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Morphological and molecular data against the monophyly of Dendromurinae (Muridae: Rodentia)

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Abstract. For the first time, the eight known genera of Dendromurinae have been studied in a comparative analysis of their morphological characteristics, mainly dental ones. Phylogenetic interpretations based on comparative morphology with other African Muridae sensu lato are discussed. The taxon Dendromurinae appears to be paraphyletic and might be composed of at least 4 independent lineages. A first one includes *Dendromus*, *Steatomys*, *Malacothrix* and *Megadendromus*; a second one groups *Prionomys* and *Dendroprionomys*. The third and fourth lineages consist of *Deomys* and *Leimacomys*, respectively, and this latter genus clusters with Gerbillinae (*Gerbillus*, *Tatera*). Results obtained from DNA-DNA hybridization experiments in which only two Dendromurinae (*Deomys* and *Steatomys*) are involved, are also discussed. Molecular and morphological data both agree on the fact that the two genera *Deomys* and *Steatomys* do not cluster in a monophyletic group. The status of the Dendromurinae has to be revised.

Key words. Rodentia, Muridae, Dendromurinae, dental morphology, DNA-DNA hybridization, phylogeny.

Introduction

Dendromurinae (tree mice and fat mice) are presently tropical African representants of the Muroidea rodents characterized by semi-insectivorous diet and ability to climb for some of them. Among the eight genera constituting this group (Musser & Carleton 1993) there are 6 taxa with narrow geographic distribution (Fig. 1) whose dental characters and affinities are still not clearly established. The different classification of Muroidea (Allen 1939; Misonne, 1969; Chaline et al. 1977; Ellerman 1940—41; Simpson 1945; Arata 1967) indicate various systematic positions of Dendromurinae as well as various numbers of genera attributed to this taxon (see summary in Meester et al. 1986). The Dendromurinae were classified among Muridae or Cricetidae by different authors, or even attributed to a separate family (Chaline et al. 1977). New molecular data (this paper) and new Miocene fossil material (Lindsay 1988) attributed to this group are today available. Moreover, no author has ever presented and discussed together the dental patterns of all eight extant dendromurine genera. The few available partial studies of selected representants of Dendromurinae have ruled out the possibility that this group is monophyletic (Rosevear 1969; Chaline et al. 1977; Carleton & Musser 1984).

First investigations on dental morphology (Petter 1966a; Lavocat 1959, 1964, 1967) have concluded that Dendromurinae derive directly from fossil Muroidea with a cricetid dental pattern as exhibited by Miocene members of the cricetid radiation.

But none of the latter authors has suggested any hypothesis on the polyphyly of the group for the reason that only the most common representants of the subfamily (*Dendromys* and *Steatomys*) were treated.

Moreover, systematical studies on fossil Muroidea give a prominent importance to the upper and lower M1 to the detriment of other teeth and especially of the upper M3/. Jacobs (1978), Jaeger et al. (1985), Lindsay (1988) discussed almost only about the upper M1/ or lower M/1 dental features. This situation cannot longer last since Denys & Michaux (1992) have recently shown the importance of the upper M3/ for phylogenetic purpose among Murinae and related taxa.

After detailing the characteristics of each of the eight genera currently accepted as Dendromurinae, the present paper will give the point of view of morphologists on the monophyly of the subfamily Dendromurinae. The phylogenetic trees derived from morphological traits and the trees obtained from molecular distances will be presented. In the latter case, DNA/DNA hybridization experiments involve a more restricted sample of only two Dendromurinae (*Deomys* and *Steatomys*), which are compared to *Cricetomys*, *Gerbillus*, *Acomys*, *Uranomys* and two Murinae. This approach is a necessary step in order to further discuss the status of some controversial Miocene fossil remains. The attribution of the fossil to one or the other sub-families of Muroidea have immediate consequences on the calibration with time of the molecular data.

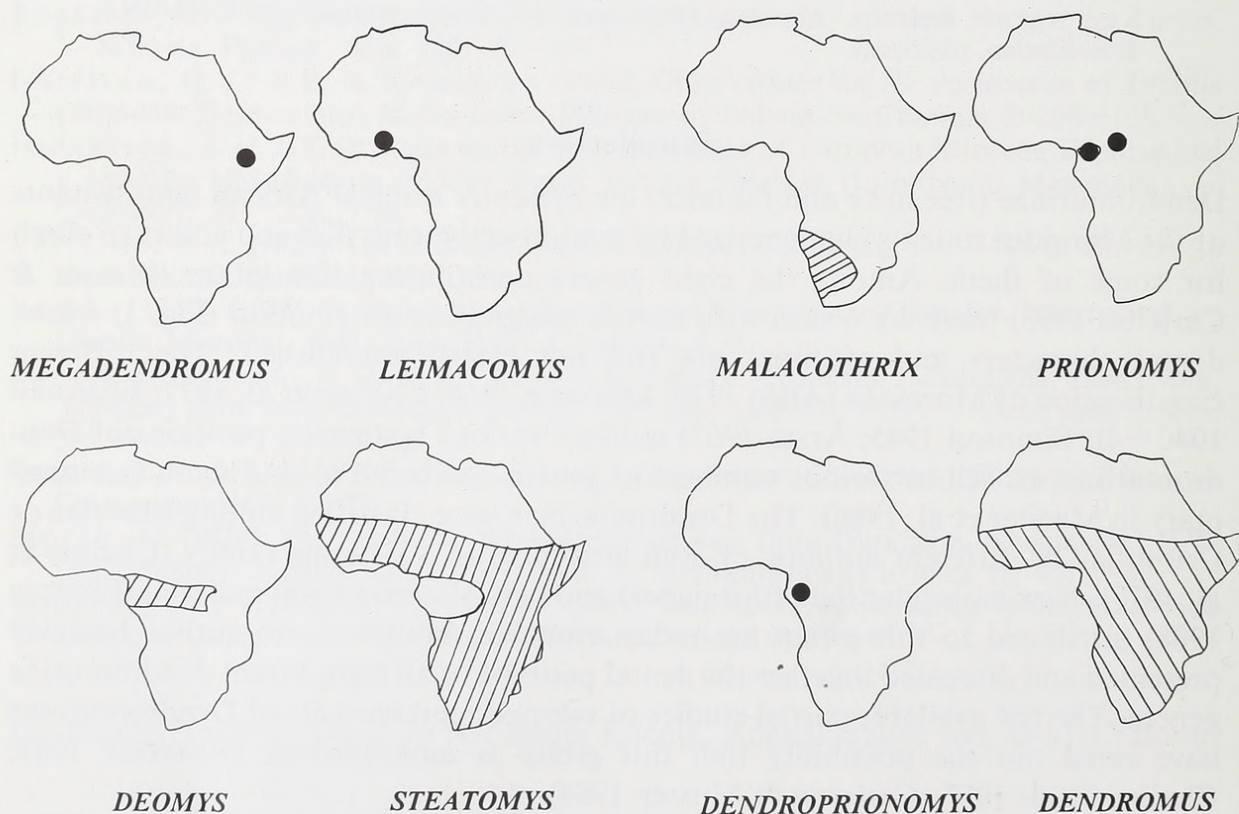


Fig. 1: Geographical distribution of the eight Dendromurinae genera according to the literature.

Review of the Dendromurinae

Alston (1876: p. 82) created the subfamily Dendromyinae characterized by "incisors convex in front; molars tuberculate. Infraorbital foramen opening not narrowed below; coronoid process very small. Ears hairy. Claws long." In this original description, the new subfamily comprised 3 genera: *Dendromus*, *Steatomys* and *Lophuromys*. The latter genus has been removed and attributed to Murinae. Since that time 6 supplementary genera have been included in the subfamily Dendromurinae. Dendromurinae are today restricted to sub-Saharan Africa (Fig. 1), and two of the eight genera traditionally constituting this taxon are rather well known for they are relatively common and widespread all over tropical African savannas: *Dendromus* and *Steatomys*. The other six dendromurine genera are monospecific and have restricted distribution areas. Some taxa are represented by less than 10 specimens and one, *Leimacomys*, is declared as almost extinct (Schlitter 1989).

The type genus is *Dendromus* Smith, 1829, which shows a high variability in morphology and is represented, according to the recent revision of Musser & Carleton (1993) by at least eleven species. This African climbing mouse or tree mouse shows a soft pelage and has a long thinly-haired and prehensile tail, longer than head and body (Tab. 1). *Dendromus* is the only dendromurine showing only three well developed digits on the forefoot, the toes being long and slender. The first digit is opposable, which is of considerable help for climbing. *Dendromus* is not really arboreal and no specimen has been trapped in a tree, but almost all species are good climbers. African climbing mice are known to make round nests of dry grasses and to climb up slender grass stems. Females have 8 mammae and there is an average of 3 or 4 young per litter (2 to 8 embryos). The genus is found in most habitats of the savannas and montane zones (up to 4300 m altitude) except true rain forest. Dieterlen (1971) has given morphological and ecological features for 5 species of central Africa. *Dendromus* favours savanna, marshes, tall dense grasses near rivers, and has been seen eating small lizards, bird eggs, nestlings, and even killing snakes (Kingdon 1974). Roberts (1951) indicates a majority of grass seeds eaten with a complement of insects. Bohman (1942) has made one of the last extensive systematic revisions of the whole genus (except for the species *D. mystacalis* and *D. melanotis*).

Steatomys Peters, 1846 is well known for its ability to accumulate fat and to estivate in deep burrows during the dry season hence its vernacular name of "fat mouse". It is characterized by four toes on the forefoot and five toes on the hind foot, but with no opposable digit. *Steatomys* has a short tail, smaller than head and body (Tab. 1). Primarily a savanna inhabitant, *Steatomys* can also be found all over Africa from semi-desertic zones to forest clearing fields or to degraded forest or forest edge. Nocturnal and terrestrial, this genus eats seeds, grass, bulbs, some termites and insects. There are 1 to 7 young per litter. At least six species have been recognized by Musser & Carleton (1993), but careful systematic revisions are needed.

Leimacomys Matschie, 1893, known as the "Togo mouse" or the "groove-toothed forest mouse", is poorly known by two specimens only. The type locality is in the high forest belt in Togo. Its short naked tail, the four digits on the forefoot as well as the hind foot with 5 toes suggest terrestrial habits (Tab. 1). In describing its skull and tooth morphology, and after opening its stomach Dieterlen (1976a) concludes to an insectivorous diet.

Megadendromus Dieterlen & Rupp, 1978 (no vernacular name known) is the last discovered Dendromurinae and is found only in the Bale Mountains and on Mt Chilalo in Ethiopia. Demeter & Topal (1982) describe a supplementary individual from Dinshu trapped in a bush of *Erica arborea* in a generally open *Hagenia* woodland. Morphologically it looks like a giant *Dendromus*. It is also known by less than 10 individuals. According to the original description, this genus has 4 digits on the forefoot but with a very small fifth one, the first one being missing. The hind foot has 5 digits with the fifth one being probably opposable. Its habitat is the ericaceous scrub moorland of high altitude (3000 to 3800 m). Nothing is known about its diet or its reproduction (Tab. 1).

Deomys Thomas, 1888 is either called the "Congo forest mouse" or the "link rat" (in Rosevear 1969). The latter vernacular name has been used to build its scientific Greek name given by Thomas, "deo" means I link, "mys", mouse. Thomas (1888: p. 132) believed this genus being in intermediate systematic position between Mures and Criceti on the basis of dental morphology. *Deomys* is a terrestrial rodent with a long hind foot and a scaly tail longer than head and body (Tab. 1). Its habitat is the true rain forest where it lives on the ground and feeds on insects (mostly termites) and other invertebrates (specially millipedes and slugs) for 40 to 65 %, the remaining of its diet consisting in vegetable matter (Genest-Villard 1980). Its nests are made of shredded leaves and vegetable fibers and are situated in holes and crevices or at the basis of the trees. It is a good climber but remains on the ground most of the time. *Deomys* seems to be territorial, found usually as a pair of male and female, or a female with young. There are 1 to 3 young per litter, most of the time only 2.

Prionomys Dollman, 1910 or "Dollman's tree mouse" is found only in Cameroon and the Central African Republic. This forest living rodent is a burrowing animal which is probably exclusively insectivorous as only ants have been found in its stomach (Genest-Villard 1980). The hand of *Prionomys* has 4 digits whereas the hind foot has 5 digits with the first being very well developed and opposable; the tail is semi-prehensile (Petter 1964, 1966b). Measurements are given in Table 1. Dollman (1910) cited also that the small ears of *Prionomys* are round and simple, with no such internal folds as in *Dendromus*. The tail is long and almost naked. Dollman concluded that *Prionomys* appears to be more closely related to *Dendromus* than to any other of the allied genera, due to its long prehensile tail. He also concluded that molar, skull and external characters distinguish this genus from other dendromurines. The original description tells nothing about the habitat and living habits of this rodent.

Dendroprionomys Petter, 1966 is known by 5 specimens from Brazzaville (Congo). Nothing is known about its habits (Tab. 1). *Dendroprionomys* shows an intermediate morphology between *Dendromus* and *Dendroprionomys* and is characterized, according to Petter (1966b), by 5 digits in the hind foot with the fifth being opposable. It is a forest living animal.

Malacothrix Wagner, 1843, the gerbil mouse or the long (large) eared mouse, is endemic to South Africa where it lives in semi-desert regions in sandy plains, grassy velds, pans with karroid vegetation (Tab. 1). This terrestrial nocturnal animal constructs deep burrows and has a granivorous diet. The pelage is long, dense and silky; the hind foot has only 4 toes contrary to *Steatomys* and *Dendromus* which have 5.

The soles are hairy, the foot is very narrow. The tail is shorter than head and body length. There are generally 2 to 7 youngs per litter after a gestation of about 22–26 days on average. See Table 1 for comparison with other genera.

When considering altogether the external characteristics of the eight dendromurine genera as well as their way of life, it is quite evident that they do not constitute a homogeneous group.

Table 1: Main measurements and characteristics of the Dendromurinae genera. TL = tail length, HB = Head and Body length, Mamm. = Number of mammae according to the literature, Number of species (NS) according to Musser & Carleton (1993).

Genus	NS	Habitat	Weight	TL	HB	MAMM
<i>Dendromus</i>	11	Savanna	5–21	65–132	50–100	8
<i>Dendroprionomys</i>	1	?Forest	?	108	77	?
<i>Deomys</i>	1	Forest	40–70	150–215	120–160	4
<i>Leimacomys</i>	?	?Forest	ca. 30	37	118	?
<i>Malacothrix</i>	1	Semi-desert	7–20	28–42	65–95	8
<i>Megadendromus</i>	1	Moorland	49–66	92–110	117–129	?
<i>Prionomys</i>	1	Forest	?	100–112	60–85	?
<i>Steatomys</i>	6	Savanna	5–70	34–59	65–145	8–16

Material and methods

Modern specimens from different regions of Africa have been examined in different collections, especially those from the MNHN (Muséum National d'Histoire Naturelle, Paris), BMNH (Natural History Museum, London), Musée Royal de l'Afrique centrale, Tervuren), ZFMK (Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn), SMNS (Staatliches Museum für Naturkunde in Stuttgart), HZM (Harrison Zoological Museum, Sevenoaks, G. B.), ZMB (Zoologisches Museum Berlin), HNM (the Hungarian Natural History Museum, Budapest), and TM (Transvaal Museum, Pretoria, South Africa).

The specimens drawn here (Fig. 2) are considered typical for the genera despite the high variability of dental patterns. The nomenclature and the terminology of teeth characteristics follow Miller (1912), Mein & Freudenthal (1971), Musser (1981), and Denys et al. (1992). Phylogenetic analyses were conducted with the aid of the PAUP 3.1 program (D. Swofford 1993). DNA-DNA hybridization methodology is explained in Chevret et al. (1993).

Dental morphology patterns and phylogenetic analyses

Phylogenetic analyses have been performed on the eight genera traditionally included in the Dendromurinae: *Dendromus*, *Dendroprionomys*, *Deomys*, *Leimacomys*, *Malacothrix*, *Megadendromus*, *Prionomys*, *Steatomys*. In order to test the monophyly of the taxon Dendromurinae as here defined, several taxa have been used as outgroups: Petromyscinae, Cricetomyinae, *Macrotarsomys* (Nesomyinae), *Mystromys* (Muridae incertae sedis), some Gerbillinae (*Gerbillus*, *Tatera*), questionable Murinae (*Acomys*, *Lophuromys* and *Uranomys*: Chevret et al. 1993) and true Murinae (*Arvicanthis*, *Mus*).

14 characters relative to cheek teeth and 6 characters relative to general morphology and skull have been used. Multistates characters have been recoded in two states characters, the total of which is 29. Outgroup comparison and paleontological information allow a definition of primitive and derived states. The taxa/characters matrix is given in Table 2. For two states characters, primitive and derived states are respectively defined as (0) and (1). The successive states of a morphocline for a three states character are indicated as follows: (0,0), (1,0) and (1,1). Two different derived states originating from the same ancestral (0,0) state are noted (1,0) and (0,1) respectively.

The interpretations of the dendromurine dental patterns are based on the hypothesis of their derivation from an ancestor with a cricetid dental pattern: upper M1 has 5 cusps (anterocone, paracone, protocone, metacone, and hypocone), upper M2 has 4 cusps (paracone, protocone, metacone, and hypocone) and upper M3 has two or three cusps (paracone, protocone, and sometimes a hypocone) (for terminology, see Lindsay 1988). Crests link these cusps. Lower molars are generally not taken into account because of the absence of relevant major morphological change. The evolution which leads to the dental pattern of Dendromurinae thus consists in the acquisition of a cusp on the labial (or internal) side of upper M1 and M2, the enterostyle or cusp t4, and loss of longitudinal crests or lophs (Petter 1966a; Lavocat 1959, 1967; Lindsay 1988). The importance of the presence of a supplementary internal cusp on upper M1 is stressed by many authors as a diagnostic criteria for the definition of the subfamily. However this character is not sufficient to define Dendromurinae as it is also present in Petromyscinae, in Murinae and Cricetomyinae. In the two latter groups this cusp is found in association with another internal cusp: one in an anterior position in Murinae, one in a posterior position in Cricetomyinae. Other dental traits involved in the comparative study deal directly with structures of the cricetid dental pattern: transverse lophs and longitudinal crests. Transverse lophs and longitudinal crests are primitive. The schematic dental morphology of the studied taxa is given in Fig. 2.

Following the traditionally accepted correspondence between cusps in Dendromurinae and Murinae, the terminology of Miller (1912) is used. Consequently, the unique lingual cusp in Dendromurinae is a t4, the two lingual ones in Murinae are respectively, t1 and t4, and a cusp t7 can be present posteriorly. Similarly, on the antero-labial side of upper M2 and M3, the cusp which can be present is a t3. These homologies are challenged according to our results and they will be discussed.

Characters and character states are defined as follows:

1. Antero-internal region on upper M2/: loph (0,0); cusp t1 (0,1), nothing (1,0). The absence of t1 on M2/ of Dendromurinae is shared with *Delanymys*, *Petromyscus*. This cusp is generally absent in Cricetomyinae but in many cases there is a small cingular inflation at its place. A loph is a primitive state and derived states are independently acquired.

2. Antero-external region on upper M2/: loph (0,0); cusp (t3) (0,1), nothing (1,0). The presence of a t3 on the upper M2/ is not a constant character in Dendromurinae defined here as including eight genera. This cusp is always observed in *Steatomys*, *Dendromus*, *Malacothrix*, *Megadendromus* and *Prionomys*. For the other genera there is either a cingular crest in the place of t3 (*Dendroprionomys*, *Deomys*) or no cusp nor crest in *Leimacomys* (known only by a unique skull). The presence of a t3 on M2/ is shared by *Petromyscus*, *Delanymys*, *Cricetomys*, *Beamys*, *Saccostomus*. In *Mystromys* there is no cusp in the place of a t3 on M2/, only a remain of a central longitudinal crest as in other Cricetinae. There is a t3 in *Acomys*, *Uranomys*, *Lophuromys* as well as in all unquestionable Murinae. In all the latter taxa a t3 is always associated with a t1 on M2/. Derived states are independently acquired.

3. Antero-internal region on upper M3/: loph (0,0); cusp "(t1?)" (0,1), nothing (1,0). Derived states are independently acquired.

4. Antero-external region on upper M3/: loph (0,0); cusp "(t3?)" (0,1), nothing (1,0). The presence of a t3 on the upper M3/ is not a constant character of the Dendromurinae. It has been seen on *Steatomys*, *Dendromus*, *Malacothrix*, *Megadendromus*, but on more derived molars patterns like in *Deomys*, *Dendroprionomys*, *Prionomys* or *Leimacomys* it is not visible. The presence of a t3 on upper M3/ is shared with *Petromyscus*, *Delanymys*, Cricetomyinae, *Acomys*, *Uranomys*, some *Lophuromys* (but not all), many Murinae (Denys & Michaux 1992). In true Murinae when present, cusp t3 on M3/ is always associated with a t1. On the contrary in Dendromurinae and Petromyscinae, as well as in *Acomys*, *Uranomys*, and *Lophuromys*, cusp t3 is present while cusp t1 is absent.

5. Cusp t1 on upper M1/: absent (0), present (1). The absence of t1 on M1/ is a primitive feature and cannot be used as a diagnostic criteria. Dendromurinae, Cricetomyinae, Gerbillinae, *Petromyscus*, *Delanymys* and *Mystromys* exhibit this primitive state.

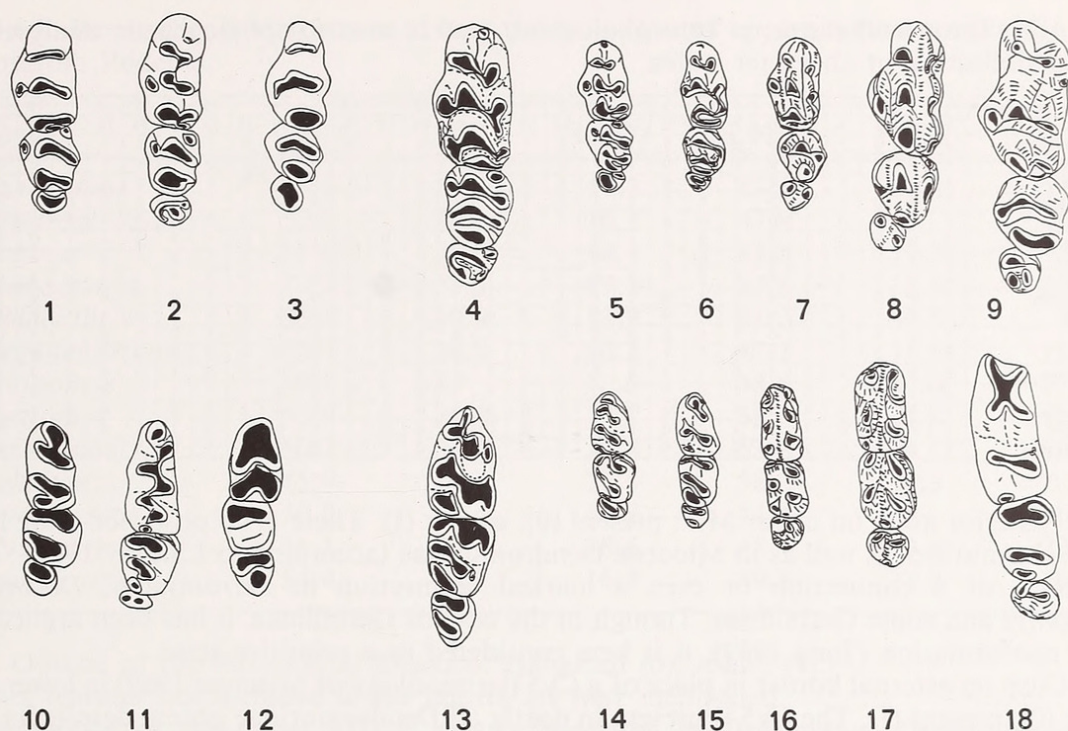


Fig. 2: Dental morphology of the eight Dendromurinae genera. Upper molar rows (1 to 9), lower molar rows (10 to 19) (\times). 1,10: *Steatomys pratensis*, SAM — ZM 14401; 2,11: *Malacothrix typica*, SAM — ZM 17090; 3,12: *Leimacomys boettneri*, holotype, ZMB — 6856 for specimen figured in 3) 4,13: *Megadendromus nikolausi*, holotype, SMNS — 23982; 5: *Dendromus melanotis*, MNHN — 1962 — 1167; 14: SAM — ZM 15084; 6,15: *Dendromus mesomelas*, MNHN — 1983 — 217; 7,16: *Dendroprionomys rousseloti*, MNHN — 1949 — 17; 8,17: *Prionomys batesi*, MNHN — 1967 — 1593; 9,18: *Deomys ferrugineus*, MNHN — 1983 — 293.

6. Cusp t4 on upper M1—2/: absent (0); present (1). The presence of a cusp in position of a t4 on M1—2/ is clearly a constant for Dendromurinae, but this feature is shared with Cricetomyinae, Petromyscinae, Murinae including the questionable ones as *Acomys*, *Uranomys*, and *Lophuromys*. There is no t4 in *Mystromys* and Gerbillinae.

7. Cusp t7 on upper M1/: absent (0); present (1). The shape of t7 on upper M1/ is highly variable. It may be longitudinally extended and crestiform as in some *Dendromus* species or a tiny cusp as in *Dendroprionomys*, or else a large one as in *Megadendromus*. T7 is found in all Cricetomyinae and some Murinae (including some *Acomys* species (Petter 1983) and in some *Lophuromys* species (Dieterlen 1976b). As t7 is observed in many modern and fossil Muroidea, it could have no phylogenetic meaning because of parallel evolution.

8. Anteroconid on lower M/1: unicuspidate (0), bicuspidate (1). In most Dendromurinae genera, the anteroconid is unicuspidate except in *Dendroprionomys*, *Prionomys*, and *Deomys*. The lower molars of the single specimen of *Leimacomys* are very worn and it is not possible to recognize the state of this character (one or two cusps) in this taxon. For *Malacothrix*, the very elongated M/1 shows two very alternating anterior cusps linked by a well marked longitudinal crest. On very young molars of *Mystromys* this anteroconid can be constituted of two cusps but in general it is unicuspidate as in *Petromyscus* and *Delanymys*, *Uranomys*. A bicuspidate prelobe is a rule for Murinae and also for *Acomys* and *Lophuromys*. Some tropical Gerbillinae like *Tatera* have a bicuspidate anteroconid.

9. Anterior mure on upper M1/: present (0); absent (1). The anterior mure is found on M1/ in *Petromyscus* and *Delanymys*. *Malacothrix* shows some reminiscence of anterior mure.

Table 2: Taxon and character (morphological) matrix used for phylogenetic analyses. See text for definition of character states.

Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Dendromus</i>	1	0	0	1	1	0	0	1	0	1	0	0	1	0	0	0	1	1	0	0
<i>Steatomys</i>	1	0	0	1	1	0	1	1	0	1	0	0	1	0	0	0	1	1	1	0
<i>Malacothrix</i>	1	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0	0	1	1	0
<i>Megadendromus</i>	1	0	0	1	1	0	0	1	0	1	1	1	0	1	0	0	1	1	0	1
<i>Leimacomys</i>	1	0	1	0	1	0	1	0	0	1	0	?	1	1	0	1	0	1	1	0
<i>Dendroprionomys</i>	0	0	0	0	1	0	1	0	0	1	0	1	1	1	0	0	0	1	1	0
<i>Prionomys</i>	0	0	0	1	1	0	0	0	0	1	0	1	1	1	0	1	0	0	0	0
<i>Deomys</i>	1	0	0	0	1	0	0	0	0	1	0	1	1	1	0	0	0	0	0	1
<i>Cricetomyinae</i>	1	0	0	1	1	0	0	1	0	1	1	1	1	1	0	0	0	0	0	0
<i>Gerbillus</i>	1	0	1	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0
<i>Tatera</i>	1	0	1	0	1	0	1	0	0	0	0	1	1	0	1	0	1	0	0	0
<i>Acomys</i>	0	1	0	1	1	0	0	1	1	1	0	1	1	1	0	0	0	0	0	0
<i>Lophuromys</i>	0	1	0	1	1	0	0	1	1	1	0	1	1	1	0	0	0	0	0	0
<i>Murinae</i>	0	1	0	1	0	1	1	0	1	1	0	1	1	1	0	0	0	1	1	0
<i>Petromyscus</i>	1	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0	1	0	0	0
<i>Mystromys</i>	1	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Macrotarsomys</i>	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0

10. Posterior mure on upper M1/: present (0); absent (1). There is no posterior mure in living dendromurines as well as in Miocene Dendromurinae (according to Lindsay 1988). There is a trace of a connection or even a marked connection in *Petromyscus*, *Delanymys*, *Mystromys* and some Gerbillinae. Though in the case of Gerbillinae, it has been argued that it is a neoformation (Tong 1989), it is here considered as a primitive state.

11. Cusp on external border in place of a Cv5 (terminology of Misonne 1969) in lower M1/: absent (0), present (1). The Cv5 is present in nearly all Dendromurinae genera despite its great variability.

12. Posterior cingulum on M1/: short crest (0,0), long crest or round and isolated cusp (0,1); absent (1,0). In some Dendromurinae there is a long posterior cingulum and the valley between the cingulum and cusps t8 and t9 is rather wide and long. The resulting structure has been named fovea by Jaeger et al. (1985) and it is found more or less developed in *Dendromus*, *Megadendromus*, *Dendroprionomys*. A fovea is also present in some *Saccostomus*, *Cricetomys*, *Beamys*. In *Malacothrix*, *Deomys* and some *Steatomys* there is a posterior cingular cusp, like in most Murinae. In *Delanymys*, *Petromyscus*, and *Mystromys*, the posterior part of the tooth is composed of hypocone and metacone and there is no posterior cingulum.

13. Longitudinal groove on upper molars: weak groove (0,0), no groove (1,0), deep groove (0,1). In Dendromurinae, the main cusps, except cusp t4, are arranged in two longitudinal rows. Main cusps are also transversally linked together by crests or they are fused in transverse laminae as in *Steatomys*, *Leimacomys* and *Malacothrix*. In the latter genera there is consequently no groove separating the two longitudinal rows of cusps. On the contrary the rows of cusps are separated by a longitudinal groove in the other genera. In *Deomys*, *Dendromus*, *Megadendromus*, transverse crests between central and external cusps are still present and cross the longitudinal groove which is not regularly deep. The groove is deep and continuous in *Dendroprionomys* and very deep in *Prionomys* where the cusps are no more transversally linked together. The latter three groups of genera illustrate a gradient that could correspond to an adaptation toward a purely insectivorous diet. Such a character of the occlusal surface — weak groove — is also exhibited by many Murinae as main cusps are arranged in longitudinal rows and transversally linked together.

14. Antero-external region of lower M2/: loph (0,0); cusp (0,1), nothing (1,0). On lower M2/, the antero-labial cingulum crest, which is present in nearly all Dendromurinae, is nevertheless unequally developed as in some Murinae and also in *Acomys*, *Uranomys*, *Lophuromys*. This crest is absent in Gerbillinae but is found well developed in *Delanymys*, *Petromyscus*, *Macrotarsomys*, *Mystromys*.

15. Tail length: shorter (0), longer than head and body length (1).

16. Length of incisor foramina: short or ending before anterior root of upper M1/ (0), long or ending between the lingual roots of the M2/ (1).

17. Upper dental rows: parallel (0) or divergent (1).

18. Upper incisors: ungrooved (0,0), with a weak groove (1,0), with a deep groove (1,1).

19. Arrangement of the upper incisors: opisthodont (0,0); orthodont (1,0); proodont (1,1).

Table 3: Relative length in percent of the total molar row of upper and lower molars in different muroid Rodents.

Genus	LM1/	LM2/	LM3/	LM1/	LM2/	LM3/
<i>Dendromus</i>	57.8	30.7	11.3	47.3	36.3	14.9
<i>Dendroprionomys</i>	52.6	30.8	16.2	47.8	33	18.8
<i>Deomys</i>	57.6	28.8	14.4	55.8	29.7	14.1
<i>Leimacomys</i>	57.7	27.3	17.5	47.8	28.9	23.3
<i>Malacothrix</i>	55.7	30.9	13.7	61.3	30.5	8.9
<i>Megadendromus</i>	55.7	30.5	16.2	47.1	31.9	21.5
<i>Prionomys</i>	57.7	35	12.6	44.6	37.8	17.9
<i>Steatomys</i>	55.9	30.2	14.2	53.8	34.8	11.5
Gerbillinae	50.7	31.9	18.5	53.8	34	12
<i>Delanymys</i>	45.9	33.7	22.5	38.6	34.3	26.8
<i>Petromyscus</i>	50.8	32.4	17.3	44.4	35	20.6
<i>Mystromys</i>	51.1	31.7	18.6	45	33.6	22.2
<i>Lophuromys</i>	54.4	30.9	16.1	49.8	28.8	16.1

20. Outline of the infraorbital foramen: elongated (0), round (1).

Other features not included in the matrix are here mentioned.

The prelobe of the upper M1/ is clearly bilobated in *Dendromus*, *Dendroprionomys*, *Prionomys*, *Megadendromus*, *Malacothrix*, but not so clearly in *Steatomys*; the prelobe is unilobated in *Delanymys*, *Petromyscus*, in worn teeth of *Mystromys*, as well as in some Gerbillinae.

The posterior cingulum, generally small on M/1, is located in the interno-posterior corner of the tooth except in *Dendroprionomys*, *Prionomys*, *Malacothrix* where it is situated in the middle of the posterior wall of the tooth. The first disposition is also observed for *Delanymys*, *Petromyscus*, *Mystromys* in which the posterior cingulum is not round and isolated like in Dendromurinae, Cricetomyinae, Murinae, but related to the postero-labial cusp and in the prolongation of the longitudinal crest. In *Leimacomys* no posterior cingulum is seen.

Generally cited as a discriminating character, the reduction of the M3/3 has never been quantified. Table 3 indicates that if the maximum of reduction is found in *Dendromus* or *Malacothrix*, the reduction of the molars is less important in *Steatomys*, *Deomys*, and especially in *Megadendromus*. As a rule, the M3/3 of Dendromurinae are more reduced than those of *Delanymys*, *Petromyscus* or *Mystromys*, and all Murinae except for *Nannomys*. There are also some differences in the proportions of the molars between Dendromurinae and true Murinae.

On lower M/1, the anterior mure is present in nearly all dendromurines except *Dendroprionomys*. The latter character is found also in Cricetomyinae, most of the Murinae, *Delanymys*, *Petromyscus*, *Mystromys*. The posterior mure is absent in Dendromurinae, while it is found in *Petromyscus*, *Delanymys*, *Mystromys* and some Gerbillinae.

The shape of cusp t4 on upper M1-2/ (as expressed in Denys et al. 1992) is peculiar in Dendromurinae where it is generally a low cusp, weakly related to the t5, sometimes elongated longitudinally and crestiform (some *Steatomys*, *Leimacomys*, *Dendromus*, *Megadendromus*). In fossil *Acomys* (Denys 1990) from Langebaanweg, the t4 of some specimens is very low and isolated from the t5. Petter (1967) has discussed the homology of the t4 of Petromyscinae and concluded to a different origin than to Dendromurinae. By the fact in genus *Petromyscus* the t4 is never isolated from the t5. T4 is as high as t5.

Results

Analyses of the morphological characters

The matrix of character states (Table 2) has been used to test the monophyly of the Dendromurinae when different outgroups are considered. A parsimony analysis

using PAUP version 3.1 (Swofford 1993) yields two equally parsimonious trees one of which (Consistency index of 0,819) being illustrated in Fig. 3. A first monophyletic group of dendromurines includes *Dendromus*, *Steatomys*, *Malacothrix*, and *Megadendromus*. The other genera of Dendromurinae are separated and linked with other Muroidea. *Prionomys* and *Dendroprionomys* cluster with Muridae and *Acomys*, *Lophuromys*, and *Deomys* is the sister group of this latter cluster. The last dendromurine, *Leimacomys*, is grouped with Gerbillinae (*Gerbillus*, *Tatera*) and *Mystromys*, a genus traditionally attributed to Cricetinae incertae sedis (Carleton & Musser 1984). *Petromyscus*, considered by some authors as a Dendromurinae, is here the sister group of an assemblage including Cricetomyinae, Murinae, Dendromurinae at the exclusion of *Leimacomys*, *Acomys*, and *Lophuromys*. Hence, *Petromyscus* is not related to Gerbillinae and *Mystromys*. There are two branchings of *Macrotarsomys*: it is either the sister group of all the previously listed taxa or it is on an independent branch of a polytomy, as distant from Gerbillinae, *Mystromys* and *Leimacomys* as from the other remaining taxa.

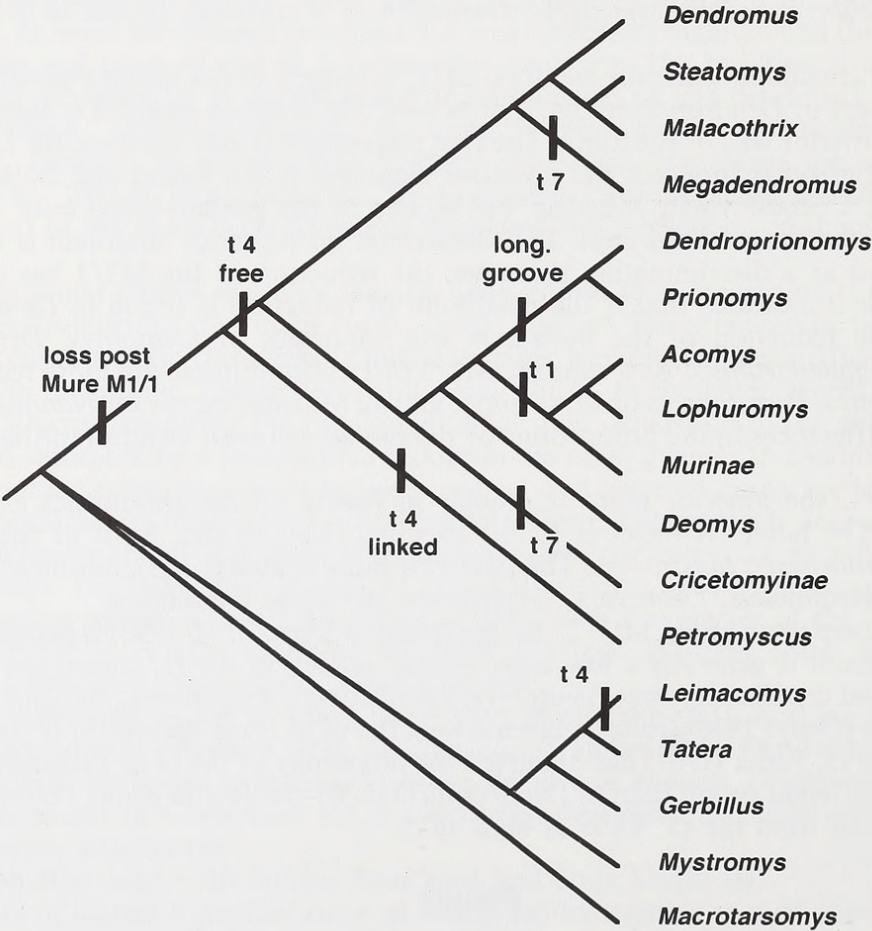


Fig. 3: One of the two most parsimonious trees derived from the characters states matrix of Table 2. The other tree differs by the relative position of *Macrotarsomys* (see text for further details).

Comparison between molecular and morphological trees

Molecular data obtained from DNA-DNA hybridization experiments are available for eight muroid taxa, among which two of the eight recognized Dendromurinae (*Deomys* and *Steatomys*). The general methodology and data treatments are explained in Chevret et al. (1993). Six genera were radioactively labelled: *Acomys*, *Lophuromys*, *Gerbillus*, *Mus*, *Arvicanthis* and *Cricetomys* (no Dendromurinae could be used as tracer because not enough DNA material was available). The results of the DNA-DNA hybridization experiments expressed in delta Tm values ($^{\circ}\text{C}$), are presented in Table 4, with the corresponding % nucleotide substitutions and datings of the different dichotomies of the tree in Figure 4. As we did not get a complete matrix of data, this tree was constructed through a simple UPGMA clustering, assuming a near-equality of rates of DNA change, an assumption which holds for murid rodents (Chevret et al. 1993). The % nucleotide substitutions estimates were calibrated with the geological time by the use of the age of the *Mus/Rattus* dichotomy estimated at ca 10 Ma (Jacobs & Pilbeam 1980; Jaeger et al. 1986), with a molecular clock hypothesis. The datings older than ca. 12 Ma must be considered as under-estimates due to saturation effects and experimental constraints. *Deomys* forms a monophyletic group with *Acomys* and *Lophuromys* and their closest relative would be *Gerbillus*. On the contrary *Cricetomys* and *Steatomys* form another separate group.

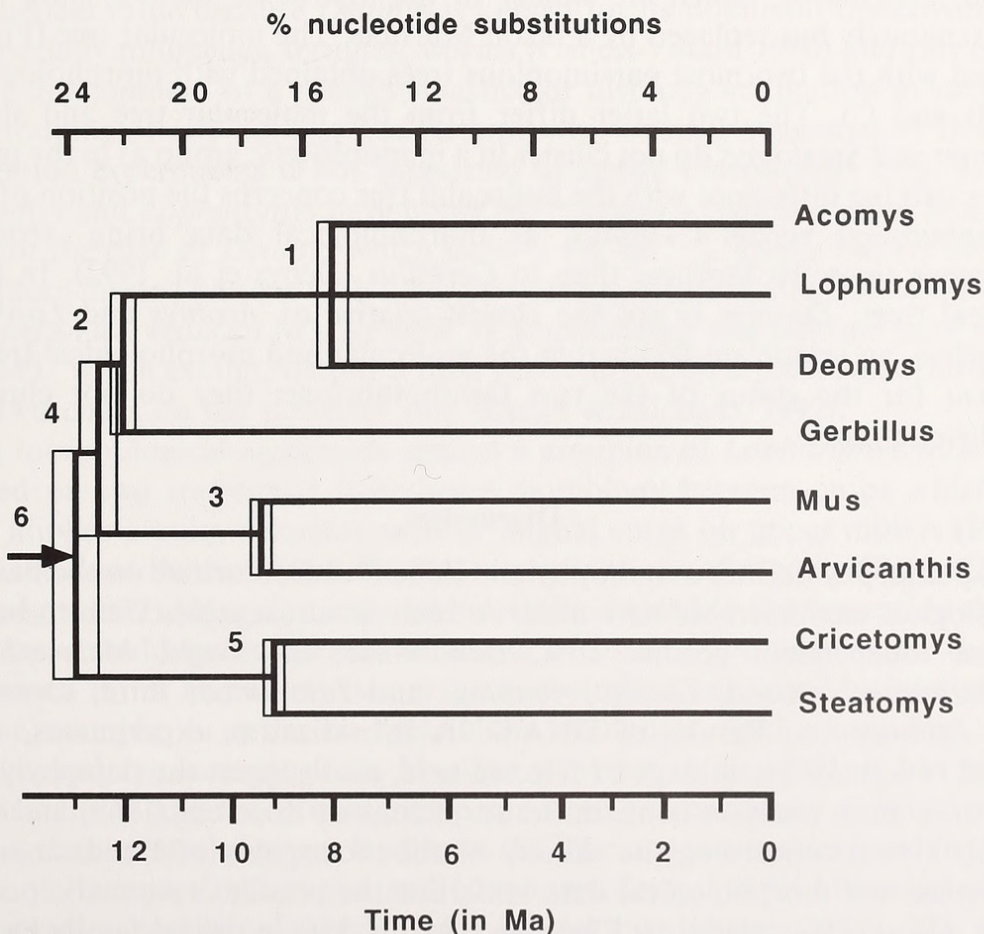


Fig. 4: Molecular tree reconstructed from delta-Tm distances of Table 4.

Table 4: DNA-DNA hybridization experiments: Delta-Tm values (in °C: average \pm standard-deviation; n: number of experiments), % nucleotide substitutions estimates, and datings of each dichotomy (in million years: Ma) derived from the molecular clock concept.

Node in Figure 4	Delta-Tm (°C)	% subst. nucl.	Time (Ma)
1) <i>Acomys</i> / <i>Lophuromys</i> / <i>Deomys</i>	11.6 \pm 0.4 (N = 9)	15.1	8.0
2) <i>Gerbillus</i> / <i>Acomys</i> et al.	16.4 \pm 0.2 (N = 14)	22.3	>11.9
3) <i>Mus</i> / <i>Arvicanthis</i>	13.2 \pm 0.2 (N = 6)	17.5	9.3
4) Murinae / <i>Gerbillus</i> + <i>Acomys</i> et al.	16.9 \pm 0.3 (N = 33)	23.1	>12.3
5) <i>Cricetomys</i> / <i>Steatomys</i>	12.8 \pm 0.2 (N = 3)	16.9	9
6) <i>Cricetomys</i> + <i>Steatomys</i> / other taxa	17.2 \pm 0.3 (N = 35)	23.7	>12.6
reference <i>Mus</i> & <i>Arvicanthis</i> / <i>Rattus</i>	14.1 \pm 0.6 (N = 10)	18.8	10

In a second step, a parsimony analysis of morphological variations has been conducted for only those taxa involved in the molecular approach. The two Murinae, *Mus* and *Arvicanthis*, which are similar in the matrix of Table 2, have not been treated separately but replaced by a taxon Murinae. The molecular tree (Fig. 5 A) is compared with the two most parsimonious trees obtained with morphological data (Fig. 5 B and C). The two latter differ from the molecular tree and show that *Cricetomys* and *Steatomys* do not cluster in a monophyletic group as in the molecular tree. The striking difference with the molecular tree concerns the position of *Acomys* and *Lophuromys* versus *Gerbillus*, as morphological data bring *Acomys* and *Lophuromys* closer to Murinae than to *Gerbillus* (Denys et al. 1992). In the morphological trees, *Deomys* is not the closest relative of *Acomys* and *Lophuromys*. Nevertheless, an important fact is that the molecular and morphological trees are in agreement for the status of the two Dendromurinae: they do not cluster in a monophyletic group.

Discussion

No synapomorphy defines a monophyletic clade Dendromurinae on the basis of the morphological characters we have used. At least dendromurines seem to be divided into four independent groups: first, *Dendromus*, *Steatomys*, *Malacothrix*, and *Megadendromus*, second, *Dendroprionomys* and *Prionomys*, third, *Deomys*, and fourth, *Leimacomys*. Results of DNA-DNA hybridization experiments, although restricted to a small assemblage of selected taxa, also suggest the paraphyly of Dendromurinae. Both analyses confirm the suspicions of Rosevear (1969) and Carleton & Musser (1984) concerning the validity of the monophyly of Dendromurinae.

Molecular and morphological data underline the peculiar systematic position of *Deomys*. *Deomys* was placed by Ellerman (1941; p. 316) in the subfamily Deomyinae on the basis of its skull characters (zygomatic plate abnormally narrowed and com-

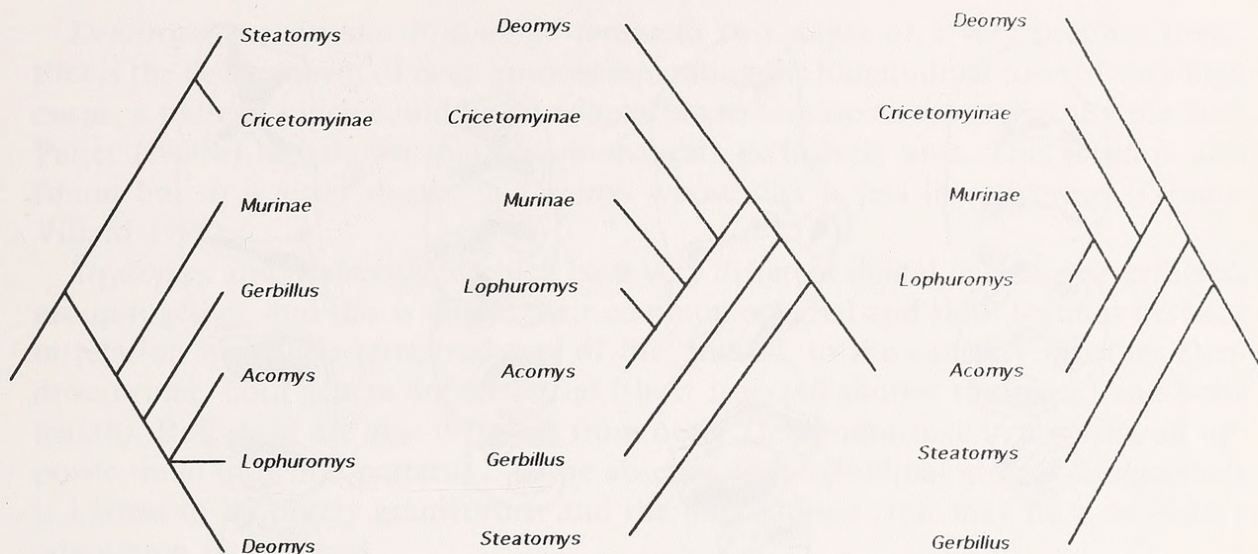


Fig. 5: Comparison of the molecular tree (A) with the two most parsimonious morphological trees (B, C) for the subset of taxa studied by both approaches.

pletely beneath the infraorbital foramen, infraorbital foramen nearly as wide as high, not narrowed below). This original skull morphology has perhaps not a phylogenetical value because *Deomys* is known for its dominant insectivorous diet, eating specially millipedes, termites, worms (Genest-Villard 1980) and this could explain the development of a peculiar masticator myology adaptation to such a diet.

The grouping of *Lophuromys* and *Acomys* with *Deomys* suggested by DNA-DNA hybridization experiments is not supported by dental morphology (Fig. 6). By the fact *Acomys* and *Lophuromys* have upper M1–2 with a typical murine morphology that is not the case of *Deomys* which lacks t1 on M1–2. Lower molars of *Deomys* show a more murine pattern with a bicuspidate anteroconid and a cv5 on lower M1. Both genera have reduced M3/3 (Table 3). *Lophuromys* and *Deomys* have relatively similar M3/ which exhibit, despite a high variability, a bicuspidate anterior lobe and one or two cusps on the posterior one (Denys & Michaux 1992).

These morphological arguments against a grouping of *Lophuromys* with *Deomys* are based on two traditional hypotheses: homology between cusps which consequently implies a unique development of lingual cusps on upper molars (following Lavocat 1967 and Petter 1966a). Careful reexaminations of modern (Petter 1967) and fossil (Jaeger 1977) Muroidae material more often lead to the suggestion that these lingual cusps could have appeared at several occasions, and in this case the lingual cusps named t1, t4 and t7 might not be homologous between Murinae and other taxa. For example, in order to explain the molecular results excluding *Acomys*, *Uranomys* and *Lophuromys* from Murinae (Chevret et al. 1993), it has been suggested that the t4 and the t1 could have appeared independently at least two times, namely in the ancestral segment leading to the Murinae sensu stricto and in the direct ancestor of *Acomys*, *Lophuromys* and *Uranomys*. Several fossil Myocricetodontinae also illustrate a parallel acquisition of a lingual cusp (Jaeger 1977). The observed polyphyly of Dendromurinae could result from a parallel acquisition, in different

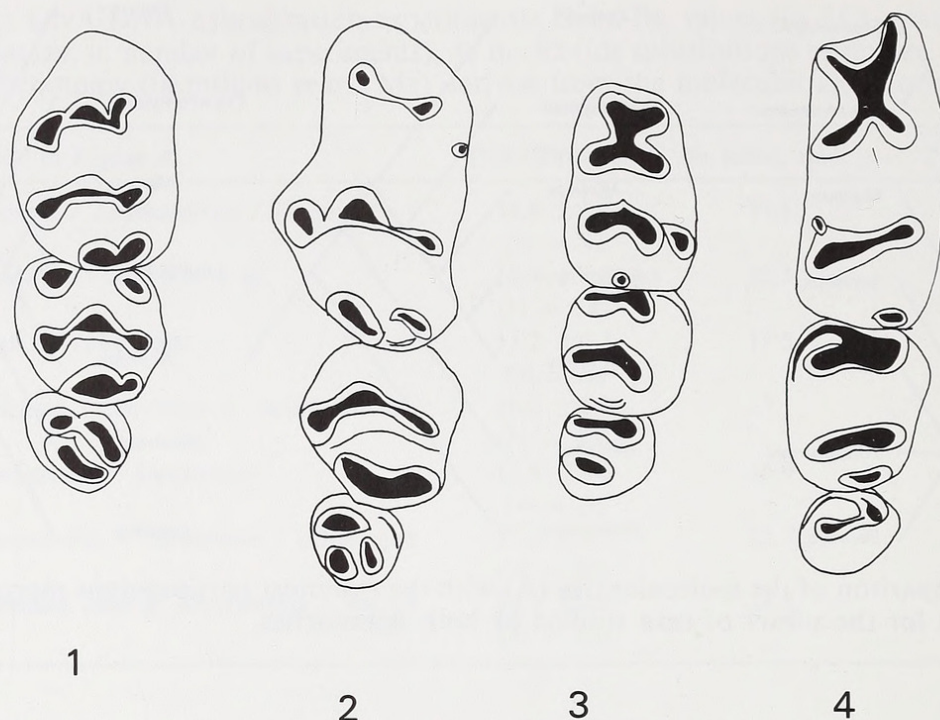


Fig. 6: Comparison of dental patterns of *Lophuromys cinereus* (1,3: type specimen, SMNS 18046) and *Deomys ferrugineus* (2,4: MNHN 1983-233).

lineages, of a centro-internal cusp (t4) from different primitive muroid ancestors. Indeed, many of the characters of Dendromurinae are shared with Petromyscinae, Delanyomyinae, Cricetomyinae, and even some Murinae of controversial position (*Acomys*, *Uranomys*, *Lophuromys*) (cf. Tab. 2).

The parsimony analysis indicates that the sister-taxon of *Leimacomys* is *Tatera* and that it belongs to a monophyletic group including *Gerbillus* and *Mystromys* (Fig. 3). The main reason for this clade is the absence in all these taxa of some cusps (absence of Cv5 on lower M/1–2, absence of t1 and t3 on upper M2–3/) found in all other Dendromurinae and Murinae. Nevertheless, *Leimacomys* do not show any sign of longitudinal crest nor any of the external or cranial characters of the Gerbillinae (Denys 1993). In opposition with *Mystromys* and the Gerbillinae, *Leimacomys* has a t4. The morphological cladogram illustrated by Figure 3 implies the appearance of t4 at least two times, one time in the ancestor of a large cluster including Cricetomyinae, *Deomys*, Murinae, *Acomys*-*Lophuromys* and six genera of Dendromurinae and in the other time, in a lineage to which belong Gerbillinae, *Mystromys*, and *Leimacomys*.

A remark can be made here concerning the position of *Mystromys*. Considered until present as a Cricetinae incertae sedis (Ellerman 1941; Carleton & Musser 1984; Denys 1991), it clusters here with Gerbillinae rather than with Murinae. According to DNA-DNA hybridization data of Rice (1974), *Mystromys* is as distant from true Murinae as from true Cricetinae. It is probable that *Mystromys* derives from an African Early Miocene radiation.

Dendroprionomys and *Prionomys* represent two stages of a very peculiar trend, that is the development of deep grooves separating the longitudinal rows of very high cusps, a pattern which could be an adaptation to an insectivorous diet. By the fact, Petter (1966b) has shown that *Prionomys* eats exclusively ants. This trend is also found but to a lesser degree in *Deomys* whose diet is less insectivorous (Genest-Villard 1980).

Steatomys and *Malacothrix* which have very different dental patterns nevertheless group together, and this is due to their common external and skull features perhaps in relation with their terrestrial way of life. Indeed, to the contrary of other Dendromurinae, both genera are terrestrial (short feet, tail shorter than head and body length). Both taxa are also different from other Dendromurinae in showing an opposite trend in dental pattern, i. e. the absence of longitudinal groove. *Malacothrix* is known to be purely granivorous and the longitudinal crest may be a secondary adaptation in this case.

Megadendromus derives clearly from *Dendromus* by acquisition of a very derived dental pattern and for its external and skull characters it looks like a giant *Dendromus* (Dieterlen & Rupp 1978). The acquisition of a t7 and of a longitudinal crest posterior to the t6 mimics the stephanodonty in Murinae (Schaub 1938; Michaux 1971; Jaeger 1983).

Conclusion

The analyses of skull and dental characters of the eight genera traditionally attributed to Dendromurinae give for the first time the extent of the morphological variability existing among this supposed monophyletic subfamily. Our data clearly suggest that Dendromurinae is not monophyletic and that the different genera belong at least to four lineages, with a parallel evolution of some morphological traits.

A first group made of *Dendromus*, *Malacothrix*, *Steatomys* and *Megadendromus*, is very consistent in all analyses and is probably monophyletic. A second group comprises *Prionomys* and *Dendroprionomys*. *Deomys* is an isolated lineage as well as *Leimacomys*. *Deomys* appears to be the sister group of *Acomys*, *Uranomys* and *Lophuromys*. In the present study, *Leimacomys* is related to Gerbillinae and to *Mystromys*.

The Dendromurinae as classically defined are the grouping of different lineages whose roots have to be traced back into at least Middle Miocene times, a time interval during which differentiated Muridae with neoformed lingual cusps (Jacobs 1978; Lavocat 1967; Lindsay 1988; Wessels et al. 1982). As fossils are only composed of dental remains and very rarely of skulls, fossil teeth will be very difficult to interpret as members of one or the other lineages recognized today because of parallel evolution in molars. Potential ancestors of the *Deomys-Acomys* lineage will be equally difficult to recognize. The dental criteria advocated by Lindsay (1988) — the presence of an enterostyle (t4) — is no longer reliable to identify Asiatic Miocene forms as members of the traditional Dendromurinae.

Despite some discrepancies between the phylogenetic interpretations of morphological and molecular data, both analyses agree on the fact that Dendromurinae

are not monophyletic. This implies that Dendromurinae do not constitute a natural taxon independently of the question of their rank in the classification of the Muroidea.

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Zusammenfassung

Alle acht bekannten Gattungen der Dendromurinae wurden erstmals vergleichend-morphologisch analysiert, mit Schwergewicht auf Merkmalen der Bezahnung. Die Ergebnisse werden im Vergleich mit anderen afrikanischen Muridae diskutiert. Das Taxon „Dendromurinae“ ist offensichtlich paraphyletisch und beinhaltet möglicherweise vier unabhängige Entwicklungslinien. Die erste umfaßt *Dendromus*, *Steatomys*, *Malacothrix* und *Megadendromus*; eine zweite *Prionomys* und *Dendroprionomys*. Eine dritte und vierte Einheit bilden *Deomys* und *Leimacomys*; letztere Gattung gruppiert nächst einigen Vertretern der Gerbillinae (*Gerbillus*, *Tatera*). Zwei Gattungen (*Deomys*, *Steatomys*) wurden mit der DNA-DNA Hybridisierungstechnik untersucht; die Resultate stützen insoweit die morphologischen Ergebnisse, als beide Gattungen keine monophyletische Gruppe bilden. Der Status des Taxon „Dendromurinae“ muß revidiert werden.

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