"Acomyinae": new molecular evidences for a muroid taxon (Rodentia: Muridae)

Pascale Chevret

François Catzeflis

Johan R. Michaux

Introduction

Until the immunological study of SARICH (1985), *Acomys*, the spiny mouse, was included in the Murinae based on its morphology. More precisely it was considered as a close relative of *Mus* (JACOBS, 1978). Sarich's results raised questions about the taxonomic affinities of *Acomys*, and other immunological works came to similar conclusions. These distance-based analyses indicated that the immunological distance between *Acomys* and Murinae was as large as between Murinae and other non-murine rodents (HAMMER *et al.*, 1987; WILSON *et al.*, 1987; FRAGUEDAKIS-TSOLIS *et al.*, 1993). MONTGELARD (1992) furthermore indicated that another Murinae, *Uranomys* might be in the same taxonomic situation. Following these first immunological data, other molecular studies came to support the exclusion of *Acomys* from Murinae, and its association with at least 2 other "murines": *Uranomys* and *Lophuromys*, such as DNA/DNA hybridizations (CATZEFLIS, 1990; CHEVRET *et al.*, 1993), 12S rRNA sequences (HÄNNI *et al.*, 1995) and a study of LINE repeated elements (FURANO *et al.*, 1994; USDIN *et al.*, 1995). A morphological reexamination of the third upper molar (DENYS and MICHAUX, 1992) evidenced also

a peculiar morphology of that tooth shared by the three genera *Acomys*, *Uranomys* and *Lophuromys*. Thus, different biochemical, molecular and morphological evidences have recently indicated that *Acomys*, *Uranomys* and *Lophuromys* cannot be considered anymore as murine rodents (see CHEVRET and HÄNNI, 1994 for more details). HÄNNI *et al.* (1995) proposed the term « Acomyinae » for this group of muroids, without providing any morphological diagnosis. In order to precise the composition of the Acomyinae, the relations among them and with their closest relatives, we performed three different molecular analysis: we completed the data sets for the DNA/DNA hybridizations (CHEVRET *et al.*, 1993) and the 12S rRNA sequences (HÄNNI *et al.*, 1995) and we included new data of the LCAT nuclear gene.

Material and methods

Material

The list of genera involved in the three different analyses is presented on table 1. DNA samples were extracted from 95% ethanol-preserved tissues housed in the collection of Preserved Mammalian Tissues of the Institut des Sciences de l'Évolution, Montpellier (CATZEFLIS, 1991).

DNA/DNA hybridizations

This approach measures the global divergence between the scnDNA (single copy nuclear DNA) of two species. We used the same methods as described in our previous papers (CHEVRET *et al.*, 1993, 1994). The 21*21 matrices of distances (delta-Tm, delta-mode) include only labelled taxa but were still rather incomplete (41% of missing cells). Prior to any distance analysis, we completed the matrices following the procedures described by LANDRY *et al.* (1996) with the RECALL program, kindly provided by F. J. Lapointe. To ascertain the stability of topologies with regards to taxonomic sampling, we used the weighted jackknife performed through the MAJACK program (LAPOINTE *et al.*, 1994).

Subfamily	Genus	DNA/DNA hybridization	12S rRNA	LCAT analysis	Combined
Acomyinae	*Acomys*	+	+	+	+
	Uranomys	+	+	+	+
	Lophuromys	+	+	+	+
	Deomys	+	+	+	+
Murinae	*Arvicanthis*	+			
	Hylomyscus	+			
	Malacomys	+			
	Mastomys	+			
	Millardia	+			
	Mus	+ (3 sp.)	+	+	+
	Myomys	+			
	Praomys	+			
	Rattus	+ (2 sp.)	+	+	+
Gerbillinae	*Gerbillus*	+	+	+	+
	Tatera	+	+	+	+
Dendromurinae	*Steatomys*	+	+	+	+
	Dendromus		+	+	+
Otomyinae	*Otomys*	+			
Cricetomyinae	*Cricetomys*	+	+		
	Saccostomus		+	+	+
Nesomyinae	*Macrotarsomys*		+	+	+
	Nesomys		+	+	+
Mystromyinae	*Mystromys*		+	+	+
Cricetinae	*Mesocricetus*		+	+	+
	Cricetulus		+	+	+
Myospalacinae	*Myospalax*		+	+	+
Sigmodontinae	*Peromyscus*		+	+	+
Arvicolinae	*Clethrionomys*		+	+	+
	Microtus		+	+	+
Spalacinae	*Spalax*		+	+	+
Rhizomyinae	*Rhizomys*		+	+	+

Table 1
List of taxa involved in the different analyses. Additional informations (species, geographic origin, collector, voucher-specimen when available) can be obtained upon request from the senior author.

The distance analyses were done with FITCH and KITSCH programs from the Phylip package (version 3.5c, FELSENSTEIN, 1993). To propose divergence times, the delta-Tm values were then transformed into% base pair mismatch (bpm) estimates by the relation of 1 °C delta-Tm = 1.18% pbm (SPRINGER *et al.*, 1992). These estimates were finally transformed into percent nucleotide substitutions (% nucl. subst.) by the JUKES and CANTOR formula (1969), which corrects for

multiple substitutions. The% nucl. subst. values are then calibrated against the geological time provided by the fossil record, in our case the *Mus-Rattus* dichotomy estimated at *ca* 12 Ma (JACOBS and PILBEAM, 1980; JAEGER *et al.*, 1986; JACOBS and DOWNS, 1994).

Sequences

Mitochondrial DNA: complete 12S rRNA gene

We performed the amplifications of the complete 12S rRNA genes with the R1 and S2 primers (SOURROUILLE *et al.*, 1995) and realised a direct sequencing with the ^{33}P sequencing kit of Amersham, using similar sequencing primers as in previous 12S studies (SOURROUILLE *et al.*, 1995, HÄNNI *et al.*, 1995; DUBOIS *et al.*, 1996). The ten new sequences have been deposited in EMBL under accession numbers AJ 250349 to AJ250358.

The sequences were manually aligned using the ED program (MUST package, PHILIPPE, 1993), and the alignment was refined in order to minimize the number of indels (insertions-deletions) in stems. The hypervariable region (47 nucleotides, position 912 to 958) was excluded from all analyses, which were realized on a final alignment of 964 positions. In order to locate homoplasy, we searched for the evidence of saturation using the method of HASSANIN *et al.* (1998). This analysis shows the importance of multiple substitutions by comparing the pairwise numbers of observed versus inferred changes, as calculated by PAUP. This saturation was checked for 4 partitions (transitions and transversions in stems and loops). The values derived from this analysis were used in a weighted analysis via a stepmatrix procedure in PAUP. In order to test the possibility to estimate the divergence time from the 12S data set we compared the likelihood of the trees constructed with a clock and non-clock hypothesis as proposed by FELSENSTEIN (1981) and calculated with Puzzle 4.0 (STRIMMER and VON HAESELER, 1996).

Nuclear DNA: LCAT (Lecithin-Cholesterol Acyl-Transferase), exons 2 to 6 (804 bp).

Two fragments of the nuclear LCAT gene were amplified using the PCR primers designed by ROBINSON *et al.* (1997). Sequencing on

both strands was done using a dye terminator (Perkin Elmer) sequencing kit and a ABI 373 (Perkin Elmer) automatic sequencer.

Previously known sequences were extracted from GenBank and aligned with the new sequences using CLUSTALW (THOMPSON *et al.*, 1994) and the ED editor (MUST package, PHILIPPE, 1993). As for the 12S gene, in order to locate those substitutions which are the most prone to saturation, we searched for the evidence of saturation by comparing the pairwise numbers of observed versus inferred changes of each substitution type (transition, transversion) at each codon position. The new sequences will be presented elsewhere (MICHAUX and CATZEFLIS, 2000). As indicated in MICHAUX and CATZEFLIS (in press), a relative rate-test was performed with RRTree, version 1.0 (ROBINSON *et al.*, 1998), with Dipodidae as outgroup for the intra-Muridae phylogeny. This leads to the exclusion of the slowest-and fastest-evolving taxa.

Combined analysis

Combining both genes resulted in a data matrix of 22 taxa x 1768 nucleotidic sites. We performed a congruence test (program ARNIE, included in the Random Cladistics Package, SIDDALL, 1996) which indicated that both data sets were not in conflict, hence the combined analysis.

Phylogenetic analysis

On the three resulting data sets (12S, LCAT and 12S + LCAT), we realized analyses with distances (Neighbor-joining, SAITOU and NEI, 1987), Maximum Parsimony (PAUP 3.11, SWOFFORD, 1993, or Paup 4.0b, SWOFFORD, 1998) and Maximum Likelihood (Puzzle 4.0, STRIMMER and VON HAESELER, 1996). The robustness of the phylogenies was assessed by bootstrap for distance and parsimony, by the Bremer Support Index (BSI) (BREMER, 1988) for parsimony, and by reliability percentages for maximum likelihood. A stepmatrix procedure was also used with PAUP with the values deduced from the different saturation analyses. The molecular clock hypothesis was tested for both data sets with Puzzle 4.0 (STRIMMER and VON HAESELER, 1996) and RRTree 1.0 (ROBINSON *et al.*, 1998).

Results and discussion

DNA/DNA hybridizations

The average consensus tree resulting from 10000 jacknife with equiprobable deletions from 4 to 17 taxa (LAPOINTE *et al.*, 1994) on the delta-Tm matrix is presented figure 1. The raw 21*21 delta-matrices can be obtained upon request from the senior author. Except for one case (see below), all ancestral segments were retrieved in all (minimum, average, maximum) consensus trees (details of the jacknife procedure can be found in LAPOINTE *et al.*, 1994). The trees built with the delta-mode and consensus trees obtained with jacknife with single deletion (LANYON, 1985) gave similar results (data not shown). On this tree with 19 ingroup taxa, the association of *Acomys*, *Uranomys* and *Lophuromys* is evidenced, confirming the previous results of CHEVRET *et al.* (1993), which were based on a smaller set of taxa. The so-called « Acomyinae » group also comprises a Dendromurinae, *Deomys,* as previously suggested by a reduced data set (DENYS *et al.*, 1995). This group is clearly separated from the other subfamilies included in this study (Gerbillinae, Murinae), and from the outgroups represented by *Cricetomys* and *Steatomys*. Other molecular studies (see below) indicate that the genera *Cricetomys/ Steatomys* can be considered as a valid outgroup for rooting the Acomyinae/Murinae/ Gerbillinae. In the jacknife procedure with single deletions, the suppression of different taxa leads to an Acomyinae-Murinae (exclusion of *Uranomys* or *Tatera*) or a Acomyinae-Gerbillinae (exclusion of *Steatomys)* association. Thus, the clustering of Gerbillinae with Murinae is not robust, which suggests that our DNA hybridization data are best interpreted as an unsolved polytomy Acomyinae - Murinae – Gerbillinae. The divergence between the Murinae, Gerbillinae and Acomyinae can be estimated at around 14.5 My (with reference to *Mus/Rattus* dichotomy at 12 My), while the four different genera among the acomyine group diverged between 10 and 8.5 millions years ago, and *Tatera* and *Gerbillus* at 8.2 My.

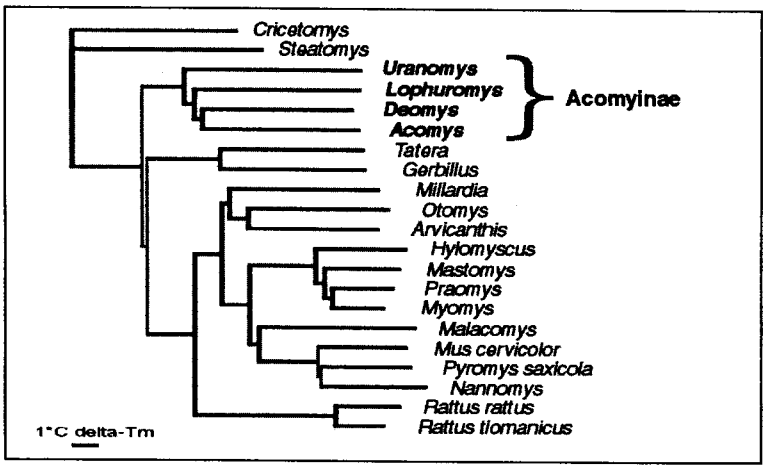

Figure 1
Average consensus tree derived from the 21*21 delta-Tm matrices produced with the weighted jacknife procedure (LAPOINTE *et al.*, 1994). Thin lines indicate two uncertainties: 1) the relationships between *Mus saxicola, M. cervicolor* and *Nannomys* were not retrieved in all jacknife combinations of the multiple-deletions procedure; 2) different branching patterns for Murinae - Gerbillinae - Acomyinae were observed in jacknife replications during the single-deletion procedure.

Sequences analysis

The results of the combined analysis of both genes are presented on the tree illustrated on figure 2. The supports for the main nodes for the different data sets and for the different phylogenetic analyses are indicated in table 2. These results do not change significantly when weighted analyses were performed (data not shown). As indicated in a previous study of the LCAT gene (ROBINSON *et al.*, 1997), *Spalax* and *Rhizomys* seem an appropriate outgroup for the rest of the murid taxa included in our analysis. Here again a robust association of the four Acomyinae (*Acomys*, *Uranomys*, *Deomys* and *Lophuromys*) is observed when both genes are concatenated. Nevertheless, the association of *Uranomys* with the three other Acomyinae is not robustly supported by the 12S rRNA data set alone, as in a previous analysis with a reduced 12S data set (see figs. 3 and 4 in HÄNNI *et al.*, 1995). Within Acomyinae, the combined analysis indicates that *Acomys* and *Deomys* are sister-taxa, followed by *Lophuromys* and *Uranomys*. The

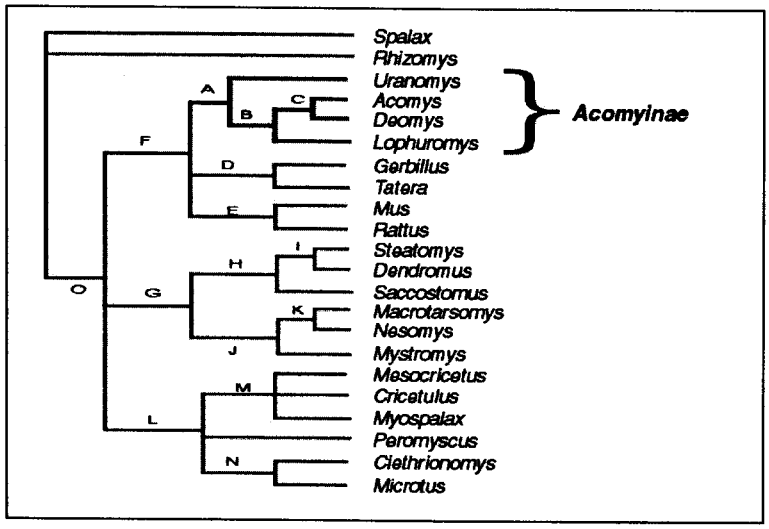

Figure 2
Consensus tree of the combined analysis of the 12S rRNA and LCAT genes using all events (TV + TS + indels) and all positions. When a node was not robustly supported or when there was desagreement between the different phylogenetic analyses, a polytomy is indicated. The different nodes are labelled A to O, the corresponding supports for the parsimony, distance and maximum likelihood analyses are indicated in table 2. Branch lengths are arbitrary.

results of the LCAT gene analysis inverse the position of *Lophuromys* and *Uranomys*, but the support of the *Uranomys/Acomys/Deomys* group is low (tabl. 2).

As with the DNA hybridization data, gene sequences were not able to precise the relationships between Acomyinae, Gerbillinae and Murinae. The different approaches lead either to a Murinae-Acomyinae or to a Acomyinae-Gerbillinae clades, with low supports in both cases. Consequently, we have depicted these three taxa as issued from an unsolved polytomy (fig. 2).

It appears that the mitochondrial 12S rRNA gene does not provide strong support for the oldest segments, such as nodes G, J, L, or M (fig. 1, tabl. 2), to the difference of the nuclear LCAT gene and the combined analysis. The association of these two genes provides the

Node	12S rRNA	LCAT	Combined analysis
A: Acomyinae	–	97/+8 99/81	96/+15 100/82
B: *Acomys/Deomys/Lophuromys*	74/+2 95/79	–	91/+9 96/94
C: *Acomys/Deomys*	–	94/+6 92/92	85/+6 61/97
D: Gerbillinae	100/+31 100/67	100/+8 99/88	100/+43 100/89
E: Murinae	85/+3 100/87	98/+11 98/91	100/+19 100/91
F: Murinae/Gerbillinae/Murinae	–	70/+4 69/<40	86/+11 72/53
G	–	40/+1 62/<40	57/+3 73/42
H	29/0 63/40	86/+7 93/76	96/+13 100/91
I	78/0 85/51	47/0 47/65	86/+6 87/75
J	–	88/+4 100/90	70/+4 92/78
K	86/+8 94/82	67/+3 67/80	95/+13 100/67
L	–	39/+1 70/69	57/+4 97/60
M	–	95/+6 99/70	83/+6 94/58
N	99/+10 100/85	100/+16 100/84	100/+27 100/85
O	100/+33 100/83	99/+14 99/99	100/+54 100/94

Table 2
Support values for ancestral segments of the phylogenetic tree of Figure 2. For each node labelled A to O: above line: Boostrap Percentage (BP parsimony) / Bremer Support Index (BSI parsimony); below line: Bootstrap Percentage (BP distance) / Reliability Percentage (RP maximum likelihood). These robustness values were obtained using all events (TV + TS + indels) and all positions: not supported at the 50% treshold.

best support for several nodes (for example, nodes F or H: fig. 1, tabl. 2), and some ancestral segments that are not robustly supported by separate analyses appear much stronger such as the African group (node G) or the association Cricetinae, *Peromyscus*, *Myospalax* and Arvicolinae (node L).

The tests of the molecular clock hypothesis lead to the rejection of the use of the 12S rRNA gene to determine the timing of divergence of our taxa, as the two Gerbillinae are some of the fastest-evolving sequences, as indicated by the RRTree analysis. Consequently gerbils should be excluded from molecular-clock tree. For the LCAT gene the same tests lead to the exclusion of Sigmondontinae, *Nesomys* and *Rhizomys*, but Gerbillinae, Acomyinae and Murinae can be used in a phylogeny constructed with a molecular clock hypothesis. This analysis, with the *Mus/Rattus* divergence at 12 My as reference, indicates that Acomyinae, Gerbillinae and Murinae diverged at 16.6 My, the four acomyines genera from 11.9 to 6.6 My, *Tatera* and *Gerbillus* at 8.7 My.

Molecules and morphology: support for the Acomyinae?

Both molecular approaches indicate the existence of an Acomyinae clade which comprises *Acomys*, *Deomys* and *Lophuromys* (for the 12S rRNA data sets) associated with *Uranomys* for the other data sets. The resolution of the different approaches are not equivalent. The 12S rRNA gene and the hybridization data sets provide less resolution for older divergences than the LCAT gene or the combined sequences. Other molecular data have also grouped some of these taxa. *Acomys* and *Uranomys* were associated by HÄNNI *et al.* (1995) and DUBOIS *et al.* (1999), but the supports for this group were low (fig. 4B, HÄNNI *et al.*, 1995; fig. 4, DUBOIS *et al.*, 1999). Other associations were also published, *Lophuromys* and *Deomys* (VERHEYEN *et al.*, 1996), *Acomys*, *Lophuromys* and *Deomys* (DENYS *et al.*, 1995), *Acomys*, *Uranomys* and *Lophuromys* (CHEVRET *et al.*, 1993). But this is the first study that clearly groups the four acomyine genera together, with the support of different molecular methods involving scnDNA hybridization, a mitochondrial and a nuclear gene.

If our data bring strong molecular support for the existence of the Acomyinae, morphological evidence uniting them is still lacking.

The four genera have been brought closer by different authors but only two at a time, with most evidences supporting an *Acomys-Uranomys* clade. *Acomys* and *Uranomys* have been effectively considered as closely related based on dental and cranial morphology since a long time (HELLER, 1911; HINTON, 1921; INGOLBY, 1929; ELLERMAN, 1941; HEIM DE BALSAC, 1963; MISONNE, 1969). More recently, HUTTERER *et al.* (1988) have associated *Acomys*, *Uranomys* and a fossil of the Canary Islands, *Malpaisomys*. This hypothesis was refuted by the immunological analysis of MONTGELARD (1992) which indicated that *Malpaisomys* was more closely related to *Mus* than to *Acomys* and *Uranomys*, without any further information concerning their relationships. DENYS *et al.* (1992), in a morphological analysis on dental characters in *Acomys*, *Uranomys* and other murid rodents, associated *Acomys* and *Uranomys*, considering them as an early offshoot of the Murinae. However, the re-examination of the third upper molar by the same authors (DENYS and MICHAUX, 1992) lead them to propose a morphological synapomorphy uniting *Acomys*, *Uranomys* and *Lophuromys*, and excluding them from the Murinae. Thus, some strong morphological support does exist for the association of these three genera, which also share precocious youngs, a fragile skin and tail, and a partially diurnal life.

Lophuromys and *Deomys* share similarities in the morphology of the zygomatic arch (ELLERMAN, 1941), but this author and DIETERLEN (1976) considered that this character state might be a convergence due to their similar diet (mostly insectivorous). A morphological re-examination of the eight living genera of Dendromurinae lead DENYS *et al.* (1995) to the conclusion that this taxon was not monophyletic. This interpretation is congruent with our results, which indicate that *Deomys* is within the Acomyinae, whereas *Dendromus* and *Steatomys* are more closely related to the Cricetomyinae (*Saccostomus* or *Cricetomys*, figs. 1 and 2). DENYS *et al.* (1995) also found that *Acomys* and *Lophuromys* are closely related, but without any close relationship with *Deomys*. Comparative morphology suggested that *Acomys* and *Lophuromys* were more closely related to Murinae than to Gerbillinae, as the morphology of the latter group appears very derived.

Thus, if the association of *Acomys*, *Uranomys* and *Lophuromys* is now supported by both molecular and morphological data, the problem of their morphological association with *Deomys* is neither explained

nor solved, as the latter genus appears completely distinct from the remaining Acomyinae.

Acomyinae within the Muridae

The sister-group of Acomyinae is either Murinae or Gerbillinae, but we cannot decide between both hypotheses. Morphology and paleontology would tend to associate Murinae and Acomyinae, notably due to the supposed derived morphology of their first upper molar which was considered a diagnostic feature of all Murinae (JACOBS *et al.*, 1989). Among Muridae, paleontologists very often associate Murinae, Dendromurinae, Gerbillinae and, sometimes, Cricetomyinae (FLYNN *et al.*, 1985; JAEGER *et al.*, 1986, 1985; TONG and JAEGER, 1993). Our results indicate that Murinae, Acomyinae and Gerbillinae are indeed sister-taxa, as proposed by TONG and JAEGER (1993). Cricetomyinae (here represented by *Saccostomus*) belong to a completely different group which comprises African (*Steatomys, Dendromus, Mystromys*) and Malagasy (*Nesomys, Macrotarsomys*) murids, which is a new phylogenetic hypothesis. The age of the divergence – 16 My – proposed by TONG and JAEGER (1993) for the Murinae/Gerbillinae split is not too different from our estimates: 16.6 (LCAT) and 14.5 My (scnDNA hybridation), considering that one of our dating (14.5 My) for such an old divergence is probably underestimated due to some DNA/DNA hybridization properties (SPRINGER and KIRSCH, 1991).

If the existence of Acomyinae and its composition might be difficult to explain morphologically, the relative position of the group within the Muridae seems more in agreement with traditional views.

Conclusion

Our data provide strong molecular support for an Acomyinae group comprising *Acomys, Uranomys, Lophuromys* and *Deomys*. If there is also some morphological support for an *Acomys, Lophuromys* and *Uranomys* clade based upon the morphology of the third upper molar (DENYS and MICHAUX, 1992), there is still no morphological evidence for the association of *Deomys* with this group. The molecular clade

Acomyinae thus raises questions concerning the definition of Dendromurinae and Murinae as based on comparative morphology, especially dental. Other morphological characters (cranial, post-cranial, internal soft anatomy) should be searched and analysed for testing our molecular findings. Additional species of *Acomys* and *Lophuromys* have now to be included in order to precise the relationships within this group. If we can propose the existence of an Acomyinae/Gerbillinae/Murinae cluster within Muridae, none of our methods can decipher clearly the relationships between these three subfamilies. The use of other molecules, especially slow-evolving protein-coding nuclear genes, the study of repeated elements and the use of other morphological data may be able to answer the question of their relationships.

Acknowledgements

We thank for their help in the laboratory: J.-Y. Dubois, J.-Y. Dubuisson and P. Sourrouille, for the use of an automatic sequencer Prof. F. Grigorescu (Institut universitaire de recherche clinique (IURC), Montpellier), all people who provided the numerous tissues used in this study, and J. Kirsch and F.-J. Lapointe for their help and advices with the MAJACK package. This work was support by European Contract "Research Network FMRX-CT9860221" and French Ministry of Education and Research ("ACC-SV7 Réseau national de biosystématique"). This is contribution ISEM 2001-128 of Institut des sciences de l'évolution de Montpellier (UMR 5554 CNRS – université Montpellier-II).

References

BREMER K., 1988 — The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* 42 (4): 795-803.

CATZEFLIS F. M., 1990 — "DNA hybridization as a guide to phylogenies: raw data in muroid rodents". *In* NEVO E., REIG O. A. (eds): *Evolution of subterranean mammals at the organismal and molecular levels.* New York, Wiley-Liss: 217-345.

CATZEFLIS F. M., 1991 — Animal tissue collections for molecular genetics and systematics. *Trends in Ecology and Evolution* 6: 168.

CHEVRET P., DENYS C., JAEGER J.-J., MICHAUX J. and CATZEFLIS F. M., 1993 — Molecular evidence that the spiny mouse *(Acomys)* is more closely related to the gerbils (Gerbillinae) than to the true mice. *Proceedings of the National Academy of Sciences, USA* 90: 3433-3436.

CHEVRET P. and HÄNNI C., 1994 — Systematic of the spiny mouse (*Acomys:* Muroidea): molecular and biochemical evidences. *Israel Journal of Zoology* 40: 247-254.

CHEVRET P., GRANJON L., DUPLANTIER J.-M., DENYS C. and CATZEFLIS F. M., 1994 — Molecular phylogeny of the *Praomys* complex (Rodentia: Muridae). *Zoological Journal of the Linnean Society, London* 112: 425-442.

DENYS C. and MICHAUX J., 1992 — La troisième molaire supérieure chez les Muridae d'Afrique tropicale et le cas des genres *Acomys, Uranomys* et *Lophuromys. Bonner Zoologische Beiträge* 43: 367-382.

DENYS C., MICHAUX J., PETTER F., AGUILAR J.-P. and JAEGER J.-J., 1992 — Molar morphology as a clue to the phylogenetic relationship of *Acomys* to the Murinae. *Israel Journal of Zoology* 38: 253-262.

DENYS C., MICHAUX J., CATZEFLIS F., DUCROCQ S. and CHEVRET P., 1995 — Morphological and molecular data against the monophyly of the Dendromurinae (Muridae, Rodentia). *Bonner Zoologische Beiträge* 45 (3-4): 173-190.

DIETERLEN F., 1976 — Die afrikanische Muridengattung *Lophuromys* Peters 1874. *Stuttgarter Beiträge zur Naturkunde* 185: 1-96.

DUBOIS J.-Y., RAKOTONDRAVONY D., HÄNNI C., SOURROUILLE P. and CATZEFLIS F. M., 1996 — Molecular evolutionary relationships of three genera of Nesomyinae, endemic rodent taxa from Madagascar. *Journal of Mammalian Evolution.* 3 (3): 239-260.

DUBOIS J.-Y., CATZEFLIS F. M. and BEINTEMA J. J., 1999 — The phylogenetic position of "Acomyinae" (Rodentia, Mammalia) as sister group of a Murinae + Gerbillinae clade: evidence from the nuclear ribonuclease gene. *Molecular Phylogenetics and Evolution* 13 (1): 181-192.

ELLERMAN J. R., 1941 — *The families and genera of living rodents.*, 2, London, British Museum (Natural History).

FELSENSTEIN, J., 1981 — Evolutionary trees from DNA sequences: a maximum likelihood approach. *Journal of Molecular Evolution* 17: 368-76.

FELSENSTEIN J., 1993 — PHYLIP (PHYLogeny Inference Package). version 3.5c. Seattle, Department of Genetics, University of Washington.

FLYNN L. J., JACOBS L. L. and LINDSAY E. H., 1985 — "Problems on Muroid phylogeny: relationship to other rodents and origin of major groups." *In* LUCKETT, W. P. and HARTENBERGER, J.-L. (eds): *Evolutionary Relationships among Rodents. A multidisciplinary analysis.*, New York and London, Plenum Press: 589-616.

FRAGUEDAKIS-TSOLIS S. E., CHONDROPOULOUS B. P. and NIKOLETOPOULOS N. P., 1993 — On the phylogeny of the genus *Acomys* (Mammalia: Rodentia). *Zeitschrift für Säugetierkunde* 58: 240-243.

FURANO A. V., HAYWARD B. E., CHEVRET P., CATZEFLIS F. and USDIN K., 1994 — Amplification of the ancient murine Lx family of long interspersed repeated DNA occurred during the murine radiation. *Journal of Molecular Evolution* 38: 18-27.

HAMMER M. F., SCHILLING J. W., PRAGER E. M. and WILSON A. C., 1987 — Recruitment of lysozyme as a major enzyme in the mouse gut: duplication, divergence and regulatory evolution. *Journal of Molecular Evolution.* 24: 272-279.

HÄNNI C., LAUDET V. and CATZEFLIS F., 1995 — Evolutionary relationships of *Acomys* and other Murids (Rodentia, Mammalia) based on complete 12S rDNA mitochondrial gene sequence. *Israel Journal of Zoology.* 41: 131-146.

HASSANIN A., LECOINTRE G. and TILLIER S., 1998 — The "evolutionary signal" of homoplasy in protein-coding gene sequences and its consequences for *a priori* weighting in phylogeny. *Comptes Rendus de l'Académie des Sciences, Paris,- Série III - Sciences de la vie* 321: 611-620.

HEIM DE BALSAC H., 1963 — L'"abrasion préalable" sous-gingivale des molaires de certains Rongeurs et Insectivores. Le cas remarquable d'*Uranomys*. *Comptes Rendus de l'Académie des Sciences, Paris* 256: 5257-5261.

HELLER E., 1911 — New species of Rodents and Carnivores from equatorial Africa. *Smithsonian Miscellaneous Collection* 17: 1-16.

HINTON M. A. C., 1921 — Some new African Mammals. *Annals and Magazine of Natural History* 7: 368-373.

HUTTERER R., LOPEZ-MARTINEZ N. and MICHAUX J., 1988 — A new rodent from Quaternary deposits of the Canary Islands and its relationships with Neogene and Recent murids of Europe and Africa. *Paleovertebrata* 18: 241-262.

INGOLBY C. M., 1929 — On the Mammals of the Gold Coast. *Annals and Magazine of Natural History* 3: 511-529.

JACOBS L. L., 1978 — Fossil rodents (Rhizomyidae and Muridae) from Neogene Siwalik deposits, Pakistan. *Museum of Northern Arizona Press, Bulletin Series* 52: 1-104.

JACOBS L. L. and PILBEAM D., 1980 — Of mice and men: Fossil-based divergence dates and molecular "Clocks". *Journal of Human Evolution* 9: 551-555.

JACOBS, L. L., FLYNN, L. J. and DOWNS, W. R., 1989 — Neogene rodents of southern Asia. *In* BLACK C. C. and DAWSON M. R. (eds): *Papers on fossil rodents in honor of Albert Elmer Wood.* Natural History Museum Los Angeles County, Los Angeles: 157-177.

JACOBS L. L. and DOWNS W. R., 1994 — "The evolution of murine rodents in Asia.". *In* TOMIDA Y., LI C. K., SETOGUSCHI T. (eds): *Rodent and Lagomorph Families of Asian Origins and their diversification.* Vol. 8. Tokyo, National Science Museum Monograph: 149-156.

JAEGER J.-J., TONG H., BUFFETAUT E. and INGAVAT R., 1985 — The first fossil rodents from the Miocene of northern Thailand and their bearing on the problem of the origin of the Muridae. *Revue de Paléobiologie* 4: 1-7.

JAEGER J.-J., TONG H. and DENYS C., 1986 — Âge de la divergence *Mus-Rattus:* comparaison des données paléontologiques et moléculaires. *Comptes Rendus de l'Académie des Sciences, Paris, Série II* 302: 917-922.

JUKES T. H. and CANTOR C. R., 1969 — "Evolution of protein molecules". *In* MUNRO, H. N. (éd.): *Mammalian protein metabolism.* Orlando, Florida, Academic Press: 21-123.

LANDRY P. A., LAPOINTE F. J. and KIRSCH J. A. W., 1996 — Estimating phylogenies from lacunose distance matrices: additive is superior to ultrametric estimation. *Molecular Biology and Evolution* 13 (6): 818-823.

LANYON S. M., 1985 — Detecting internal inconsistencies in distance data. *Systematic Zoology* 34 (4): 397-403.

LAPOINTE F. J., KIRSCH J. A. W. and BLEIWEISS R., 1994 — Jacknifing of weighted trees: validation of phylogenies reconstructed from distance matrices. *Molecular Phylogenetics and Evolution* 3 (3): 256-267.

MICHAUX J. R. and CATZEFLIS, F., 2000 — The bushlike radiation of muroid rodents is exemplified by the molecular phylogeny of the LCAT nuclear gene. *Molecular Phylogenetics and Evolution,* 17 (2) : 280-293.

MISONNE X., 1969 — African and Indo-Australian Muridae. Evolutionary trends. *Annales du musée royal d'Afrique centrale, Tervuren* 172: 1-219.

MONTGELARD C., 1992 — Albumin preservation in fossil bones and systematics of *Malpaisomys insularis* (Muridae, Rodentia), an extinct rodent of the Canary islands. *Historical Biology* 6: 293-302.

PHILIPPE H., 1993 — MUST: a computer package of Management Utilities for Sequences and Trees. *Nucleic Acids Research* 21: 5264-5272.

ROBINSON M., CATZEFLIS F., BRIOLAY J. and MOUCHIROUD D., 1997 — Molecular phylogeny of rodents, with special emphasis on Murids: evidence from nuclear gene LCAT. *Molecular Phylogenetics and Evolution* 8 (3): 423-434.

ROBINSON M., GOUY M., GAUTIER C. and MOUCHIROUD D., 1998 — Sensitivity of the relative-rate test to taxonomic sampling. *Molecular Biology and Evolution* 15: 1091-1098.

SAITOU N. and NEI M., 1987 — The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution* 4: 406-425.

SARICH V. M., 1985 — "Rodent macromolecular systematics". *In* LUCKETT, W. P., HARTENBERGER, J.-L. (eds): *Evolutionary relationships among rodents.* New York, Plenum Press: 423-452.

SIDDALL M. E., 1996 — Random Cladistics manual. Gloucester Point, Virginia Institute of Marine Science.

SOURROUILLE P., HÄNNI C., RUEDI M. and CATZEFLIS F. M., 1995 — Molecular systematics of *Mus crociduroides,* an endemic mouse of Sumatra (Muridae, Rodentia). *Mammalia* 59 (1): 91-102.

SPRINGER, M. S. and KIRSCH, J. A., 1991 — DNA hybridization, the compression effect, and the radiation of diprotodontian marsupials. *Systematic Zoology* 40: 131-151.

SPRINGER M. S., DAVIDSON E. H. and BRITTEN R. J., 1992 — Calculation of sequence divergence from the thermal stability of DNA heteroduplexes. *Journal of Molecular Evolution* 34: 379-382.

STRIMMER K. and VON HAESELER A., 1996 — Quartet puzzling: a quartet maximum-likelihood method for reconstructing tree topologies. *Molecular Biology and Evolution* 13 (7): 964-969.

SWOFFORD D. L., 1993 — PAUP 3.1.1: Phylogenetic analysis using parsimony. version 3.1.1, Illinois Natural History Survey, Champaign.

SWOFFORD D. L., 1998 — PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. 0b, Sinauer Associates, Sunderland, Massachusetts.

THOMPSON J.D., HIGGINS D.G. and GIBSON T.J., 1994 — CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, positions-specific gap penalties and weight matrix choice. *Nucleic Acids Research,* 22: 4673-4680.

TONG H. and JAEGER J.-J., 1993 — Muroid rodents from the Middle Miocene Fort Ternan locality (Kenya) and their contribution to the phylogeny of muroids. *Paleontographica Abteilung A* 229 (1-3): 51-73.

USDIN K., CHEVRET P., CATZEFLIS F. M., VERONA R. and FURANO A. V., 1995 — L1 (LINE-1) retrotransposable elements provide a "fossil" record of the phylogenetic history of Murids rodents. *Molecular Biology and Evolution* 12: 73-82.

VERHEYEN E., COLYN M. and VERHEYEN W., 1996 — A mitochondrial cytochrome b phylogeny confirms the paraphyly of the Dendromurinae Alston, 1896 (Muridae, Rodentia). *Mammalia* 60 (4): 780-785.

WILSON A. C., OCHMAN H. and PRAGER E. M., 1987 — Molecular time scale for evolution. *Trends Genetics* 3 (9): 241-247.