Molecular phylogeny of the sciurognath rodent families Gliridae, Anomaluridae and Pedetidae

Morphological and paleontological implications.

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Introduction

Tullberg's classification (1899) of rodents was based on the angle of the lower jaw and included two suborders: Sciurognathi and Hystricognathi. Since that time, the monophyly of Hystricognathi, which includes 18 Recent families (WILSON and REEDER, 1993), has received increasing support from palaeontological data (LUCKETT and HARTENBERGER, 1985; JAEGER, 1988; WYSS *et al.*, 1993; HARTENBERGER, 1998), anatomical (LAVOCAT and PARENT, 1985; BUGGE, 1985; LUCKETT, 1985; WOOD, 1985), and molecular (CATZEFLIS *et al.*, 1995; NEDBAL *et al.*, 1996; HUCHON *et al.*, 1999, 2000). On the other hand, neither morphological nor molecular data provide support to the Sciurognathi clade and phylogenetic relationships among the diverse "non-Hystricognathi" families are obscure

and hotly debated. The suborder Sciurognathi includes 11 families (WILSON and REEDER, 1993): Aplodontidae, Sciuridae, Castoridae, Geomyidae, Heteromyidae, Dipodidae, Muridae, Anomaluridae, Pedetidae, Ctenodactylidae, and Gliridae. Among them, we focus here on three taxa: Gliridae (dormice), Anomaluridae (scaly-tailed squirrels) and Pedetidae (springhare). Gliridae includes three subfamilies: the Eurasian Leithiinae (four genera) and Glirinae (three genera) and the African Graphiurinae (one genus). Anomaluridae (three genera) and Pedetidae (one genus) are two African families, for which LUCKETT and HARTENBERGER (1985) stated that their affinities "are among the most obscure of all rodents".

We were before all interested to test the morphological and palaeontological hypotheses (VIANEY-LIAUD and JAEGER, 1996) having stated that *Graphiurus*, [which exhibits many peculiar traits relative to other glirids; see BENTZ and MONTGELARD, 1999 for a review] could be more closely related to the African Anomaluridae than to the remaining Gliridae. On the other hand, Anomaluridae is grouped with Pedetidae by some anatomical characters, such as middle-ear features (LAVOCAT and PARENT, 1985) or the carotid arterial pattern (BUGGE, 1985). Conversely, some palaeontological (JAEGER, 1988) and morphological data based on enamel incisor microstructure (MARTIN, 1995) do not corroborate this hypothesis. No molecular study has yet included Anomaluridae and the papers of NEDBAL *et al.* (1996) and MATTHEE and ROBINSON (1997), which include *Pedetes* only, do not identify a possible sister group for this species. In our study, the taxonomic sampling appears relevant to test these various hypotheses and the molecular study is based on two mitochondrial (cytochrome *b* and 12S ribosomal RNA) and one nuclear (LCAT: Lecithin Cholesterol Acyl Transferase) genes.

Molecular analysis

The whole molecular analysis was performed on 18 taxa among which 14 species represent five sciurognath rodent families. The study included six of the eight extant genera of Gliridae: *Dryomys nitedula* and *Eliomys quercinus* for the Leithiinae subfamily; *Glis glis*,

	Genus	Species	Family	Geographic origin	Collector/Donator
T-1787	*Anomalurus*	*sp.*	Anomaluridae	Cameroon: Djoum	J.-C. Gautun (V-804)
T-0768	*Dryomys*	*nitedula*	Gliridae	Georgia: north-west Caucasus	M. Baskevitch (0-22)
T-1110	*Glaucomys*	*volans*	Sciuridae	Audubon Zoo, New Orleans, USA	R.M. Zink & D. Reynolds
T-1715	*Glirulus*	*japonicus*	Gliridae	Japan	H. Suzuki (HS 443)
T-0472	*Graphiurus*	*murinus*	Gliridae	Burundi: Buagaramu	T. Maddalena (IZEA 2702)
T-1728	*Idiurus*	*macrotis*	Anomaluridae	Ivory Coast	M. Colyn (R-24210)
T-1451	*Muscardinus*	*avellanarius*	Gliridae	Switzerland: Lausanne	P. Vogel (IZEA 4927)
T-1701	*Pedetes*	*capensis*	Pedetidae	South Africa: Willem Pretorius Nature Reserve	C. Matthee (DMSO-2)

Table 1
Origin of the animals sequenced for the LCAT gene (EMBL accession numbers AJ401283 to AJ401297)
Tissue numbers (T-) are those from the Collection of Mammalian Tissues of Montpellier. Numbers in parenthesis are specimen's references from collectors or donators.

Muscardinus avellanarius and *Glirulus glirulus* for the Glirinae, and *Graphiurus murinus* for the Graphiurinae. Other sciurognath rodents are represented by two Anomaluridae (*Anomalurus sp.* and *Idiurus macrotis*), one Pedetidae (*Pedetes capensis*), three Muridae (*Mus musculus*, *Rattus norvegicus* and *Spalax ehrenbergi*), and two Sciuridae (*Sciurus aestuans* or *griseus* and *Glaucomys volans*). Two representatives of Hystricognathi (*Cavia porcellus* and *Octodon lunatus* or *O. degus*) were also included and two primates (*Papio anubis* or *P. hamadryas* and *Homo sapiens*) were used as outgroups. Eight new sequences are here presented for the LCAT gene of *Graphiurus*, *Glirulus*, *Muscardinus*, *Dryomys*, *Glaucomys*, *Pedetes*, *Anomalurus* and *Idiurus*, and were deposited at the EMBL database with accession numbers AJ401283 to AJ401297; Table 1 indicates the biological origin for these new data. However, exon 6 (about 500 pb) from *Pedetes* was not successfully amplified. Other LCAT sequences are from ROBINSON *et al.* (1997). References for cytochrome *b* and 12S rRNA sequences can be found in BENTZ and MONTGELARD (1999) and in writing to the senior author.

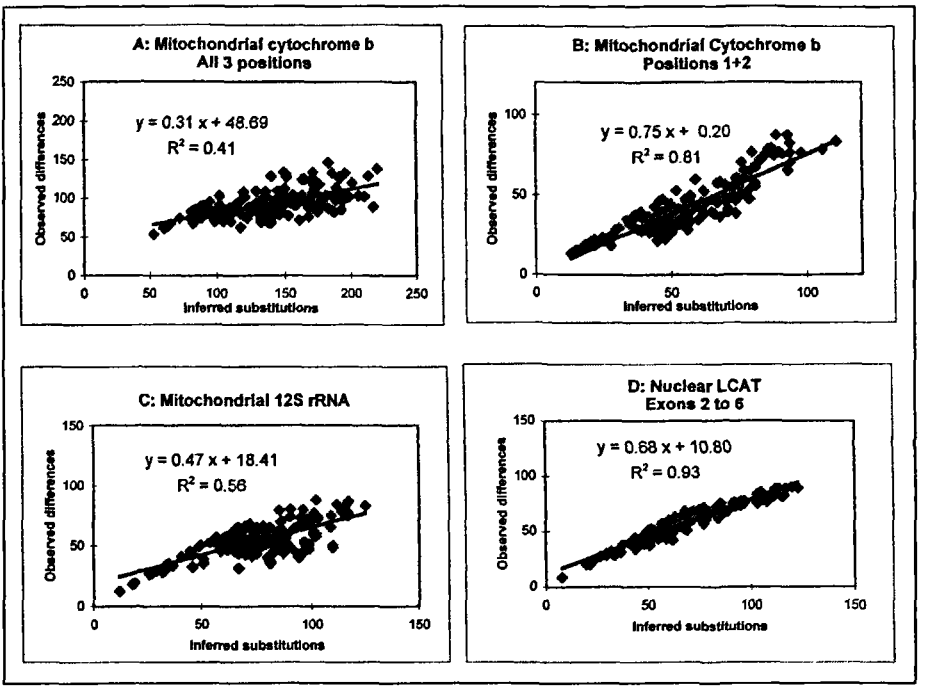
Saturation analysis

Analysis of gene saturation was performed using maximum parsimony reconstruction, according to the procedure of PHILIPPE *et al.* (1994) and HASSANIN *et al.* (1998): the observed differences from pairwise comparisons are plotted against the corresponding number of substitutions inferred from a parsimony analysis. The slope (S) of the linear regression is used to estimate the level of saturation, S decreasing towards zero as the level of saturation increases. Calculations were performed with PAUP 3.1.1 (SWOFFORD, 1993) using the option "patristic distance".

As commonly observed (figure 1), more homoplasy is detected for the cytochrome *b* (A: S = 0.31) than for the 12S rRNA (C: S = 0.47). Saturation in the cytochrome *b* is much reduced when positions 1 and 2 only are considered (B: S = 0.75). Coding sequences of the nuclear gene LCAT (concatenation of exons 2 to 6) appear the least saturated (D:S = 0.68) and also show the least scatter in points (R = 0.93). In order to diminish DNA sequence homoplasy (due to multiple substitutions at the same site), the most saturated sites (position 3 of the cytochrome *b* and LCAT introns) and sites with alignment ambiguities (indels of the 12S rRNA and LCAT introns) were excluded from analyses. The combined analysis was then performed on 2495 sites (1062 Variable and 738 Informative characters) including: (1) 760 positions (272 V, 185 I) for the first and second positions of cytochrome *b*, (2) 875 positions (424 V, 325 I) for the 12S rRNA when indels are omitted, (3) 860 positions (366 V, 228 I) for exons 2 to 6 of LCAT when introns are excluded. Homogeneity between the three partitions was evaluated with PAUP*4.0 (option HOMPART, 1000 replicates) using the test ILD (FARRIS *et al.*, 1995) on variable sites only. This test indicates that there is no statistical incongruence between the three genes ($P = 0.41 > 0.05$).

Phylogenetic results

Phylogenetic reconstructions were performed in Maximum Parsimony (MP) with PAUP 3.1.1 using informative sites equally weighted, and in Maximum Likelihood (ML) using the quartet puzzling approach (PUZZLE 4.0; STRIMMER and VON HAESELER, 1996) with the Tamura-



I Figure 1
Graphic estimation of the level of saturation according to the procedure of HASSANIN et al (1998): pairwise numbers of observed nucleotide differences are plotted against the corresponding number of substitutions inferred from the maximum parsimony tree. Inferred distances were obtained with PAUP using 529 Informative sites for the whole cytochrome *b* (A) and 185 I when position 3 is excluded (B), 325 I for the 12S rRNA (C), and 228 I for LCAT (D). Equation of the linear regression and correlation coefficient are indicated.

Nei model and a gamma distribution with eight categories for substitution rates. In MP, robustness of the nodes was assessed with bootstrap percentages (BP) after 1000 replicates and with the decay index (DI; BREMER, 1988). With ML, robustness was estimated by Reliability Percentages (RP) with 1000 puzzling steps.

Results from the three genes in combination are presented in Figure 2. In parsimony, only one MP tree is recovered (L = 1219, CI = 0.467, RI = 0.473). The sole difference between ML and MP trees concerns

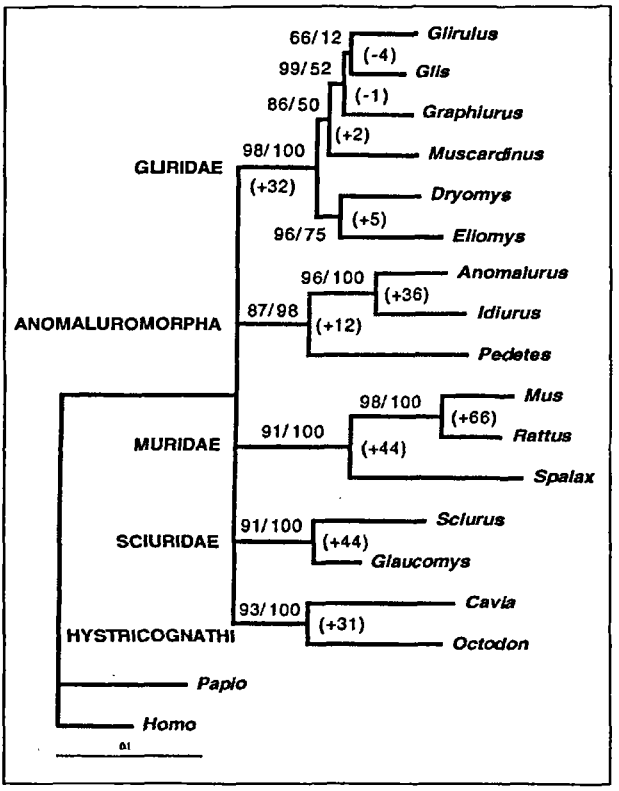


Figure 2
Maximum likelihood quartet puzzling tree from the combined cytochrome *b* (codon positions 1 and 2), 12S rRNA (excluding indels), and LCAT (exons 2 to 6) genes. Numbers above branches refer to reliability percentages (1000 quartet puzzling steps with PUZZLE) in likelihood analysis on the left, and to bootstrap percentages in maximum parsimony (1000 replicates with PAUP) on the right. Decay indexes [numbers of extra steps to break (+) or to build (–) a grouping] are indicated in parentheses.

the branching pattern of *Glis* which clusters with *Muscardinus* in the MP tree, with *Graphiurus* in the bootstrap tree in parsimony (BP = 37%) and with *Glirulus* in the puzzling tree (RP = 66%). Otherwise, the molecular analysis reveals that *Graphiurus* is clearly a member of the Gliridae (98% in ML, 100% in MP, DI = + 32). The monophyly of Leithiinae (here represented by *Dryomys* and *Eliomys*) appears well supported (96%, 75%, + 5), whereas there is no support for the subfamily Glirinae which should have included, according to WAHLERT *et al.* (1993), *Glis*, *Glirulus* and *Muscardinus*. The African *Graphiurus* appears nested among Glirinae, with affinities for the Eurasian *Glirulus* and *Glis* genera. However, these associations are strongly supported in ML (86% and 99%, respectively), but very weakly in MP (50% and 52%). Such a discrepancy between reconstruction methods was already reported by CAO *et al.* (1998) who

mentioned that the quartet puzzling approach can sometimes give reliability values misleadingly high as compared to bootstrap resampling.

The Anomaluridae family, here represented by the two genera *Anomalurus* and *Idiurus*, (the third genus, *Zenkerella*, is lacking) is very well defined (96%, 100%, + 36). The other strong result of this molecular analysis is the robust relationship between the two African Anomaluridae and Pedetidae families (87%, 98%, + 12). This relationship appears equally supported by each gene separately (data not shown): cytochrome *b* (89%, 78%, + 2), 12S rRNA (76%, 59%, + 3) and LCAT (58%, 62%, + 1). In the latter case, the support may be weakened due to the lack of exon 6 for *Pedetes*. In the combined analysis, the association between Anomaluridae and Pedetidae appears almost as strongly supported as are other rodent families, such as Sciuridae, Gliridae or Muridae.

Discussion

About the Gliridae, adding the nuclear LCAT gene allows to corroborate and reinforce previous results obtained with the two mitochondrial genes only (BENTZ and MONTGELARD, 1999). That is, the combined analysis confirms that *Graphiurus* belongs to the Gliridae family and strengthens the monophyly of the Leithiinae clade (*Dryomys* and *Eliomys* in this study). *Graphiurus* appears nested among Glirinae but the association *Glis-Graphiurus-Glirulus* is supported only in ML (99%). Thus, the systematic position of *Graphiurus* among Glirinae does not appear fully resolved, suggesting a possible multi-lineages radiation within this subfamily. This result should be validated by including additional *Graphiurus* representatives as only one species is considered here out of the 14 recognized in WILSON and REEDER (1993).

The position of *Graphiurus* among Gliridae contrasts with the palaeontological hypothesis of a *Graphiurus*-Anomaluridae relationship (VIANEY-LIAUD and JAEGER, 1996). Moreover, the molecular analysis reveals a close relatedness between the two African Anomaluridae and Pedetidae families. These two lineages thus appear as a natural

clade among sciurognath rodents, and are included in the suborder Anomaluromorpha. This clade was defined 25 years ago by BUGGE (1974) on the basis of the carotid arterial pattern and is also supported by middle-ear features (PARENT, 1980; LAVOCAT and PARENT, 1985). This relationship remains at odds with some palaeontological data (FLYNN *et al.*, 1986; JAEGER, 1988) as well as with conclusions derived from the study of incisor enamel microstructure, which clusters Pedetidae among a clade including Hystricognathi as well as Recent and fossil Ctenodactyloidea (MARTIN, 1995). However, Ctenodactylidae were proposed as a possible sister group to Hystricognathi by several morphological and palaeontological studies (LUCKETT and HARTENBERGER, 1985; BRYANT and MCKENNA, 1995). Such a hypothesis was recently corroborated by molecular data (HUCHON *et al.*, 2000) on the basis of nuclear vWF sequences, defining the clade Ctenohystrica. In this study, the clusterings of Pedetidae as sister group to Hystricognathi or Ctenodactylidae are statistically rejected. Thus, although our own study does not include ctenodactylid representatives, the possibility of a Ctenodactylidae-Pedetidae relationships remains unlikely. The two points of discordance (palaeontological data and enamel microstructure) raised by the association between Pedetidae and Anomaluridae are developed in the following discussion.

Palaeontological data

If the present African distribution of Pedetidae (southern Africa) and Anomaluridae (western and central Africa) appears consistent with their close relationships, a rather different picture emerges when palaeontological data only are considered.

The Anomaluridae lineage can be traced back until the late Eocene (42 Myr) in Algeria where *Nementchamys lavocati* is described as the oldest known fossil of Anomaluridae (JAEGER *et al.*, 1985). More recent anomalurid fossils were attributed to the genera *Paranomalurus, Anomalurus,* and *Zenkerella* in early and middle Miocene (13-20 Myr) deposits from Kenya (DENYS and JAEGER, 1992; WINKLER, 1992; LAVOCAT, 1973). Moreover, the fossil family Zegdoumyidae described from the late early Eocene (45-50 Myr) of Tunisia and Algeria, was considered as the ancestral stock of the Anomaluridae

(VIANEY-LIAUD *et al.*, 1994). So, until now, the fossil history of the anomalurid lineage is restricted to Africa.

Concerning Pedetidae, the fossil record is sparse and represented in Africa by *Megapedetes pentadactylus* (MACINNES, 1957) from Kenya and *Parapedetes namaquensis* from Namibia (STROMER, 1926), both from the early Miocene (20 Myr). Besides Africa, *Megapedetes aegaeus* (SEN, 1977) is described from the Middle Miocene (12-13 Myr) of Western Anatolia (Turkey). *Diatomys* found in middle Miocene (18-19 Myr) of China (LI, 1974) and Thailand (MEIN and GINSBURG, 1985) has been proposed as a possible ancestor for *Pedetes*, thus suggesting an Asiatic origin for Pedetidae. However, this hypothesis was recently challenged (MEIN and GINSBURG, 1997) because new fossils of *Diatomys* found in Thailand do not present the jumping adaptation which was already achieved in Pedetidae from the lower Miocene. A plausible ancestor for *Diatomys* is represented by the ctenodactyloid genus *Fallomus* from the Miocene of Baluchistan (FLYNN *et al.*, 1986; MEIN and GINSBURG, 1997), but the relationship between the Asiatic *Fallomus-Diatomys* and the African *Parapedetes*-Pedetidae lineages remains to substantiate. Therefore, the pre-Miocene (beyond 20 Myr) fossil history and the origin of Pedetidae stays unknown (HARTENBERGER, 1998).

Finally, a close relationship between pedetids and anomalurids appears not congruent with palaeontological data mainly because of the gap between the record of fossil Pedetidae (not older than 20 Myr) and the long history of the Anomaluridae lineage (42 Myr). Thus, a common ancestor to Anomaluromorpha would have to be searched in the early Tertiary, possibly from ischyromyoids (BUGGE, 1974), an early Eocene fossil family from which several sciurognath rodents could be issued.

As our molecular data do not evidence a rate constancy among the different lineages (data available upon request), we refrain from applying the molecular clock concept. Thus, no attempt of dating the different molecular dichotomies was done, pending a better sampling of sciurognath and hystricognath families for applying various local molecular clocks.

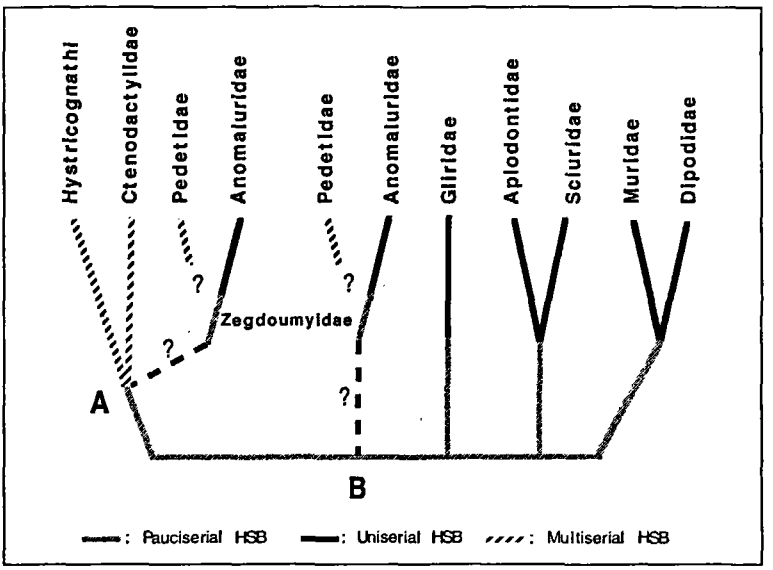
Implications for the microstructure of incisor enamel

In rodents, three basic types of incisor enamel microstructure (Hunter-Schreger Bands = HSB) are described and used as a phylogenetic tool at the familial or suprafamilial levels (review in MARTIN, 1997). The first type, called pauciserial, characterizes the most primitive rodents and represents the ancestral condition for the Rodentia (see figure 3). The two other types, uniserial and multi-serial HSB, are derived states. Recent Ctenodactylidae, Hystricognathi and Pedetidae show the multi-serial condition which was therefore considered as a synapomorphy for this group (MARTIN, 1997). The uniserial condition characterizes all other sciurognath lineages and this state is thought to have evolved several times independently in some rodent lineages derived from the extinct Ischyromyoidea (MARTIN, 1993).

If, as suggested by molecular data and some morphological characters, Pedetidae and Anomaluridae are related, how then to interpret the multi-serial condition of Pedetidae as opposed to the uniserial type of Anomaluridae? Two hypotheses can be advanced:

– Hypothesis A in Figure 3: As stated by MARTIN (1995), the multi-serial condition is a synapomorphy of Ctenodactylidae, Hystricognathi and Pedetidae, inherited from Paleogene ctenodactyloid ancestors. Under this hypothesis, the uniserial condition of Anomaluridae could have evolved from the pedetid multi-serial condition. However, according to MARTIN (1995, p. 696), "there is no way that uniserial HSB can evolve from the derived multi-serial condition". Moreover, Zegdoumyidae, considered as the ancestral stock of anomalurids, show HSB that are transitional from the ancestral pauciserial to the derived uniserial condition (MARTIN, 1993). This hypothesis is clearly not consistent with the Pedetidae-Anomaluridae relationships because at the present time no palaeontological data supports the assumption of any ctenodactyloid origin for the anomalurid lineage.

– Hypothesis B in Figure 3: The multi-serial condition in Pedetidae has been achieved convergently with that of Ctenodactylidae and Hystricognathi. As convergent evolution has been described for the uniserial HSB, we may assume that the multi-serial condition also appeared independently in two lineages. Recently, MARTIN (1999) found that several representatives of the Paleogene fossil family



I Figure 3
Evolution of incisor enamel microstructure: two hypotheses (A and B, see text) to interpret, on the basis of a Pedetidae-Anomaluridae relationship, the uniserial condition (in black) of Anomaluridae, and the multi-serial HSB (hachured) of Pedetidae. Incisor enamel data are from MARTIN (1993), and phylogenetic relationships are from LUCKETT and HARTENBERGER (1985) and VIANEY-LIAUD *et al.* (1994) for the fossil family Zegdoumyidae.

Theridomyidae were characterized by a pseudo-multiserial HSB. If this condition does not indicate a close phylogenetic relationships with Ctenodactylidae or hystricognath rodents (MARTIN, 1999), it nevertheless suggests that parallel evolution does exist for the multi-serial state. Under the assumption of independent origin, multi-serial HSB can then be considered as homologous in the clade Hystricognathi-Ctenodactylidae, but not for the Pedetidae lineage. Consequently, Pedetidae inherited their multi-serial HSB from ancestors which are presently unknown because even the possible relative genera *Fallomus* and *Diatomys* already present the mutiserial state (FLYNN *et al.*, 1986; MARTIN, 1995).

In conclusion, the molecular analyses performed on three genes (two mitochondrial and one nuclear markers) provide strong support for

the inclusion of *Graphiurus* in the Gliridae family, and for the clade Anomaluromorpha uniting the two African families Anomaluridae and Pedetidae. This relationship clearly contradicts the hypothesis of a unique appearance of the multi-serial state of incisor enamel microstructure but does not appear really in conflict with palaeontological interpretations because of the lack of fossil data for Pedetidae. It is clear that the acquisition of more molecular data (other genes and all sciurognath lineages) as well as the finding of fossils documenting the ancestral lineage for Pedetidae will greatly improve our understanding of the relationships between Anomaluridae and Pedetidae.

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References

BENTZ S., MONTGELARD C., 1999 — Systematic position of the African dormouse *Graphiurus* (Rodentia, Gliridae) assessed from cytochrome *b* and 12S rRNA mitochondrial genes. *Journal of Mammalian Evolution*, 6: 67-83.

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

BUGGE J., 1974 — The cephalic arterial system in insectivores, primates, rodents and lagomorphs, with special reference to the systematic classification. *Acta Anatomica*, 87 (Suppl. 62): 1-160.

BUGGE J., 1985 — "Systematic value of the carotid arterial pattern in rodents". *In* LUCKETT W.P., HARTENBERGER J.-L. (eds.) : *Evolutionary relationships among rodents: a multidisciplinary analysis*, New York,Plenum Press : 355-379.

CAO Y., ADACHI J. and HASEGAWA M., 1998 — Comment on the quartet puzzling method for finding maximum-

likelihood tree topologies. *Molecular Biology and Evolution,* 15: 87-89.

CATZEFLIS F. M., HÄNNI C., SOURROUILLE P. and DOUZERY E., 1995 — Molecular systematics of hystricognath rodents: the contribution of sciurognath mitochondrial 12S rRNA sequences. *Molecular Phylogenetics and Evolution,* 4: 357-360.

DENYS C. and JAEGER J.-J., 1992 — Rodents of the Miocene site of Fort Ternan (Kenya). I: Phiomyids, Bathyergids, Sciurids and Anomalurids. *Neues Jahrbuch für Geologie und Palãontologie, Abhandlungen,* 185: 63-84.

FARRIS J. S., KÄLLERSJÖ M., KLUGE A. G. and BULT C., 1995 — Testing significance of incongruence. *Cladistics,* 10: 315-319.

FLYNN L. J., JACOBS L. L. and CHEEMA I. U., 1986 — Baluchimyinae, a new ctenodactyloid rodent subfamily from the Miocene of Baluchistan. *American Museum Novitates,* 2841: 1-58.

HARTENBERGER J.-L., 1998 — Description de la radiation des Rodentia (Mammalia) du Paléocène supérieur au Miocène; incidences phylogénétiques. *Comptes rendus de l'Académie des Sciences, Paris,* 326: 439-444.

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,* 321: 611-620.

HUCHON D., CATZEFLIS F. M. and DOUZERY E. J. P., 1999 — Molecular evolution of the nuclear von Willebrand factor gene in mammals and the phylogeny of rodents. *Molecular Biology and Evolution,* 16: 577-589.

HUCHON D., CATZEFLIS F. M. and DOUZERY E. J. P., 2000 — Variance of molecular datings, evolution of rodents and the phylogenetic affinities between Ctenodactylidae and Hystricognathi. *Proceedings of the Royal Society of London B,* 267: 393-402.

JAEGER J.-J., 1988 — "Rodent phylogeny : new data and old problems". *In* BENTON M. J. (ed.) : *The phylogeny and classification of the tetrapods,* Oxford, Clarendon Press: 177-199.

JAEGER J.-J., DENYS C. and COIFFAIT B., 1985 — "New Phiomorpha and Anomaluridae from the Late Eocene of North-West Africa: phylogenetic implications". *In* LUCKETT W.P., HARTENBERGER J.-L. (eds.) : *Evolutionary relationships among rodents: a multidisciplinary analysis,* New-York, Plenum Press: 567-588.

LAVOCAT R., 1973 — *Les Rongeurs du Miocène d'Afrique Orientale. I. Miocène Inférieur.* Montpellier, École pratique des hautes études, 284 p.

LAVOCAT R. and PARENT J.-P., 1985 — "Phylogenetic analysis of middle ear features in fossil and living rodents". *In* LUCKETT W.P., HARTENBERGER J.-L. (eds.) : *Evolutionary relationships among rodents: a multidisciplinary analysis,* New York, Plenum Press : 333-354.

LI C. K., 1974 — A probable geomyoid rodent from the middle Miocene of Linchu, Shantung. *Vertebrata PalAsiatica,* 12: 43-53.

LUCKETT W. P., 1985 — « Superordinal and intraordinal affinities of rodents: developemental evidence from the dentition and placentation ». *In* LUCKETT W.P., HARTENBERGER J.-L. (eds.) : *Evolutionary relationships among rodents: a multidisciplinary analysis*, New York, Plenum Press : 227-276.

LUCKETT W. P. and HARTENBERGER J.-L., 1985 — « Evolutionary relationships among rodents: comments and conclusions ». *In* LUCKETT W.P., HARTENBERGER J.-L. (eds.) : *Evolutionary relationships among rodents: a multidisciplinary analysis*, New York, Plenum Press : 685-712.

MACINNES D. G., 1957 — A new Miocene rodent from East Africa. *British Museum (Natural History) Publications*, 12: 1-36.

MARTIN T., 1993 — Early rodent incisor enamel evolution: phylogenetic implications. *Journal of Mammalian Evolution*, 1: 227-254.

MARTIN T., 1995 — Incisor enamel microstructure and phylogenetic interrelationships of Pedetidae and Ctenodactyloidea (Rodentia). *Berliner Geowissenschaftliche Abhandlungen*, 16: 693-707.

MARTIN T., 1997 — "Incisor enamel microstructure and systematics in rodents". *In* KOENISGSWALD W.V., SANDER P.M. (eds.) : *Tooth enamel microstructure*, Rotterdam, Balkema : 163-175.

MARTIN T., 1999 — Evolution of incisor enamel microstructure in Theridomyidae (Rodentia). *Journal of Vertebrate Paleontology*, 19:550-565.

MATTHEE C. A. and ROBINSON T. J., 1997 — Molecular phylogeny of the springhare, *Pedetes capensis*, based on mitochondrial DNA sequences. *Molecular Biology and Evolution*, 14: 20-29.

MEIN P. and GINSBURG L., 1985 — Les rongeurs Miocène de Li (Thaïlande). *Comptes rendus de l'Académie des Sciences, Paris*, 301: 1369-1374.

MEIN P. and GINSBURG L., 1997 — Les mammifères du gisement Miocène inférieur de Li Mae Long, Thaïlande: systématique, biostratigraphie et paléoenvironnement. *Geodiversitas*, 19: 783-844.

NEDBAL M. A., HONEYCUTT R. L. and SCHLITTER D. A., 1996 — Higher-level systematics of rodents (Mammalia, Rodentia) : Evidence from the mitochondrial 12S rRNA gene. *Journal of Mammalian Evolution*, 3: 201-237.

PARENT J.-P., 1980 — *Recherche sur l'oreille moyenne des rongeurs actuels et fossiles : Anatomie, valeur systématique.* Thèse de l'université des Sciences et Techniques du Languedoc, Montpellier, 286 p.

PHILIPPE H., SÔRHANNUS U., BAROIN A., PERASSO R., GASSE F. and ADOUTTE A., 1994 — Comparison of molecular and paleontological data in diatoms suggests a major gap in the fossil record. *Journal of Evolutionary Biology*, 7: 247-265.

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

SEN S., 1977 — *Megapedetes aegaeus* n. sp. (Pedetidae) et à propos d'autres "rongeurs africains" dans le Miocène d'Anatolie. *Geobios,* 10: 983-986.

STRIMMER K. and VON HAESELER A., 1996 — Quartet Puzzling: A quartet Maximum-Likelihood method for reconstructing tree topologies. *Molecular Biology and Evolution,* 13: 964-969.

STROMER E., 1926 — "Reste Land- und Süsswasser-bewohnender Wirbeltiere aus den Diamantenfeldern Deutsch-Südwestafrikas". *In* KAISER E. (ed.) : *Die Diamantenwüste Südwest-Afrikas,* Berlin, Reimer D. : 107-153.

SWOFFORD D. L., 1993 — *PAUP 3.1.1: Phylogenetic analysis using parsimony, version 3.1.1.* Computer program distributed by the Illinois Natural History Survey, Champain.

TULLBERG T., 1899 — Über das System der Nagetiere: eine phylogenetische Studie. *Nova Acta Regiae Societatis Scientiarum Uppsaliensis, Uppsala,* 18: 1-514.

VIANEY-LIAUD M., JAEGER J.-J., HARTENBERGER J.-L. and MAHBOUBI M., 1994 — Les rongeurs de l'Eocène d'Afrique Nord-Occidentale (Glib Zegdou (Algérie) et Chambi (Tunisie)) et l'origine des Anomaluridae. *Palaeovertebrata,* 23: 93-118.

VIANEY-LIAUD M. and JAEGER J.-J., 1996 — A new hypothesis for the origin of African Anomaluridae and Graphiuridae (Rodentia). *Palaeovertebrata,* 25: 349-358.

WAHLERT J. H., SAWITZKE S. L. and HOLDEN M. E., 1993 — Cranial anatomy and relationships of dormice (Rodentia, Myoxidae). *American Museum Novitates,* 3061: 1-32.

WILSON D. E. and REEDER D. M. (eds.), 1993 — *Mammal species of the world: a taxonomic and geographic reference.* Washington and London, Smithsonian Institution Press, 1207 p.

WINKLER A. J., 1992 — Systematics and biogeography of middle Miocene rodents from the Muruyur beds, Baringo district, Kenya. *Journal of Vertebrate Paleontology,* 12: 236-249.

WOOD A. E., 1985 — "The relationships, origin and dispersal of the hystricognathous rodents". *In* LUCKETT W. P., HARTENBERGER J.-L. (eds.) : *Evolutionary relationships among rodents: a multidisciplinary analysis,* New York, Plenum Press : 475-513

WYSS A. R., FLYNN J. J., NORELL M. A., SWISHER C. C., CHARRIER R., NOVACEK M. J. and MCKENNA M. C., 1993 — South America's earliest rodent and recognition of a new interval of mammalian evolution. *Nature,* 365: 434-437.