table 2), raw Tm values (Table 3), raw Mode values (Table 4) and delta-Mode values. When using Tm and Mode values, we take into account the variability of the different homolog hybrids, a source of variation which is ignored by the delta-values. For each of the four matrices, 1500 bootstrap replications were done, from which a single, identical majority consensus tree was obtained (Fig. 3).

From the delta-Tm values, the consensus tree has each ancestral segment supported at the 100% level, hence there is only one branching pattern. This same pattern is supported at 95.2% for delta-Mode, 97.1% for Tm and 97.2% for Mode. We also obtain two minority trees (Fig. 3), which differ from the majority consensus tree in the position of three genera: *Mastomys, Praomys* and *Myomys*. One of these minority tree groups *Mastomys* and *Praomys* and the other, only observed with delta-Mode (0.1%) and Mode (2.7%), groups *Mastomys* with *Myomys*.

TABLE 3.—*continued*

	Tracer: *Praomys tullbergi*					
Nannomys	73.53	73.84	73.48	73.49		
Mus	73.76	73.64	74.31			
Cricetomys	66.94	66.93				
Mastomys	80.05	80.15	79.89	80.09	79.59	79.48
Praomys	85.20	85.25	85.18	85.05	85.06	
Hylomyscus	79.37	79.14	78.86			
Myomys	81.14	81.11	79.48			
Rattus	71.65	70.90	71.46			
	Tracer: *Hylomyscus stella*					
Nannomys	73.19	72.69	72.59			
Mus	73.40	73.51	73.17	73.01		
Cricetomys	67.53	66.69				
Mastomys	78.56	78.67	78.22	78.48	77.79	
Praomys	78.65	78.43	78.25			
Hylomyscus	84.85	84.46	84.45	84.62	84.32	84.27
Myomys	79.11	78.59	78.80			
Rattus	70.28	70.71	70.62	70.52		
	Tracer: *Myomys daltoni*					
Nannomys	73.07	73.21	72.64			
Mus	73.87	73.86	73.46	73.33		
Cricetomys	67.88	66.58				
Mastomys	79.44	79.37	79.58	78.92	78.64	79.73
Praomys	80.39	80.39	80.35			
Hylomyscus	78.74	78.61	78.60			
Myomys	84.46	84.35	84.13	84.62	83.81	
Rattus	70.53	70.81	70.23	70.62		
	Tracer: *Rattus tiomanicus*					
Nannomys	69.35	69.30				
Mus	69.49	69.08	69.78			
Cricetomys	66.53	66.71	66.56			
Mastomys	69.50	69.44	69.27			
Praomys	69.40	69.50	69.66			
Hylomyscus	69.46[b]					
Myomys	69.46[b]					
Rattus	81.72	82.20	82.58	82.09	81.92	82.13

[a]: Average value of **Mus/Mastomys* and **Mus/Praomys* hybrids.
[b]: Average value of **Rattus/Mastomys* and **Rattus/Praomys* hybrids.

Tree built for 17 taxa by direct clustering

Table 2 gives the delta-Tm values of all different hybrid comparisons based on the eight tracer taxa. At the bottom of Table 2 are indicated the correcting factors used to correct for non-reciprocity, which are derived from the symmetrization procedure on the 8×8 complete matrix. The corrected delta-Tm values are used for inferring the % nucl. subst. estimates from which the tree of Figure 4 has been drawn by a simple UPGMA clustering. All dichotomies are clearly separated from each other, except for nodes 3 and 6; these latter two nodes are nevertheless statistically different (*t*-test, $P < 0.005$).

The resulting tree is presented in Figure 4, and the average and standard deviation of delta-Tm values for each node, as well as the corresponding % nucl. subst. value and dating for each dichotomy are presented in Table 5.

The tree reconstructed by direct clustering largely agrees with the eight taxa consensus tree (Fig. 3), i.e. *Praomys* and *Myomys* are sister taxa, followed by

TABLE 4. Raw, uncorrected, Mode values (in °C) for the 8*8 complete matrix subjected to the bootstrap procedure.

	Tracer: *Nannomys* cf *setulosus*					
Nannomys	88.20	88.16	88.11	88.29	88.27	
Mus	81.35	81.28	81.29			
Cricetomys	64.41	64.58	63.49			
Mastomys	76.79	76.50	76.75			
Praomys	76.44	76.26	76.07			
Hylomyscus	76.20	76.39	76.11	76.39		
Myomys	76.41	76.84	76.34			
Rattus	71.79	72.29				
	Tracer: *Mus cervicolor*					
Nannomys	80.11	80.07	80.49	80.39	80.74	80.24
Mus	87.42	87.40	87.65	87.37	87.58	87.32
Cricetomys	63.32	63.29				
Mastomys	75.50	75.38				
Praomys	75.35	75.88	76.37			
Hylomyscus	75.70[a]					
Myomys	75.70[a]					
Rattus	72.15	71.53	72.07			
	Tracer: *Cricetomys gambianus*					
Nannomys	62.92	64.00				
Mus	63.92	63.63	62.86			
Cricetomys	86.44	86.25	86.46			
Mastomys	62.38	62.54	63.93			
Praomys	63.04	62.55	64.63			
Hylomyscus	64.27	62.91	62.78			
Myomys	64.91	65.04	65.19			
Rattus	64.30	64.61	63.69			
	Tracer: *Mastomys huberti*					
Nannomys	74.51	74.40	73.87	73.87		
Mus	74.81	74.87	73.90			
Cricetomys	62.51	62.64				
Mastomys	86.78	86.43	86.67	86.41	86.48	86.61
Praomys	81.69	81.78	81.71	82.07		
Hylomyscus	80.55	80.55	80.79			
Myomys	81.72	81.76	81.81			
Rattus	66.79	66.74				

Mastomys and finally *Hylomyscus*, which is the most divergent taxon within the *Praomys* group.

Specifically, Figure 4 indicates that the four taxa *Praomys, Myomys, Mastomys* and *Hylomyscus* build up a monophyletic group well separated from the other Murinae, and more related to *Mus* than to *Rattus*. *Myomys,* represented only by *M. daltoni*, is more related to *Praomys* than to *Mastomys* but *Praomys jacksoni* is as distant from *Praomys tullbergi* as from *Mastomys*. *Hylomyscus* is issued from the deepest speciation within the *Praomys sensu lato* group. All species of *Mastomys* so far examined build up a monophyletic entity clearly separated from the other genera, and whose species are very close to each other. The molecular time scale suggests a separation of 300 000 years for *M. huberti*, *M. natalensis* and *M. erythroleucus*, and of *c.* 1 Myr for *M. coucha* when Tm is considered. Nevertheless, when using the modal approach, we obtain the same estimate of % nucl. subst. between *Mastomys coucha* and the two other *Mastomys* species when *Mastomys huberti* is the tracer; these conflicting results are interpreted by a dotted line on the tree of Figure 4. The difference of branching pattern for

TABLE 4.—*continued*

	Tracer: *Praomys tullbergi*						
Nannomys	75.92	76.14	75.64	75.61			
Mus	75.90	75.81	76.44				
Cricetomys	62.75	62.56					
Mastomys	82.48	82.58	82.82	82.58	82.75	82.50	
Praomys	87.69	87.69	87.49	87.30	87.48	87.54	87.34
Hylomyscus	81.93	81.62	81.98				
Myomys	83.67	83.70	83.93				
Rattus	72.17	70.91	72.27				
	Tracer: *Hylomyscus stella*						
Nannomys	75.25	74.54	74.19				
Mus	75.72	75.76	75.46	75.08			
Cricetomys	64.00	62.70					
Mastomys	81.30	81.45	81.09	81.45	80.42		
Praomys	81.82	80.97	80.99				
Hylomyscus	87.24	86.92	87.18	86.99			
Myomys	81.71	81.14	81.84				
Rattus	70.07	70.83					
	Tracer: *Myomys daltoni*						
Nannomys	75.10	75.58	74.51				
Mus	76.08	76.14	75.71	75.36			
Cricetomys	64.43	63.36					
Mastomys	82.09	82.22	82.22	81.42	81.27	82.43	
Praomys	83.11	82.79	82.91				
Hylomyscus	81.51	81.31	81.27				
Myomys	86.96	86.91	86.93	87.11	86.84	86.23	
Rattus	70.03	70.92					
	Tracer: *Rattus tiomanicus*						
Nannomys	64.98	65.47					
Mus	66.20						
Cricetomys	64.05	63.71	63.79				
Mastomys	66.57						
Praomys	65.64	65.77	66.75				
Hylomyscus	66.18[b]						
Myomys	66.18[b]						
Rattus	85.66	85.94	86.32	85.55	85.46	85.90	

[a]: Average value of **Mus/Mastomys* and **Mus/Praomys* hybrids.
[b]: Average value of **Rattus/Mastomys* and **Rattus/Praomys* hybrids.

Mastomys coucha may be due to the poor quality of the driver DNA which seems to affect more Tm than Mode. Indeed, the poor DNA quality of this sample is also reflected in the low NPH values (*c.* 71%) obtained with the tracer *Mastomys huberti* as compared to an average NPH value of *c.* 93% for the two other species of *Mastomys*.

A search for the heterogeneity of molecular evolutionary rates of change along the different lineages indicates that no difference in sister branch lengths is larger than 5% for the different pairs of taxa under comparison. This allowed us to accept the hypothesis of a near equality of rates, hence supporting the clustering procedure leading to the 17-taxa tree of Figure 4.

DISCUSSION

Relationships between the different taxa of the Praomys *complex*

The consensus tree (Fig. 3A) based on bootstrapping is in agreement with the enlarged UPGMA-reconstructed tree (Fig. 4). The branching pattern derived

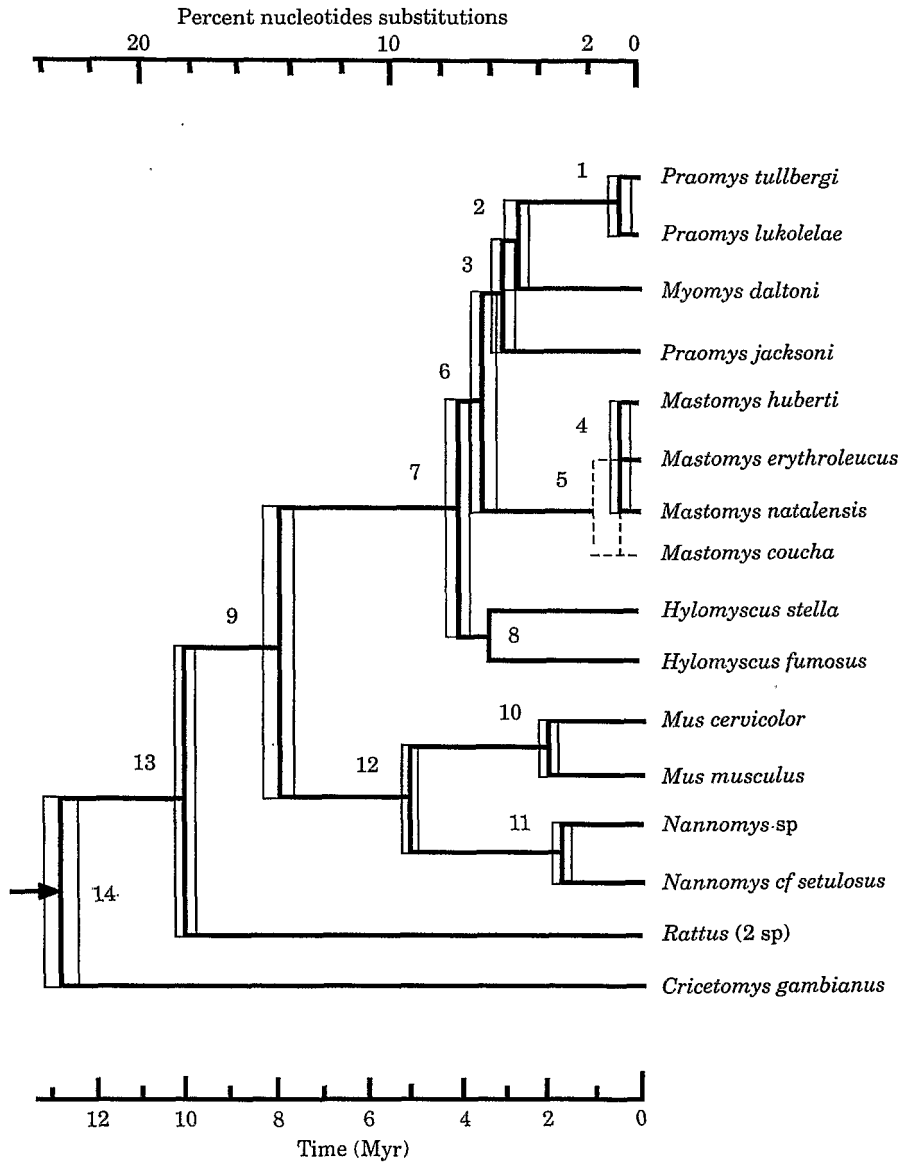

Figure 4. Phylogenetic tree reconstructed from the data of Table 2 by direct clustering and with a molecular clock hypothesis. The thin boxes bordering each node represent the standard deviation, the number at each node refers to three values (delta-Tm, % nucl. subst. and dating) in Table 5. The molecular time scale is calibrated by the age of the *Mus-Rattus* dichotomy estimated at ca 10 Myr. The dashed lines represent the uncertain position of *Mastomys coucha*, whose exact relation differs according to Tm or Mode indexes (see text for further details). Only 16 taxa are represented in this tree, for the results of both species of *Rattus* have been pooled and as the data concerning *Mus saxicola* and *M. caroli* are too incomplete for a secure placement within the genus *Mus*.

from this study is also in agreement with those obtained by Van der Straeten (1979) and Britton-Davidian *et al.* (1995). Two other trees, which are much less represented, have been obtained by bootstrapping, and they challenge the order

TABLE 5. Average delta-Tm values (in °C), estimates of percent nucleotides substitutions (% nucl. subst.), and dating (in Million Years: Myr) of the different dichotomies numbered in Fig. 4.

Node	Delta-Tm	% nucl. substit.	Dating
1. Praomys tullbergi/P. lukolelae	0.6±0.2 (*n*=3)	0.7	0.4 Myr
2. Praomys tullbergi/Myomys daltoni	4.0±0.1 (*n*=6)	4.9	2.7 Myr
3. P. jacksoni/P. tullbergi & *M. daltoni*	4.5±0.3 (*n*=6)	5.5	3.0 Myr
4. Mastomys huberti/M. natalensis & *M. erythroleucus*	0.5±0.2 (*n*=5)	0.6	0.3 Myr
5. Mastomys huberti/M. coucha	1.5, 1.5	1.8	1.0 Myr
6. Praomys & *Myomys/Mastomys*	5.0±0.4 (*n*=21)	6.2	3.4 Myr
7. Praomys & *Mastomys/Hylomyscus*	5.9±0.3 (*n*=20)	7.3	4.0 Myr
8. Hylomyscus stella/H. fumosus	4.8, 4.8	5.9	3.3 Myr
9. Praomys sensu lato/Mus & *Nannomys*	11.2±0.4 (*n*=47)	14.5	8.0 Myr
10. Mus cervicolor/Mus musculus	4.5±0.2 (*n*=3)	5.5	3.0 Myr
11. Nannomys sp/*Nannomys* cf *setulosus*	4.0±0.3 (*n*=3)	4.9	2.7 Myr
12. Mus/Nannomys cf *setulosus*	7.2±0.2 (*n*=11)	9.0	5.0 Myr
13. Mus & *Praomys/Rattus*	13.7±0.3 (*n*=30)	18.1	10.0 Myr
14. Murinae/Cricetomys gambianus	16.9±0.5 (*n*=36)	23.2	>12.8 Myr[a]

[a]: For delta-Tm values >15°C, the proposed datings are underestimates, as there is a strong saturation effect on such large values (see text for further details).

of relationship between *Mastomys*, *Praomys* and *Myomys*. One of these minority trees agrees with the hypothesis of Van der Straeten & Dieterlen (1983), who brought together *Myomys* to *Mastomys*.

In the genus *Praomys* we note two very related species, *P. tullbergi* and *P. lukolelae* (dichotomy estimated at *c.* 400 000 years) and a third one, *Praomys jacksoni*, which is almost as distant from *Praomys* (*P. tullbergi* and *P. lukolelae*) as is *Mastomys*, which raises the problem of its generic affiliation. *Praomys tullbergi* and *P. lukolelae* are also considered as closely related by Van der Straeten & Dieterlen (1987) and Van der Straeten & Dudu (1990), on the basis of skull biometry. For these authors and Petter (1965, 1975), *P. jacksoni* constitutes a more clearly differentiated species complex, an opinion which seems to be supported by our results. The molecular data, which indicate a well-marked genetic differentiation between *P. tullbergi* and *P. jacksoni*, are in strong opposition to the opinion of Ellerman, Morrison-Scott & Hayman (1953) who considered *tullbergi* and *jacksoni* as mere subspecies of *Praomys morio*. On the other hand Petter (1975) considered that *P. tullbergi* and *P. lukolelae* as subspecies of *P. morio*. Our DNA/DNA hybridization results are also in conflict with the chromosomal data of Qumsiyeh *et al.* (1990) and isozyme data of Iskandar & Bonhomme (1984) discussed in Britton-Davidian *et al.* (1995), for whom *Praomys jacksoni* and *P. tullbergi* are very close to each other.

According to our experiments, *Myomys daltoni* is closer to *Praomys tullbergi* and *P. lukolelae* than to *Mastomys*. The same relationship was found by Van der Straeten (1979), who challenged the validity of the genus *Myomys* and included it in the genus *Praomys*, an hypothesis that our data tend to support. The problem of the genus *Myomys* is complicated by its possible relationship to *Myomyscus*, which would need further research.

In our study, *Hylomyscus* is always the most distant taxon of the *Praomys* group, and from this result alone one could well consider *Hylomyscus* as a separate genus. For Misonne (1969), *Hylomyscus* might be the most derived member of the *Praomys sensu lato* group. Due to several dental and cranial

characters unique to *H. fumosus*, Misonne (1969) created the genus *Heimyscus* for this taxon, and noted that *H. (Heimyscus) fumosus* was morphologically related to *Dephomys*, an African genus belonging to the *Arvicanthis* division of Murinae. Musser & Carleton (1993: 595) treated *Heimyscus* as a "very distinctive genus whose closest phylogenetic affinities have yet to be resolved". According to the DNA/DNA hybridization data, the species [*Heimyscus*] *fumosus* appears indeed very well differentiated from *H. stella*, a difference of the same order of magnitude (*c.* 6% nucl. subst: see Table 5) as the one between *Mastomys* and '*Praomys+Myomys*'. This would reinforce the use of *Heimyscus*, at least at a subgeneric rank.

Monophyly of Mastomys

The monophyly of the taxon *Mastomys*, clearly separated from the other genera, is in agreement with other studies based upon morphology (Rosevear, 1969), biometry (Van der Straeten, 1979), protein electrophoresis (Iskandar & Bonhomme, 1984) and chromosome analysis (Britton-Davidian *et al.*, in press). All these results suggest that *Mastomys* may be considered as a valid genus, and its taxonomic content has been suggested by Robbins & Van der Straeten (1989). Nevertheless, due to technical constraints and limitations, our approach does not permit deciphering the relationships between the different species studied, which issued from a multitomy dated at *c.* 300 000 years ago.

The non-repeated fractions of the genome of the three closely related species *M. natalensis*, *M. erythroleucus* and *M. huberti* differ by at most 1% nucl. subst. These species, whose systematics were addressed by Duplantier, Britton-Davidian & Granjon (1990a), are characterized by different karyotypes, and live in sympatry in some parts of Africa. Laboratory crosses have yielded viable hybrids with low reproductive success (Duplantier *et al.*, 1990a), supporting the hypothesis of a rather recent divergence of these taxa. The recency of this interspecific divergence in *Mastomys* is also supported by protein electrophoresis (Duplantier *et al.*, 1990b) and albumin study (C. Montgelard: personal communication).

Relationships of Praomys sensu lato *within the subfamily* Murinae

The three recognized genera (*Praomys*, *Mastomys* and *Hylomyscus*) constitute a monophyletic entity which is clearly separated from *Mus*, *Rattus* and *Nannomys*, as well as from several other African and Asian Murinae so far tested (*Arvicanthis*, *Millardia*, *Malacomys*, *Apodemus*, *Maxomys*, *Niviventer* and *Hybomys*: unpublished data).

The *Praomys* group is clearly more related to *Mus* than to *Rattus* (Catzeflis & Denys, 1992). The separation between the *Praomys* group and the *Mus* lineage may be estimated at *c.* 8 Myr, if we use the molecular clock concept calibrated by the *Mus/Rattus* dichotomy estimated at *c.* 10 Myr.

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