A NEW HYPOTHESIS FOR THE ORIGIN OF AFRICAN ANOMALURIDAE AND GRAPHIURIDAE (RODENTIA)

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ABSTRACT

A new hypothesis for the phylogenetic relationships of Recent anomalurids and graphiurids is proposed, based on information from evolutionary lineages of Paleogene European rodents, particularly Gliridae, and Eocene Algerian Zegdoumyidae. Differences in first occurrences, in paleogeography, and in infraorbital structure in glirids (protrogomorphy and pseudomyomorphy) and graphiurids (hystricomorphy) separate Graphiuridae from Gliridae (Graphiurinae is here raised to family rank). Similar considerations, and dental morphology, suggest that Anomaluridae (appearing in the late Eocene) and Graphiuridae (appearing in the Pliocene) are related to early Eocene Zegdoumyidae.

RESUME

Une nouvelle hypothèse sur les relations phylogénétiques entre les rongeurs africains graphiures et anomalures est proposée. Elles reposent sur les données issues de l'étude des lignées évolutives de rongeurs paléogènes européens, Gliridae en particulier, ainsi que sur celles fournies par les rongeurs Zegdoumyidae de l'Eocène d'Algérie. Les Graphiuridae sont exclus de la famille des Gliridae, sur la base de l'analyse de leur région infra-orbitaire (protrogomorphie et pseudo-myomorphie des Gliridae, et hystricomorphie des Graphiuridae), ainsi que d'après les données relatives à leur distribution géographique au moment de leur première apparition. Ces mêmes éléments, auxquels s'ajoutent les caractères dentaires, permettent de mettre en évidence des relations de parenté entre Anomaluridae et Graphiuridae, qui semblent partager un ancêtre commun au sein des Zegdoumyidae.

INTRODUCTION

New information and a reappraisal of older facts has led us to formulate a new hypothesis concerning the phylogenetic relationships of three rodent groups: Gliridae are European, while Graphiurinae and Anomaluridae (scaly-tailed rodents) are African in present-day distribution. The new information is provided by a detailed fossil record: that of Gliridae is one of the most complete known, and many evolutionary lineages have been identified and studied (Vianey-Liaud 1989, 1994). Our new hypothesis relies on two sources of evidence. The first consists of evidence provided by European Paleogene rodents, which suggests that Gliridae are rooted in Microparamyinae (Hartenberger 1971) and that myomorphy has been achieved convergently by glirids and muroids — the earliest glirids (Gliridae) being protrogomorphous (Vianey-Liaud 1974a, 1985, 1989, 1994) and the earliest muroids (Cricetidae) hystricomorphous (Vianey-Liaud 1974b, Wang & Dawson 1994). The second source of evidence is based on the study of recently-discovered Eocene rodents from Algeria and their assignment to a new family, Zegdoumyidae, which has been recognized as the ancestral group for the Anomaluridae (Vianey-Liaud *et al.* 1994).

ORIGIN AND RELATIONSHIPS OF GLIRIDAE : THE QUESTION OF GRAPHIURS

Gliroidea (= Myoxoidea) are mainly Palearctic rodents, including representatives from northern and tropical Africa. The subfamily Graphiurinae, that we presently propose to remove from Gliroidea, is found exclusively in sub-Saharan Africa. Gliridae have often been considered closely related to Muroidea on the basis of their myomorphy. The glirid dental formula is I^1/I_1, P^{3-4}/P_4, M^{1-3}/M_{1-3}. The teeth are brachydont and lophodont, with crests more or less numerous. The hypocone is weakly developed in the earliest forms.

Although the Recent Eurasiatic and North African glirids are myomorphous, the African Graphiurinae are hystricomorphous, without any indication of a distinct anterior head of the masseter lateralis. On the basis of their hystricomorphy, Miller and Gidley (1918) placed them within the Dipodoidea. Ellerman (1940), following Winge (1924) and Weber (1928), and taking into account the alleged similarities of their dental pattern with that of *Eliomys*, put them into the Gliridae. The rather reduced P4, the lack of a well developed hypocone, and the lophodonty of the graphiurines is found in all the glirids, not only in *Eliomys*. However, the type of complexity of the ridges in some species, related to the development of surrounding walls, is an apomorphic graphiurine character that is not observed in either the Recent glirids, nor among the numerous European Paleogene rodents (Hartenberger 1971, 1994, Vianey-Liaud 1974a, 1989, 1994), with the exception of anomalurids (Fig. 1 and Fig. 2). On the basis of their supposed similarities of dental pattern, Ellerman (1940) suggested that the hystricomorphy of the graphiurines was the primitive condition for glirids, i.e., that the masseter medialis first lengthened anteriorly, before lengthening of the masseter lateralis and compression of the infraorbital foramen. Skull remains of the oldest fossil glirids do not corroborate Ellerman's hypothesis.

Hartenberger (1971) described the oldest known glirids, *Eogliravus wildi* from the latest early Eocene of Europe, and *Eogliravus hammeli* from the middle Eocene of Europe. On the basis of tooth pattern, he considered these earliest Gliridae to be derived from the ischyromyid genus *Microparamys*, which is known both in Europe and North America. At least ten glirid lineages have since been identified in the European Eocene (Vianey-Liaud 1994). The size of teeth and the dental pattern as well as infraorbital structures show a great diversity by the late Eocene, suggesting an earlier radiation. The genera *Gliravus* and *Bransatoglis* are protrogomorphous. While the anterior root of the zygomatic arch is horizontal in *Gliravus*, it is tilted slightly upwards in *Bransatoglis*. Another genus, *Glamys*, is sciuromorphous, with a rather small infraorbital foramen, compressed by the anterior lengthening of the masseter lateralis. In addition to this compression, the skull of the early Miocene *Vasseuromys* shows enlargement of the infraorbital foramen, as found in Recent glirids. Cranial morphology of these early glirids indicates that the myomorphy of Recent Gliridae is derived from a protrogomorphous ancestral condition, without any hystricomorphous transition (Vianey-Liaud 1974a, 1985, 1989a, 1994).

Thus, the myomorphy of the modern glirids seems to have a different origin from that observed in muroids. It has been called pseudomyomorphy (Vianey-Liaud 1985) in

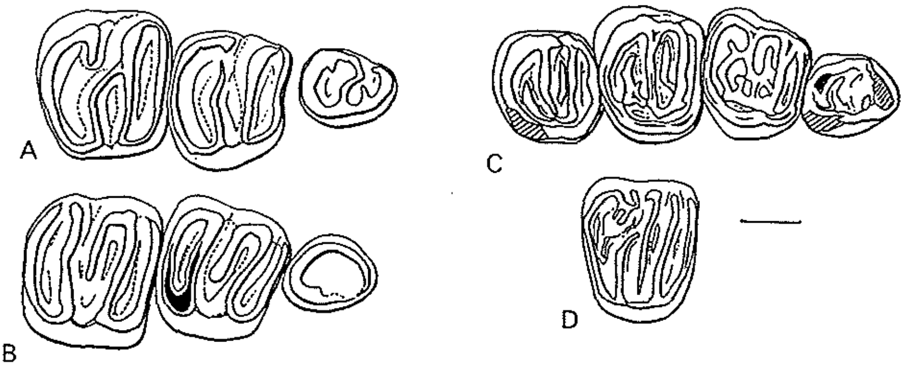

Figure 1.— Dental patterns of Recent Graphiuridae. *Graphiurus crassicaudatus* (MNHN 1992-111, Paris): A, RDP^4–M^2; B, LDP$_4$–M$_2$. *Graphiurus murinus* (MNHN 1992-97, Paris): C, LP$_4$–M$_3$; D, RM^2. The scale represents 1 mm.

contrast to the true myomorphy of muroids ("true" because the term was defined based on murids).

Among the oldest muroids, early Oligocene cricetids like *Eucricetodon atavus*, *Pseudocricetodon*, and *Cricetops* are hystricomorphous (Vianey-Liaud 1974b). The oldest known cricetid, belonging to the genus *Pappocricetodon* recently described by Wang and Dawson (1994) from a middle Eocene fissure filling in southern China, is clearly hystricomorphous. On the basis of known information from China and North America, the authors concluded that Cricetidae are the sister group of protrogomorphous Sciuravidae, both evolving from primitive Ischyromyidae.

Wahlert *et al.* (1993) have challenged the phylogenetic relationships for glirids described above. Wahlert *et al.* concluded that "*Graphiurus* retains the condition of hystricomorphy," in other words, they considered that hystricomorphy is the primitive condition for glirids, which is, however, refuted by the fossil record. A PAUP analysis performed on 43 cranial and 11 dental characters led them to consider that Myoxoidea (= Gliroidea) are both monophyletic and include Graphiurinae, Leithiinae, and Myoxinae. Graphiurinae were considered to be the sister group of other Gliroidea. Moreover, Wahlert *et al.* concluded that there are close relationships between Muroidea and Gliroidea.

The analysis of Hartenberger (1985), mainly on dental features (20), with some cranial characteristics (4), led to a different conclusion. Hartenberger concluded that Gliroidea are close to Reithroparamyinae, near Sciuridae, and clearly distinct from Muroidea. Bugge (1985) emphasized differences in the cephalic arterial supply between Gliridae and typical Muroidea. Like Lavocat and Parent (1985), he drew attention to similarities between glirids and sciurids in middle ear anatomy. On the basis of the ear, Meng (1990) suggested close relationships between Gliridae, Sciuridae, Aplodontidae, and Reithroparamyinae.

It appears that varying use of cranial, auditory, or dental characteristics by the different authors leads to different phylogenetic trees. Recognition of polarities seems

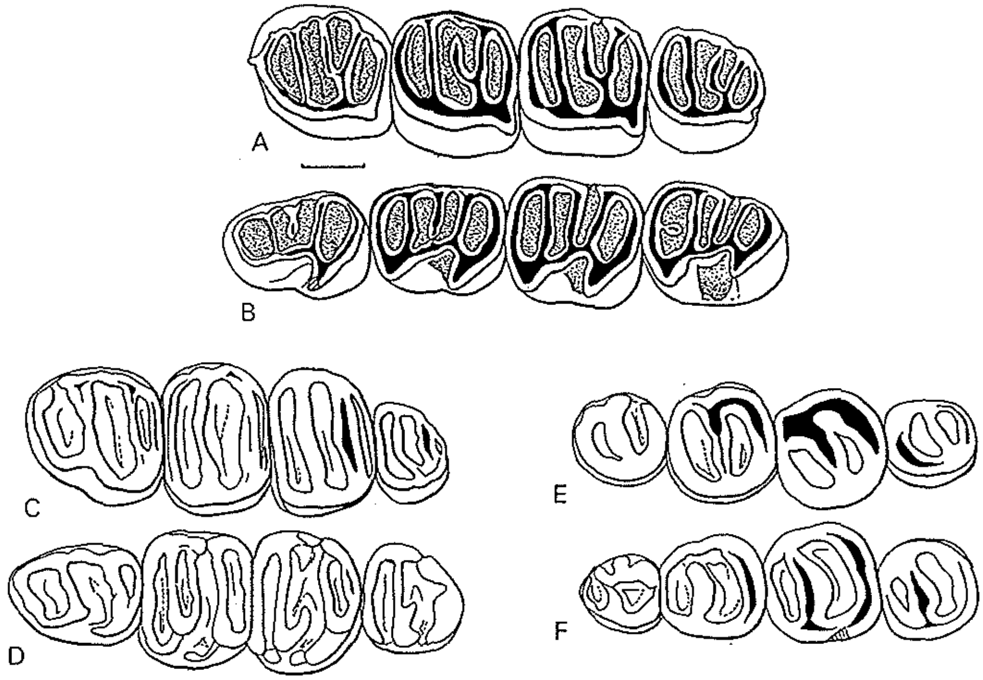

Figure 2.— Dental patterns of Recent Anomaluridae. *Anomalurus peli* (MNHN 1984-1160, Paris): **A**, LP^4–M^3; **B**, LP$_4$–M$_3$. *Idiurus macrotis* (MNHN 1985-220, Paris): C, LP^4–M^3; **D**, LP$_4$–M$_3$. *Zenkerella* sp.(MNHN 1984-1160, Paris): **E**, LP^4–M^3; **F**, LP$_4$–M$_3$. The scale represents 1 mm.

difficult, and varies among authors.

As seen above, first, the hystricomorphy of Graphiurinae is not the primitive condition for Gliridae; second, the oldest evidence supports independent origins for the myomorphy of Recent Gliroidea and Muroidea. Graphiurines cannot be considered as primitive glirids on the basis of their hystricomorphy. If graphiurines are really members of Gliridae, their hystricomorphy should be derived from the protrogomorphy of some Eurasiatic Paleogene glirids. If this is the case, when did dispersal from Europe to Africa take place? One problem in answering this question is the scarcity of graphiurines in the fossil record. The glirid *Graphiurops* was described by Bachmayer and Wilson (1978, 1980) from the upper Miocene of Kohfidisch (Austria). Because of the simple dental pattern of the lower molars (the only known teeth), these authors emphasized their resemblance to graphiurids. After comparisons with some species of *Graphiurus*, and particularly with *Graphiurus murinus*, Bachmayer and Wilson noted that "the shape of the lower molars are much more typically glirid than in the African genus," because of the conspicuously high metalophid. The dental pattern of *Graphiurops* is very close to that of the small European upper Eocene glirid *Tenuiglis* (Vianey-Liaud 1994). This simplified pattern occurs sometimes among glirids, but in those cases the transverse inner crests are always as high as the outer ones (antero- and posterolophids). In graphiurines, the crests running inside the basins are much lower than the border crests.

The earliest known typical graphiurines are from the South African Pliocene (Pocock 1976). Denys (1987) has figured a single tooth from the early Pleistocene of west Natron (East Africa). Graphiurines are not reported from the well sampled early Miocene faunas described by Lavocat (1973). The first North African glirids, supposed to be derived from European genera, are not recorded before the early middle Miocene (Lavocat 1973, Jaeger 1977). Moreover, even if the localities are presently not numerous, there are neither glirids nor graphiurines in the Paleogene rodent faunas from North Africa and Oman (Thomas *et al.* 1992). To date, nothing in the fossil record can therefore support a glirid origin for the graphiurines.

For these reasons, and because of their distinctive morphological and biogeographical characteristics, it is better to raise the taxon to family level as Graphiuridae. Some diagnosic cranial and dental characters of this family compared to those of Gliridae are summarized below.

DIAGNOSIS OF SUBSAHARAN AFRICAN GRAPHIURIDAE BASED ON CRANIAL AND DENTAL CHARACTERISTICS

Hystricomorphous; no separate tubercle or area for the origin of masseter lateralis superficialis; sciurognathous; P3 absent; DP4 and P4 reduced; upper and lower M3 smaller than M1–2 and larger than P4; brachydont lophate teeth; surrounding crests higher than the central crests (lophs, lophids and accessory crest); central crests very low; basined lower molars without mesoconid; protocone sometimes clearly separated from the hypocone and sometimes connected; hypocone poorly developed; protoloph connected to the protocone and metaloph (without metaconule) to the hypocone.

DIAGNOSIS OF EUROPEAN THEN ASIATIC AND NORTH AFRICAN GLIRIDAE BASED ON CRANIAL AND DENTAL CHARACTERISTICS

Protrogomorphous to pseudomyomorphous; separate tubercle or area for the origin of masseter lateralis superficialis; sciurognathous; P3 present to absent; DP4 and P4 reduced; upper and lower M3 smaller than M1–2 and larger than P4; brachydont lophate teeth; no surrounding crests; central crests as high as the lophs and lophids; mesoconid generally present; protocone generally connected to the hypocone; hypocone poorly developed; protoloph connected to the protocone and metaloph (without metaconule) to the hypocone.

ORIGIN OF AFRICAN FAMILIES ANOMALURIDAE AND GRAPHIURIDAE : THE CONTRIBUTION OF ZEGDOUMYIDAE

Until now, only two late early Eocene North African localities have yielded isolated teeth of rodents: there are 25 teeth from Glib Zegdou (Algeria), and 4 teeth from Chambi (Tunisia). Although slightly different in size and shape, these teeth have a similar occlusal pattern and have been attributed to a new family, Zegdoumyidae (Vianey-Liaud *et al.* 1994). The teeth of Zegdoumyidae are brachydont and lophodont. The incisor has a transitional pauciserial-uniserial enamel microstructure (Martin 1993). Premolars and deciduous teeth are molarized. Upper molars are square, with the hypocone as well developed as the protocone. Transverse crests, at least the protoloph and metaloph, are well developed. The longitudinal crest is absent or weak and incomplete. On the lower molars, the talonid and trigonid are of similar height. The anterior cingulid is always present and well developed, and it is as high as the talonid basin. A distinct mesoconid is clearly separated from the protoconid, and this is generally elongated into a mesolophid. As a rule, there is no longitudinal crest (ectolophid). There is also no hypoconulid. Thus, Zegdoumyidae, which are the oldest African rodents known to date, already show several apomorphic characteristics. Among them, some can be recognized as autapomorphies (molarization of D4 and P4; square upper molars with a hypocone linked to the metaloph), and the others as synapomorphies with sciuravids, glirids and anomalurids. It seems unambiguous that anomalurids arose from members of Zegdoumyidae, as shown by the characteristics of one of them, *Glibemys* (Vianey-Liaud *et al.* 1994: 108-109, 112-113). European glirids and American sciuravids could be considered as vicariant groups of the African Zegdoumyidae, the three families originating from a common ancestor in Ischyromyidae. Theridomyidae were until recently considered to be closely related to Anomaluridae (Hartenberger 1990). However, it appears to us that Theridomyidae and Zegdoumyidae have separately followed divergent evolutionary trends (Vianey-Liaud *et al.* 1994). If Zegdoumyidae are the ancestors of Anomaluridae, then Theridomyidae cannot be closely related to Anomaluridae (Vianey-Liaud *et al.* 1994: 111-114). This scenario implies communication between Euramerica and North Africa, not earlier than the early Eocene, followed by a period of endemism which led to the adaptive radiation of Zegdoumyidae. Such a trans-Tethyan communication has been suggested for the beginning of the Paleocene by Gheerbrant (1992) to explain similarities between European and Moroccan insectivore faunas.

As discussed above (p. 353-354), late Eocene and Oligocene African faunas have not yet yielded any glirid that could have given rise to graphiurids. The ancestors of graphiurids are likely to be found among Zegdoumyidae, which show some glirid-like characteristics (elongated mesolophid, no ectolophid,...). If this hypothesis of an ancestor-descendent relationship between zegdoumyids and graphiurids is correct, then graphiurids should be phylogenetically closer to anomalurids than to glirids. This hypothesis is supported by analysis of dental and cranial features of the Recent Anomaluridae from sub-Saharan Africa. Three Recent genera are known. *Anomalurus* and *Idiurus* have a gliding membrane, *Zenkerella* has none. Their zygomasseteric structure is hystricomorphous, as in graphiurids. P4 may be reduced or unreduced (Fig. 2). The cheek teeth are flat-crowned, generally low-crowned and lophodont. The longitudinal crest (= mure) may be interrupted. Anomaluridae generally show a labial and lingual wall on upper molars and, often, a lingual wall on the lower ones. Of the three Miocene pentalophodont anomalurids, *Paranomalurus bishopi* and *P. walkeri* show an endoloph and surrounding walls on the upper molars, an ectolophid and a lingual wall on the lower molars, while *Paranomalurus soniae* displays neither an endoloph nor a mure (Lavocat 1973). The genus *Zenkerella*, with its simplified teeth (a surrounding wall, a central basin separated by a central transverse crest), is known since the Miocene (Lavocat 1973). The late Eocene *Nementchamys* (Jaeger *et al.* 1985) has a more complicated pattern, with numerous extra-ridges, endoloph and mure, and surrounding walls.

Although graphiurids have a lophodont dental pattern resembling that of glirids, the development of a surrounding wall on lower molars (see Fig. 1C for *Graphiurus murinus*) and, partly, upper molars, is not typical of glirids but occurs in some anomalurids (Fig. 2). The pattern of a juvenile specimen of *Graphiurus crassicaudatus* (Fig. 1A) shows a general similarity to glirids but, on upper molars, the protocone is clearly separated from the hypocone by a wide but shallow valley. Such a wide valley is never observed among glirids. Partly because of this valley, and because of the kind of connections between the cusps and transverse crests, the lower molars display a pattern nearly symmetrical to that of the upper molars. We have never observed such symmetry among glirids, but this condition appears in some anomalurids such as *Zenkerella*. Moreover, the lower teeth of *Zenkerella* shows neither entolophid nor mesoconid, although these are generally developed in glirids.

In other words, and to summarize: (1) the diversity observed in the dental patterns of anomalurids could include that of graphiurids; (2) one anomalurid (*Zenkerella*) is not volant and shows the general shape of a dormice although it is scaly-tailed; (3) both graphiurids and anomalurids are hystricomorphous; (4) the oldest (late early Eocene) African rodents are the zegdoumyids which could represent a vicariant group of glirids; (5) anomalurids originated from the zegdoumyids; and (6) the oldest known African glirids are not older than the middle Miocene and belong to typical European genera.

We maintain a distinct family rank for graphiurids and anomalurids, but it might be desirable to emphasize their close relationships by including both in the same family; a decision on this is deferred pending additional fossil evidence.

CONCLUSION

We conclude that there is a close relationship between graphiurids and anomalurids, as descendents of zegdoumyids. Graphiurids appear clearly separated from glirids, and can be raised to family rank. As shown above, this is strongly supported by morphological, chronological, paleogeographical, and biogeographical information. This new light on the relationships of these families is based on both Recent and fossil evidence. We emphasize that contradictory phylogenetic results have been obtained by several authors using cladistics, largely because of difficulties in recognizing character polarities. It is important to test cladistic results with fossil data in order to identify homoplasies, which are important in rodent evolution (manuscript in preparation).

Further, our hypothesis of phyletic relationships should be tested by means of molecular analysis of the extant species of graphiurids, anomalurids, glirids, muroids, and sciurids.

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REFERENCES

BACHMAYER, F. & WILSON, R.W., 1978. — A second contribution to the small mammal fauna of Kohfidisch, Austria. *Annalen Naturistorisches Museum*, Wien, 81: 129-161.

BACHMAYER, F. & WILSON, R.W., 1980. — A third contribution to the small mammal fauna of Kohfidisch, Austria. *Annalen Naturistorisches Museum*, Wien, 83: 351-386.

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. Plenum Press, New York, 355-379.

DENYS, C., 1987. — Micromammals from the West Natron Pleistocene deposits (Tanzania). Biostratigraphy and paleoecology. *Sciences Géologiques*, Bulletin, 40 (1-2): 185-201.

ELLERMAN, J.R., 1940. — The Families and Genera of Living Rodents. Vol. 1. Trustees of the British Museum, London, 689 pp.

GHEERBRANT, E., 1992. — Les mammifères paléocènes du Bassin d'Ouarzazate (Maroc). I. Introduction générale et Paleoryctidae. *Palaeontographica*, Stuttgart, A, 224: 67-132.

HARTENBERGER, J.-L., 1971. — Contribution à l'étude des genres *Gliravus* et *Microparamys* (Rodentia) de l'Eocène d'Europe. *Palaeovertebrata*, Montpellier, 4: 98-135.

HARTENBERGER, J.-L., 1985. — The order Rodentia: Major questions on their evolutionary origin, relationships and suprafamiliar systematics. *In*: LUCKETT, W.P. & HARTENBERGER, J.-L. (Eds.), Evolutionary Relationships Among Rodents: A Multidisciplinary Analysis. Plenum Press, New York, 1-33.

HARTENBERGER, J.-L., 1990. — L'origine des Theridomyoidea (Mammalia, Rodentia): données nouvelles et hypothèses. *Comptes Rendus de l'Académie des Sciences, Paris*, 311: 1017-1023.

HARTENBERGER, J.-L., 1994. — The evolution of the Gliroidea. *National Science Museum Monographs*, Tokyo, 8: 19-33.

JAEGER, J.-J., 1977. — Les rongeurs du Miocène moyen et supérieur du Maghreb. *Paleovertebrata*, Montpellier, 8: 1-166.

JAEGER, J.-J., DENYS, C. & COIFFAIT, C., 1985. — New Phiomorpha and Anomaluridae from the late Eocene of North Africa: phylogenetic implications. *In*: LUCKETT, W.P. & HARTENBERGER, J.-L. (Eds.), Evolutionary Relationships Among Rodents: A Multidisciplinary Analysis. Plenum Press, New York, 567-588.

LAVOCAT, R., 1973. — Les rongeurs du Miocène d'Afrique orientale. I. Miocène inférieur. *Mémoire de l'Ecole Pratique des Hautes Etudes*, Montpellier, 1: 1-284.

LAVOCAT, R. & 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. Plenum Press, New York, 333-354.

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

MENG, J., 1990. — The auditory region of *Reithroparamys delicatissimus* (Mammalia, Rodentia) and its systematic implications. *American Museum Novitates*, 2972: 1-35.

MILLER, G.S. & GIDLEY, J.W., 1918. — Synopsis of the supergeneric groups of rodents. *Journal of the Washington Academy of Sciences*, 8: 431-448.

POCOCK, T.N., 1976. — Pliocene mammalian microfauna from Langebaanweg: a new fossil genus linking the Otomyinae with the Murinae. *South African Journal of Science*, 72: 58-60.

THOMAS, H., ROGER, J., SEN, S. & AL-SULAIMANI, Z., 1992. — Early Oligocene vertebrates from Dhofar (Sultanate of Oman). *In*: Geology of the Arab World, Cairo University, 283-293.

VIANEY-LIAUD, M., 1974a. — Les rongeurs de l'Oligocène inférieur d'Escamps. *Palaeovertebrata*, Montpellier, 6: 197-241.

VIANEY-LIAUD, M., 1974b. — L'anatomie des genres *Eucricetodon* et *Pseudocricetodon* (Cricetidae, Rodentia, Mammalia). *Géologie Méditerranéenne*, Aix-en-Provence, 14: 111-132.

VIANEY-LIAUD, M., 1974c. — *Palaeosciurus goti* nov. sp., écureuil terrestre de l'Oligocène moyen du Quercy. Données nouvelles sur l'apparition des Sciuridae en Europe. *Annales de Paléontologie (Vertébrés)*, Paris, 60: 103-122.

VIANEY-LIAUD, M., 1985. — Possible evolutionary relationships among Eocene and lower Oligocene rodents of Asia, Europe and North America. *In*: LUCKETT, W.P. & HARTENBERGER, J.-L. (Eds.), Evolutionary Relationships Among Rodents: a Multidisciplinary Analysis. Plenum Press, New York, 277-309.

VIANEY-LIAUD, M., 1989. — Parallelism among Gliridae (Rodentia): the genus *Gliravus* Stehlin and Schaub. *Historical Biology*, 2: 213-226.

VIANEY-LIAUD, M., 1994. — La radiation des Gliridae (Rodentia) à l'Eocène supérieur en Europe Occidentale, et sa descendance Oligocène. *Münchner Geowissenschaftlichen Abhandlungen*, (A), 26: 117-160.

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

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

WANG, B. & DAWSON, M.R., 1994. — A primitive Cricetid (mammalia, Rodentia) from the middle Eocene of Jiangsu province, China. *Annals of Carnegie Museum*, 63: 239-256.

WEBER, J., 1928. — Die Saugetiere, vol. II: Systematischer Teil. Gustav Fischer, Jena, 898 pp.

WINGE, H., 1924. — Pattedyr-Slaegter II: Rodentia, Carnivora, Primates. 376 pp. (Translated from Danish by E. DEICHMANN & G.M. ALLEN: The interrelationships of the mammalian genera, 1941-42, Copenhagen.)