Molecular evidence that the spiny mouse (*Acomys*) is more closely related to gerbils (Gerbillinae) than to true mice (Murinae)

(molecular systematics/Rodentia/DNA hybridization)

Pascale Chevret, Christiane Denys, Jean-Jacques Jaeger, Jacques Michaux, and François M. Catzeflis*

Institut des Sciences de l'Evolution, Unité Recherche Associée 327, Centre National de la Recherche Scientifique, Université Montpellier II, Case courrier 064, 34095 Montpellier, France

ABSTRACT   Spiny mice of the genus *Acomys* traditionally have been classified as members of the Murinae, a subfamily of rodents that also includes rats and mice with which spiny mice share a complex set of morphological characters, including a unique molar pattern. The origin and evolution of this molar pattern, documented by many fossils from Southern Asia, support the hypothesis of the monophyly of *Acomys* and all other Murinae. This view has been challenged by immunological studies that have suggested that *Acomys* is as distantly related to mice (*Mus*) as are other subfamilies (e.g., hamsters: Cricetinae) of the muroid rodents. We present molecular evidence derived from DNA·DNA hybridization data that indicate that the spiny mouse *Acomys* and two African genera of Murinae, *Uranomys* and *Lophuromys*, constitute a monophyletic clade, a view that was recently suggested on the basis of dental characters. However, our DNA·DNA hybridization data also indicate that the spiny mice (*Acomys*) are more closely related to gerbils (Gerbillinae) than to the true mice and rats (Murinae) with which they have been classified. Because *Acomys* and the brush-furred mice *Uranomys* and *Lophuromys* share no derived morphological characters with the Gerbillinae, their murine morphology must have evolved by convergence, including the molar pattern previously considered to support the monophyly of the Murinae.

The genus *Acomys* includes at least eight species of small murid rodents, called spiny mice, that have been placed in the Murinae, which includes mice (*Mus*), rats (*Rattus*), field mice (*Apodemus*), etc. (1, 2). The relationships of *Acomys*, which was considered to be a close relative of *Mus sensu lato*, the true mice (3–5), have been challenged by immunological data published by Sarich (6) who suggested that quantitative precipitin assays involving *Acomys*, *Mus*, *Rattus*, *Praomys*, and other murid rodents related to the Murinae showed that *Acomys* is as distantly related to *Mus* as are some other subfamilies of the Muridae. This conflict between biochemical and morphological evidence was cited by Wilson *et al.* (7) as evidence that the traditional classification of rodents is incorrect.

The spiny mouse *Acomys* was placed in the Murinae because it shares a unique and complex tooth pattern with the Murinae (1, 5, 8). Jacobs *et al.* (9) defined the Murinae by the presence of two additional lingual cusps on the first upper molar (M1/), a derived character also found in *Acomys*. However, the spiny mice were also characterized by the structure of their third upper molar (M3/), (10) and this morphological pattern, also found in two other African genera of murids, is not present in most fossil and living murines (11).

The fossil record pertaining to the origin and evolution of the spiny mouse does not help, because the oldest *Acomys*, from the Lower Pliocene (dated at 4.5 to 6.0 million years B.P.) of Langebaanweg, South Africa, look like recent taxa; hence, they yield no clues to the affinities of this genus (12).

In response to the challenge of the immunological data (6, 7), two phylogenetic studies based on cladistic analyses of morphological characters suggested that *Acomys* was either a murine (13) or an early offshoot of the murine radiation (14). A taxonomic survey of murid rodents by isozyme electrophoresis (15) indicated that *Acomys* was more closely related to the Murinae than to the other subfamilies tested, but nevertheless emphasized its isolated position within the Murinae. Similarly, chromosomal studies by G-banding (16) did not exclude *Acomys* from the Murinae but suggested that the spiny mouse, as well as other murine genera such as *Uranomys*, *Mus*, or *Rattus*, were derived from the ancestral murid karyotype.

To resolve this contradiction between molecules and morphology, we have used liquid-phase DNA·DNA hybridization of the nonrepeated fraction of the genome. This method, which has been critically examined for its use in evolutionary systematics (17–19), produced evidence that *Acomys* and its two sister genera, *Uranomys* and *Lophuromys*, form a monophyletic group that is not allied to the Murinae but clusters with the gerbils (subfamily Gerbillinae). These data, confirming and expanding the hypothesis of Sarich (6), support the dental morphology that has united *Acomys*, *Lophuromys*, and *Uranomys* (11).

METHODS

DNA samples were extracted and purified from ethanol-preserved tissues of the rodents listed in Table 1. Based on morphological, paleontological, and biochemical data (20–22), *Cricetomys gambianus* (Cricetomyinae) was included in the study as an outgroup to the Murinae and Gerbillinae. The procedures for single-copy nuclear DNA (scnDNA) hybridization experiments used here are similar to those published by Sibley and Ahlquist (23) and Werman *et al.* (24) and are identical to those used in previous papers (18, 25). DNAs were sheared to fragments with an average size of 500 bp (range, 300–1000 bp). The scnDNA fractions were isolated by removing, on hydroxyapatite (Bio-Gel HTP, Bio-Rad) columns, the highly repeated sequences that reassociate by a $C_0 t$ value of 1000 M·s ($C_0 t$ is the product of the DNA concentration and the time of reassociation) in 0.48 M sodium phosphate (pH 8.0) at 55.0°C. Tracer scnDNAs were chemically labeled with ^{125}I, and their average fragment length ranged from ≈300 to ≈700 bp, as measured on sizing gels (24, 26).

Table 1. ΔT_{m} of the tracer scnDNAs of *Acomys cahirinus,*
Uranomys ruddi, and *Lophuromys sikapusi*

Driver	T_{m}, °C		
	*Acomys	*Uranomys	*Lophuromys
Acomys	0.00	12.5 ± 0.5‡	12.0 ± 0.1†
Uranomys	13.5 ± 0.3†	0.00	12.8 ± 0.8†
Lophuromys	12.9 ± 0.2†	12.1 ± 0.8§	0.00
Gerbillus	18.0 ± 0.1†	15.2, 14.8	16.5 ± 0.1†
Tatera	17.7 ± 0.2†	15.3 ± 0.4§	16.5 ± 0.3†
Arvicanthis	18.2, 18.3	16.2, 16.2	16.9 ± 0.2†
Millardia	18.6 ± 0.1†	16.0, 16.1	16.7 ± 0.3†
Mus	18.8 ± 0.3†	16.2, 16.3	16.9 ± 0.2†
Rattus	18.9 ± 0.1†	—	17.1 ± 0.3†
Mastomys	19.0 ± 0.1†	—	17.2, 17.2†
Praomys	18.7 ± 0.5†	—	16.9 ± 0.3†
Cricetomys	19.2 ± 0.3†	—	17.4 ± 0.4†

Data are the average ± SD of three or more comparisons or the data obtained. —, No data available; 0.00, homologous reaction. Labeled tracer species are indicated by an asterisk. The origins of the animals [and their DNA sample numbers] are as follows: Murinae: *Acomys cahirinus* (4103, 4242, 4281), Saudi Arabia, collected by F. Catzeflis; *Arvicanthis niloticus* (4092), Mali, F. Petter; *Lophuromys nudicaudus* (4430) and *Lophuromys sikapusi* (4424), Congo, L. Granjon; *Mastomys erythroleucus* (4491), Congo, L. Granjon; *Mastomys huberti* (4101), Senegal, J.-M. Duplantier; *Milliardia meltada* (4406), India, F. Catzeflis; *Mus caroli* (4108), laboratory strain, F. Bonhomme; *Mus cervicolor* (4106, 4105), laboratory strain, F. Bonhomme; *Mus musculus* (57), laboratory strain, F. Bonhomme; *Mus saxicola* (4486), India, F. Catzeflis; *Praomys lukolelae* (4592), Congo, L. Granjon; *Praomys tullbergi* (4633), Gabon, V. Nancé; *Rattus norvegicus* (3753b, 4047), laboratory strain, Yale University; *Rattus tiomanicus* (4294), Borneo, R. Stuebing; *Uranomys ruddi* (4413), Ivory Coast, F. Petter. Gerbillinae: *Gerbillus agag* (4143), Burkina Fasso, J.-C. Gautun; *Tatera brantsii* (4272), South Africa, M. Perrin; *Tatera gambiana* (4415), Senegal, J.-M. Duplantier. Cricetomyinae: *Cricetomys gambianus* (4240, 4431, 4433), Senegal, J.-M. Duplantier.
†Three comparisons.
‡Six comparisons.
§Four comparisons.

DNA·DNA hybrids were permitted to reassociate after heat denaturation to a C_0t of 16,000 M·s at 60.0°C in 0.48 M sodium phosphate (pH 8.0). Thermal elutions were begun at 55°C in increments of 2.5°C up to 95°C in an apparatus similar to those described in refs. 23 and 27, and the raw data are the radioactive cpm eluted at each temperature, as illustrated for rodents (18).

Among the statistics that can be used to estimate the difference between the thermal elution curves of the homoduplex and heteroduplex hybrids (17, 18, 23), we present here the results based on the median temperature at which 50% of the hybrid DNA has been dissociated (T_{m}) in the 62.5–95.0°C range (Fig. 1). In the experiments listed in Tables 1 and 2, T_{m} and Mode (the temperature of the peak of the modal elution curve) are well correlated ($r = 0.88$; $n = 151$), as observed (17), and both statistics yield the same results as far as the branching pattern is concerned. Due to lower-temperature secondary peaks interfering with the true Mode in several hybrid comparisons (as illustrated in ref. 18), the Mode statistics were rejected in favor of T_{m}. The individual ΔT_{m} values of Table 2 were examined for their robustness by a bootstrapping procedure (28); 1000 samplings with replacement, each being adjusted for asymmetry by the procedure of Sarich and Cronin (29), yielded pseudoreplicate matrices and from each matrix a best-fit tree was constructed by the least-squares approach of Fitch and Margoliash (30) by using the FITCH program (default options: $P = 0.0$; Y for writing each tree topology onto a file treated by CONSENSE program) from the PHYLIP package (31). The phylogenetic tree of Fig. 2 was constructed by averaging the branch lengths of a random sample of 50 pseudoreplicate FITCH trees, all having the same topology.

RESULTS AND DISCUSSION

The nonrepeated DNA fractions of a dozen murid and gerbillid genera and of a cricetomyine for outgroup were radioactively labeled. Tables 1 and 2 list the results for the following eight taxa: *Acomys cahirinus, Cricetomys gambianus, Gerbillus agag, Lophuromys sikapusi, Mus cervicolor, Rattus tiomanicus, Tatera brantsii,* and *Uranomys ruddi.* Fig. 1 *A* and *B,* respectively, illustrates the melting curves for several DNA·DNA hybrids made with either *Acomys* or *Mus* tracer DNAs, each curve being the average of two to four replicates with standard deviation values represented by vertical bars. The bootstrapping procedure on the individual ΔT_{m} values of Table 2 yielded an identical branching pattern (illustrated in Fig. 2) for the 1000 pseudoreplicate trees. This pattern, which is also observed in trees reconstructed with the assumption of a molecular clock (data not shown), indicates that *Cricetomys gambianus* is an outgroup to the other taxa, as was expected from traditional systematics (1, 21, 22). All segment lengths of Fig. 2 are significantly different from zero, as judged from the ratio between each
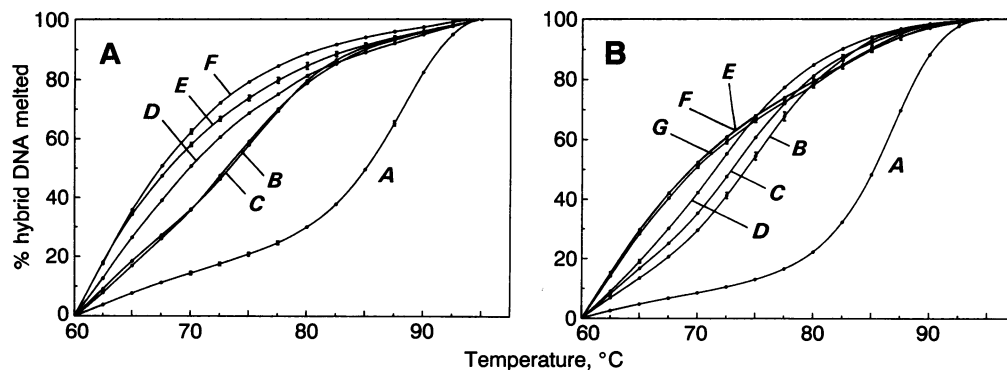

FIG. 1.   Melting curves of DNA·DNA hybrids versus temperature for calculating the T_{m}. Numbers of replicate comparisons used for drawing each curve are in parentheses, and vertical bars represent standard deviation of the mean. (*A*) The scnDNA tracer is *Acomys cahirinus.* Curves: A, homolog *A. cahirinus/A. cahirinus* (4); B, *A. cahirinus/Lophuromys sikapusi* (3); C, *A. cahirinus/Uranomys ruddi* (3); D, *A. cahirinus/Tatera brantsii, Tatera indica* (3); E, *A. cahirinus/Mus cervicolor, Mus saxicola* (3); F, *A. cahirinus/Cricetomys gambianus* (3). (*B*) The tracer species is *Mus cervicolor.* Curves: A, *M. cervicolor/M. cervicolor* (4); B, *M. cervicolor/Praomys lukolelae* (3); C, *M. cervicolor/Arvicanthis niloticus* (3); D, *M. cervicolor/Rattus norvegicus, Rattus tiomanicus* (3); E, *M. cervicolor/Lophuromys sikapusi* (2); F, *M. cervicolor/Acomys cahirinus* (2); G, *M. cervicolor/Gerbillus agag* (2).

Table 2. Matrix of individual uncorrected ΔT_m values among six species of Gerbillinae and Murinae and the outgroup *Cricetomys gambianus*

Driver	*Acomys	*Lophuromys	*Gerbillus	*Tatera	*Mus	*Rattus	*Cricetomys
Acomys	0.0	12.0	14.4	13.2	15.9	15.6	15.9
		12.1	14.6	13.1	15.7	15.4	16.5
		12.0	14.6	12.8		15.4	16.5
Lophuromys	12.7	0.0	14.7	13.4	15.8	15.1	16.3
	13.0		14.8	13.5	15.8	15.1	16.2
	12.9		14.6	13.0			
Gerbillus	18.0	16.6	0.0	9.2	15.6	15.2	16.0
	18.1	16.6		9.0	15.3	15.1	16.1
	17.9	16.4		8.9			
Tatera	17.6	16.7	8.7	0.0	16.0	14.9	16.2
	17.6	16.6	8.9		15.8	14.4	16.2
		16.2	9.0			14.8	15.9
Mus	19.1	16.7	15.0	13.7	0.0	12.2	16.4
	18.8	17.0	15.0	13.6		12.8	16.2
	18.5	17.1				13.1	16.5
Rattus	19.0	17.3	15.7	13.2	14.0	0.0	16.3
	18.9	17.2	15.6	13.2	13.6		16.3
	19.0	16.8		13.7			16.0
Cricetomys	19.6	17.7	15.6	14.2	16.1	15.6	0.0
	19.0	17.4	15.0	13.6	16.3	15.2	
	19.0	17.0		13.6		15.4	

Labeled tracer species are indicated by an asterisk.

mean branch length and its standard deviation computed from a random sample of 50 pseudoreplicate FITCH trees.

Among the taxa studied (those listed in Table 1 plus ≈10 additional genera currently placed in the Murinae; data not shown), *Uranomys* and *Lophuromys* are more closely related to *Acomys* than to any other rodent (Table 1 and Fig. 1). These rodents, called brush-furred (or harsh-furred) mice, are found exclusively in Africa. These three genera appear to form a monophyletic group and seem to be more closely related to the Gerbillinae than to the Murinae (Tables 1 and 2 and Figs. 1 and 2). Although the SEM values are rather large in some comparisons (Table 1) due to the experimental scatter of the data, the branching pattern of Fig. 2 appears
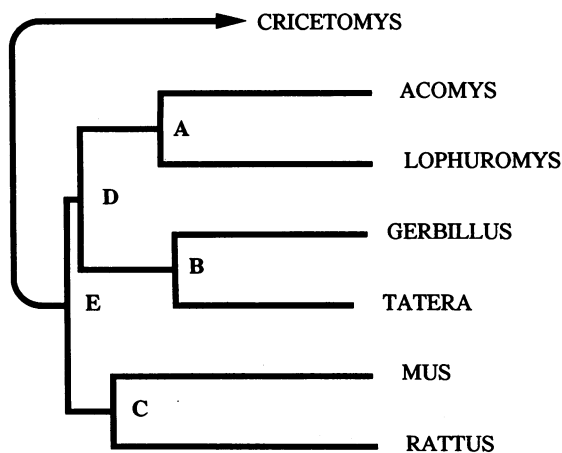

FIG. 2. Phylogenetic tree derived from the least-squares approach, with no assumption of a molecular clock. The branch lengths are based on the average of 50 best-fit trees obtained by resampling the individual ΔT_m distances of Table 2. The values of the branch lengths are as follows: node A to *Acomys*, 5.53 ± 0.03°C; node A to *Lophuromys*, 5.47 ± 0.03°C; node B to *Gerbillus*, 5.03 ± 0.40°C; node B to *Tatera*, 4.75 ± 0.05°C; node C to *Mus*, 6.70 ± 0.09°C; node C to *Rattus*, 6.83 ± 0.06°C; node E to *Cricetomys*, 8.19 ± 0.05°C; between nodes A and D, 2.20 ± 0.04°C; between nodes B and D, 2.56 ± 0.04°C; between nodes D and E, 0.25 ± 0.03°C; between nodes C and E, 1.17 ± 0.07°C.

stable and robust. The DNA·DNA hybridization tree illustrated in Fig. 2 is supported by another molecular study concerning the taxonomic distribution of the Lx repeated nuclear genes (32), amplification of which has been found in several genera of the Murinae, but not in *Acomys, Uranomys*, Gerbillinae, Cricetomyinae, Cricetinae, Arvicolinae, or other muroid rodents (F.M.C. and A. V. Furano, unpublished data). Thus, the amplification of Lx can be interpreted as a molecular synapomorphy defining the Murinae *sensu stricto* (ancestral segment EC on Fig. 2) and excluding the spiny mouse and its relatives. In summary, the results from DNA·DNA hybridization experiments suggest that *Acomys, Uranomys*, and *Lophuromys* do not belong to the Murinae but rather belong to a clade of the murid rodents represented in this study by the Gerbillinae. The clustering of *Acomys* with *Uranomys* and *Lophuromys* (Fig. 2) was unexpected, although morphological observations suggested that the spiny mice were similar to *Uranomys* (4, 5). Hutterer *et al.* (13) proposed a monophyletic clade including *Acomys, Uranomys*, and the fossil *Malpaisomys* based on their unique long palatal bridge [as noted by Rosevaer (33)], but this structure does not appear in *Lophuromys*. A study (11) of the third upper molar tooth (M3/) confirmed previous observations (10, 34), emphasizing a peculiar morphological pattern on M3/ not found in any other living or fossil murid rodent (Fig. 3, arrows). If this morphological character is valid, it would be a synapomorphy uniting the monophyletic group *Acomys*—*Uranomys*—*Lophuromys* to the exclusion of the Murinae. These three genera also tend to bear precocial young after a rather long gestation period (ref. 35 and M. Tranier, personal communication), but there is no common life-history trait uniting *Lophuromys, Uranomy*, and *Acomys* to the exclusion of other African murids. The nine species of *Lophuromys* are insectivorous and exclusively terrestrial, living in the edges of subtropical and tropical forests (34). The single species of *Uranomys* (2) is a terrestrial mouse-like rodent living in savannahs. The eight species of *Acomys* (10, 36) are omnivorous desert dwellers, and their spiny dorsal hair is thought to help in thermoregulation. The brush-furred mice, *Lophuromys* and *Uranomys*, have stiff, not spiny, hair on the dorsum (37), but this characteristic probably has no
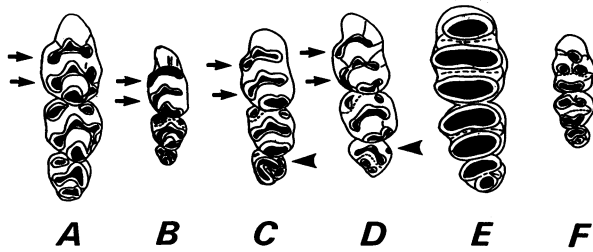
FIG. 3. Upper tooth rows of some murid and gerbillid rodents. The arrows point to the M3/ structure defining *Acomys, Uranomys,* and *Lophuromys* and to the presence of cusps t1 and t4 on the M1/ of the true Murinae (*Millardia* and *Mus*). (*A*) *Millardia meltada*. (*B*) *Mus setulosus*. (*C*) *Uranomys ruddi*. (*D*) *Acomys cahirinus*. (*E*) *Tatera nigricauda*. (*F*) *Gerbillus nigeriae*.

phylogenetic significance because it occurs in several unrelated true murines and other muroid rodents (1).

The spiny mouse *Acomys* is not a mouse and should not be placed in the Murinae. Traditional classifications included *Acomys, Uranomys,* and *Lophuromys* in the Murinae, due to several morphological (skull and teeth) characters, especially the cusp pattern of the first upper molar (M1/) tooth (Fig. 3). Jacobs and colleagues (9, 38) defined all Murinae by the presence of two lingual cusps on M1/, numbered t1 and t4 and united by transverse crests to their labial cusps t2 and t5, respectively. This pattern was considered characteristic of the Murinae, and its earliest fixed occurrence is found in the fossil *Progonomys*, the previously supposed common ancestor of all Murinae that appeared in Southern Asia, Africa, and Europe about 12 million years ago (39–41). *Progonomys* derives from the southern Asian genus *Antemus*, which documents the transition from an ancestor with one lingual cusp to an advanced murine molar pattern between 14 and 12 million years ago (38, 40). This molar pattern is unknown in any fossil or living Gerbillinae (42). Moreover, the living Gerbillinae are characterized by a series of dental and skull traits that are not observed in the Murinae or in *Acomys* and its sister genera (1, 42). If these morphological characters (lingual t1 and t4 cusps on M1/) found in *Acomys, Uranomys, Lophuromys,* and the Murinae prove to be convergent, then our molecular results illustrate the possibility that these identical apomorphies (previously thought to define exclusively the Murinae) evolved in parallel from similar or different precursors.

Although chromosomal (16), biochemical (15), and morphological investigations (for reviews, see refs. 1 and 42) examined these taxa, no other synapomorphy unites the monophyletic group of the spiny mice and its sister genera with the Gerbillinae. Our DNA·DNA hybridization results will, therefore, have to be tested by other molecular methods. If other studies of fossil and living muroid rodents find shared molecular and morphological traits that join the Gerbillinae and the spiny mice (and its sister genera), they will confirm our hypothesis.

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