

Molecular phylogeny of the

and Pedetidae

and hotly debated. The suborder Sciurognathi includes 11 families (WILSON and REEDER, 1993): Aplodontidae, Sciuridae, Castoridae, Geomyidae, Heteromyidae, Dipodidae, Muridae, Anomaluridae, Pedetidae, Gliridae and Caviidae. Anomaluridae, Geomyidae, Heteromyidae, Muridae, and Pedetidae are African families, while the remaining six are Eurasian or Palearctic. The suborder Sciurognathi is the most diverse of the three suborders, with 11 families and 1,100 genera (WILSON and REEDER, 1993).

here on three taxa: Gliridae (dormice), Anomaluridae (scaly-tailed squirrels) and Pedetidae (springhare). Gliridae includes three sub-families: 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 (JAEGER and BENTZ, 1995) and the ossified stapes (BENTZ

	Genus	Species	Family	Geographic origin	Collector/Donator
T-1787	<i>Anomalurus</i>	<i>sp.</i>	Anomaluridae	Cameroon: Djoum	J.-C. Gautun (V-804)
T-0768	<i>Dryomys</i>	<i>nitedula</i>	Gliridae	Georgia: north-west Caucasus	M. Baskevitch (0-22)
T-1110	<i>Glaucomys</i>	<i>volans</i>	Sciuridae	Audubon Zoo, New Orleans, USA	R.M. Zink & D. Reynolds

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.

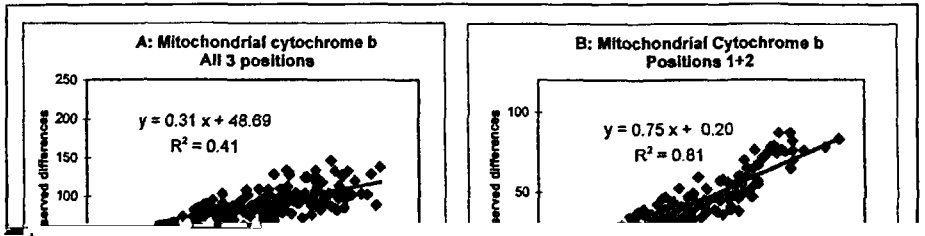
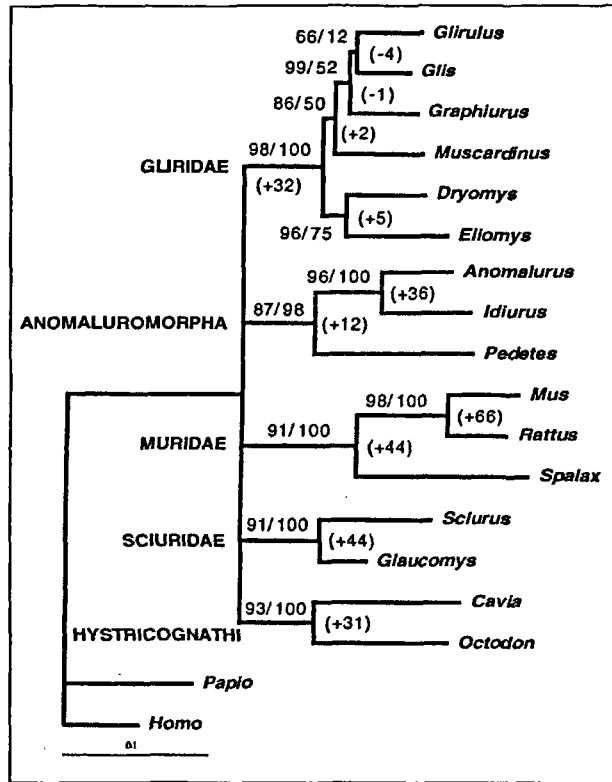


Figure 2
Maximum likelihood quartet puzzling tree from the combined cytochrome *b* (codon positions 1 and 2), 12S rRNA (excluding indels), and LCAT (exons 2 to 6) genes. Numbers above branches refer to reliability percentages (1000 quartet puzzling steps with PUZZLE) in likelihood analysis on the left, 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 *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 reli-

ability 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, suggest-

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 Zegdomyidae described from the late early Eocene (45-50 Myr) of Tunisia and Algeria, was considered as the ancestral stock of the Anomaluridae

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

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, *Pedetidae* is considered as the ancestral state of *Anomaluridae*.

show HSB that are transitional from the ancestral pauciserial to the derived uniserial condition (MARTIN, 1993). This hypothesis is clearly

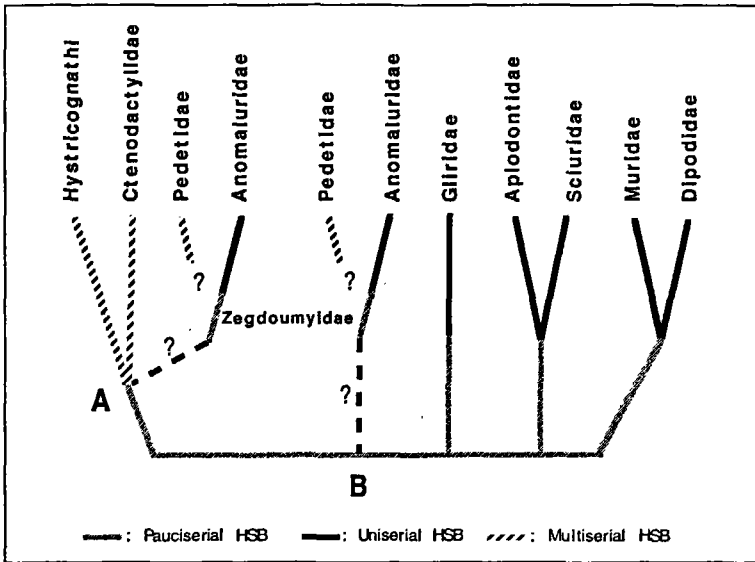


Figure 3

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 Zegdomyidae.

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 *Fallomys* 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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