

## PATTERNS OF MYOXID EVOLUTION IN THE PLIOCENE AND PLEISTOCENE OF EUROPE

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**ABSTRACT** – The origin of recent species belonging to the genera *Myoxus*, *Muscardinus*, *Glirulus*, *Eliomys*, *Dryomys* and *Myomimus* is discussed. Evolution of myoxids in the Pliocene and Pleistocene is expressed by gradual size increase of their cheek teeth. No gradual change in the dental pattern is observed.

**Key words:** Evolution, Myoxidae, Dental pattern, Pliocene, Pleistocene.

**RIASSUNTO** – *Modelli di evoluzione dei Mioxidi nel Pliocene e Pleistocene in Europa* – Viene discussa l'origine delle specie recenti appartenenti ai generi *Myoxus*, *Muscardinus*, *Glirulus*, *Eliomys*, *Dryomys* e *Myomimus*. L'evoluzione dei Mioxidi nel Pliocene e nel Pleistocene è espressa da un graduale aumento delle dimensioni dei molari. Non è stato osservato alcun cambiamento graduale nel pattern dentale.

**Parole chiave:** Evoluzione, Myoxidae, Struttura dentale, Pliocene, Pleistocene.

### INTRODUCTION

The Miocene flowering of dormice (Myoxidae) was already over by the Pliocene (Daams, 1981; Daams & de Bruijn, 1995). On the mainland of Europe, only the extant genera *Myoxus* Zimmermann, 1780 (= *Glis* Brisson, 1762), *Muscardinus* Kaup, 1829, *Glirulus* Thomas, 1905, *Eliomys* Wagner, 1840, *Dryomys* Pallas, 1778 and *Myomimus* Ognev, 1924 as well as the extinct genera *Dryomimus* Kretzoi, 1959 and *Plioselevinia* Sulimski, 1962 survived the Messinian crisis, which probably took place around the Miocene/Pliocene boundary. It is also generally assumed that the Mediterranean islands were colonised by *Eliomys* at this time and, as a result of isolation, soon became differentiated there into peculiar myoxids (treated as subgenera of *Eliomys*): *Hypnomys* Bate, 1918 (Balearic Islands), *Eivissia* Alcover et Agusti, 1985 (Balearic Islands), *Tyrrhenoglis* Engesser, 1976 (Sardinia) and *Maltamys* Zammit Maempel et de Bruijn, 1982 (Malta and Sicily) and by a giant dormice *Leithia* Adams, 1863 (Malta and Sicily) of unknown origin (Agusti & Moyá-Solá, 1990; Zammit Maempel & de Bruijn, 1982). These Mediterranean dormice were relatively common in the above mentioned islands during the Pleistocene but they have gradually become extinct, to be replaced by the present fauna (including *Eliomys* s.s. and *Myoxus*).

At present the Myoxidae comprises about 28 species belonging to 8 genera (Holden, 1993) from which 3 species (*Myoxus glis* Linnaeus, 1766, *Muscardinus avellanarius* (Linnaeus, 1758), *Eliomys quercinus* (Linnaeus 1766) are almost entirely of European distribution. *Dryomys nitedula* (Pallas, 1778) is present in Europe, Asia Minor, Afghanistan and Iran while *Myomimus roachi* (Bate, 1937) occurs in the Balkan peninsula and Asia Minor (Storch, 1978). On the basis of

studies undertaken on cranial morphology and enamel ultrastructure, *Selevinia* Belosludov et Bashanov, 1939 and *Plioselevinia* should also be incorporated into the Myoxidae (Koenigswald, 1993; Storch, 1995; Wahlert et al., 1993).

In the present paper the origin and evolution of the extant mainland European myoxids and *Glirulus* during the last 5-6 million years (Pliocene and Pleistocene) are discussed.

## ORIGIN AND PLIOCENE-PLEISTOCENE HISTORY OF THE EUROPEAN GENERA

### FAIR DORMICE (*Myoxus*)

The genus is known from almost all parts of Europe since the beginning of the Miocene, although in most fossil assemblages it is extremely rare (Agusti, 1981; Daams, 1976; de Bruijn & Rumke, 1974; Kowalski, 1967; Mayr, 1979; Van der Meulen & de Bruijn, 1982). In spite of this limited information it seems that the few specimens found so far belong to different species (e.g. *M. major* (de Bruijn et Rümke, 1974), *M. truyolsi* (Daams, 1976), *M. apertus* (Mayr, 1979), *M. vallesiensis* (Agusti, 1981), *M. galitopouli* (Van der Meulen et de Bruijn, 1982). However, it is impossible on the basis of present knowledge to decide which of these Miocene species would be the ancestor of the lineage leading to the extant species.

It seems that in the Pliocene and Pleistocene only one well established lineage is present (*M. minor* (Kowalski, 1956) - *M. sackdillingensis* Heller, 1930 - *M. glis* Linnaeus, 1766). The following changes are observed in the stratigraphical sequence of the fossil *Myoxus* assemblages during this time:

- (1) a change from relatively complicated morphotypes of molars to simpler ones, which is best seen in  $M^2$  (the simplification constitutes the loss of extra ridges) (Fig. 1) and
- (2) a gradual size increase of the molars although the oldest two assemblages do not form part of this size trend (Fig. 2) (cf. Daoud, 1993).

### COMMON DORMICE (*Muscardinus*)

The genus has a slightly shorter history than *Myoxus*. The Middle and Late Miocene taxa apparently represent 2-3 lineages of different size and dental morphology (Hugueney & Mein, 1965; de Bruijn, 1966; Hartenberger, 1966; Van de Weerd, 1976). They are represented by *Muscardinus* (*Muscardinus*) and *M. (Eomuscardinus)* which probably have a common ancestor. The *M. hispanicus* de Bruijn, 1966 - *M. vireti* Hugueney et Mein, 1965 group represents the lineage of *Muscardinus* (sensu stricto) of smallest dimensions. The Pliocene descendant of this lineage is possibly *M. helleri* (Fejfar & Storch, 1990) (Fig. 3). Already in the Late Miocene there appear *Muscardinus* species (*M. heintzi* Aguilar, 1981 and *M. davidi* Hugueney et Mein, 1965) with relatively wide molars the length of which is comparable with that of the recent species (Aguilar, 1982). The third lineage is represented by the *M. pliocaenicus* - *avellanarius* group which has survived to recent times. Large sized *Muscardinus* species (*M. dacicus* Kormos, 1930, *M. giganteus* Janossy, 1974, *M. cyclopeus* Agusti, Moya-Sola et Pons Moya, 1982) are also present in the Pliocene (Agusti & Moyá-Solá, 1990; Daoud, 1993; Jánossy, 1974; Kowalski, 1963). Thus, during the Pliocene the common dormice

were much more diversified than at present. In many localities 2-3 species of *Muscardinus* occurred sympatrically. Towards the end of this period most of them vanished and since the Middle Pleistocene only the extant species has been present in European faunas.

Stratigraphy	Types				N	Species
	M <sup>2</sup>					
	Loc.	1	2	3		
Recent	REC	47	—	—	47	<i>M. glis</i>
	LQ	3	—	—	3	
Pleistocene	KG	22	12	62	96	<i>M. sackdillingensis</i>
	ZAI	1	—	5	6	
	KII	13	7	15	35	
	KA	6	1	41	48	
	KDI	2	—	1	3	
Pliocene	RK1A	5	—	4	9	<i>M. minor</i>
	WE1	14	—	7	21	
	PN	2	—	2	4	
	PO	17	—	4	21	

Fig. 1 – Variation of M<sup>2</sup> in the *Myoxus* lineage from Early Pliocene to Recent in Central Europe. Important change of the frequency of morphotypes occurs around the Pliocene / Pleistocene boundary (KDI / KA, suggests replacement of *M. minor* by *M. sackdillingensis*) and in the end of Early Pleistocene (KG / LQ, appearance of the extant species *M. glis*). Localities: PO - Podlesice, PN - Panska Gora, WE1 - Wefe 1, RK1A - Rebielice Królewskie 1A, KDI - Kadzielnia 1, KA - Kamyk, KII - Kielniki 1, ZAI - Zalesiaki 1, KG - Kozi Grzbiet, LQ - Late Quaternary, REC - recent population (for details see Daoud, 1993).

Changes similar to those that were observed in the *Myoxus* lineage are seen in the stratigraphical sequence of fossil *Muscardinus pliocaenicus* Kowalski, 1963 - *M. avellanarius* (Linnaeus, 1758) assemblages in the Pliocene and Pleistocene:

- (1) a change of relatively complicated morphotypes to simpler ones, evidenced mainly in M<sup>1</sup> (the simplification consists of the loss of extra ridges) (Fig. 4) and
- (2) a size increase of the molars (Fig. 3) (Daoud, 1993).

#### FOREST DORMICE (*Dryomys*)

The origin of *Dryomys* is enigmatic because of the scarcity of fossil remains of this genus. Its close relationship with some *Microdryomys* de Bruijn, 1966 species is sometimes suggested (Daams, 1995). The oldest remains of forest dormice come from the Middle and Upper Miocene of North Africa (Jaeger, 1975, Lavocat, 1961). However, teeth with dental patterns similar to those of *Dryomys* have also been recognized in Europe in the Upper Miocene and Pliocene. *Dryomys* remains from the Pleistocene record (e.g. Latomi 1, Kozi Grzbiet) probably belong to the

extant species (Daoud, 1993; Storch, 1975). No evolutionary trends of the dental pattern are observed in this lineage. Thus, the reconstruction of the Plio-Pleistocene evolution of *Dryomys nitedula* (Pallas, 1778) is impossible on the basis of present knowledge.

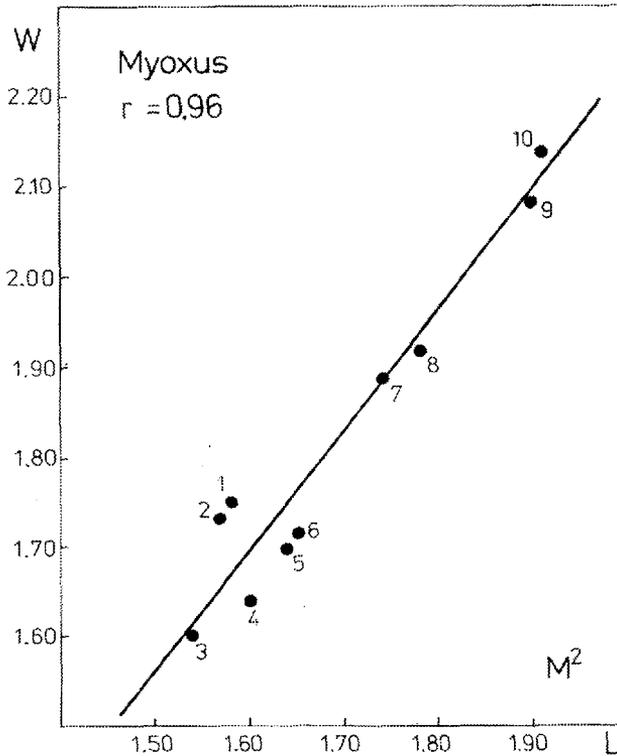


Fig. 2 – Relation (mean values) between length (L) and width (W) of the  $M^2$  assemblages of the Pliocene and Pleistocene *Myoxus* in Middle Europe. Locality numbers 1-10 indicate stratigraphical order. 1 - Pańska Góra (N = 4), 2 - Podlesice (N = 21), 3 - Weże 1 (N = 21), 4 - Rebiclice Królewskie 1A (N = 9), 5 - Kamyk (N = 48), 6 - Kielniki 1 (N = 35), 7 - Zalesiaki 1 (N = 6), 8 - Kozi Grzbiet (N = 96), 9 - Late Quaternary (N = 3), 10 - recent population (N = 47) (for details see Daoud, 1993).

#### GARDEN DORMICE (*Eliomys*)

The first fossil evidence of *Eliomys* is from the Middle Miocene of Spain (Daams & de Bruijn, 1995). Most probably it is a descendant of *Microdryomys*. In the Late Miocene the genus was probably diversified into 3-5 species (e.g. *E. assimilis* Mayr, 1979, *E. reductus* Mayr, 1979, *E. truci* Mein et Michaux, 1970) which can be distinguished on the basis of morphology of both lower and upper molars (Adrover, 1986; Mayr, 1979). Around the Mio / Pliocene boundary in the south of Europe *E. intermedius* Friant, 1953 appears. This species is larger than *E. truci* and differs in some details of the morphology of upper molars (Van de Weerd, 1976). Probably at that time an immigration of *Eliomys* to the Mediterranean Islands and rapid radiation into *E. (Hypnomys)*, *E. (Eivissia)*, *E.*

(*Tyrrhenoglis*) and *E. (Maltamys)* (Zammit Maempel & de Bruijn, 1982) took place. The extant species *E. quercinus* (Linnaeus, 1766) makes its appearance most probably in the Pliocene but its ancestry is enigmatic. Morphologically it is more similar to some rare fossil species such as *E. assimilis* and *E. reductus* than to the species common in Europe during the Late Miocene and Pliocene (*E. truci* and *E. intermedius*). During the Pliocene and Pleistocene no important changes in the morphology and tooth size of the garden dormouse took place.

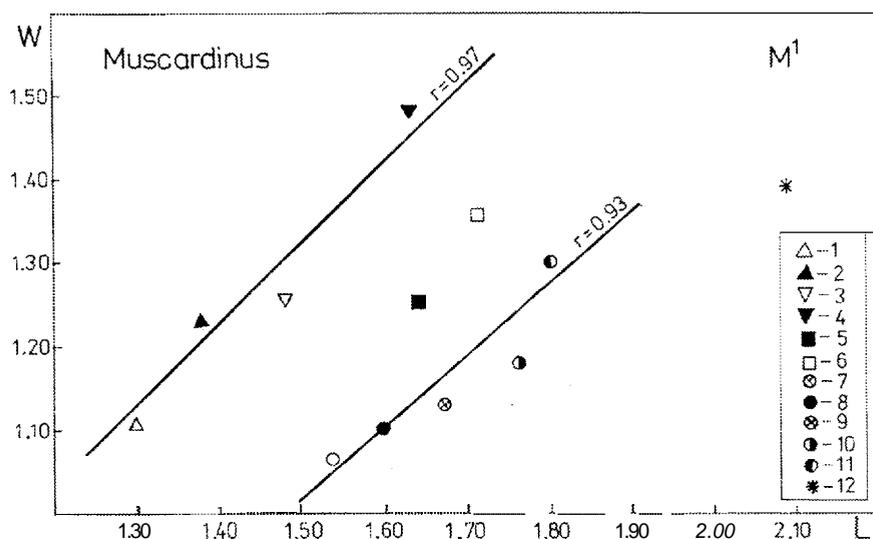


Fig. 3 – Relation (mean values) between length (L) and width (W) of the  $M^1$  assemblages of different species of *Muscardinus* s. s. 1 - *M. hispanicus*, Pedregueras 2C, Late Miocene (Vallesian), N = 20 (Van de Weerd, 1976); 2 - *M. hispanicus*, Can Llobateres, Late Miocene (Vallesian), N = 8, (Van de Weerd, 1976); 3 - *M. vireti*, Lissieu, Late Miocene (Turolian), N = 14 (Hugueney & Mein, 1965); 4 - *M. helleri*, Gundersheim, Early Pliocene (Ruscinian), N = 3 (Fejfar & Storch, 1990); 5 - *M. davidi*, Lissieu, Late Miocene (Turolian), N = 3 (Hugueney & Mein, 1965); 6 - *M. heintzi*, Montredon, Late Miocene (Vallesian), N = 7 (Aguilar, 1982); 7 - *M. pliocaenicus*, Panska Góra, Early Pliocene (Ruscinian), N = 2 (Daoud, 1993); 8 - *M. pliocaenicus*, Podlesice, Early Pliocene (Ruscinian), N = 17 (Daoud, 1993); 9 - *M. pliocaenicus*, Rebielice Królewskie 1A, Late Pliocene (Villanyian), N = 3 (Daoud, 1993); 10 - *M. avellanarius*, Kozi Grzbiet, Early Pleistocene, N = 25 (Daoud, 1993); 11 - *M. avellanarius*, recent population, N = 60 (Daoud, 1993); 12 - *M. dacicus*, Podlesice, Early Pliocene (Kuscinian), N = 5 (Daoud, 1993).

#### JAPANESE DORMICE (*Glirulus*)

The only extant species of the genus, *Glirulus japonicus* (Schinz, 1845) inhabits Japan. However, fossil representatives are found in the Neogene of Europe. The genus appeared in the Early Miocene but its origin is uncertain; possibly it is descended from *Microdyromys* or *Bransatoglis* Hugueney, 1967 (Van der Meulen & de Bruijn, 1982). The Middle Miocene taxa are included in a separate subgenus *G. (Paraglrulus)* represented by two species *G. (Paraglrulus) werenfelsi* (Engesser, 1972) and *G. (P.) agelakisi* (Van der Meulen et de Bruijn, 1982). The development of the subgenus *Glirulus* was often reconstructed by the

lineage: *G. (Glirulus) diremptus* (Mayr, 1979) - *G. (G.) lissiensis* Huguency et Mein, 1965 - *G. (G.) pusillus* Heller, 1936 - *G. (G.) japonicus* (Daxner-Hock & de Bruijn 1981; Van der Meulen & de Bruijn, 1982). The first two species evolved in Europe during the Late Miocene. Recent discovery of fossilised soft parts of the body of *G. lissiensis* (Mein & Romaggi, 1991) showed adaptations to a gliding mode of life. The third fossil species, *G. pusillus* is a rare member of the Pliocene faunas of Europe and survived until the Early Pleistocene. Around the Pliocene / Pleistocene boundary the ancestral form of *G.japonicus* possibly emigrated from Europe to Japan where the genus survived to recent times. The Pliocene populations of *G. pusillus* do not differ morphologically from the extant species. However, their teeth are distinctly smaller than those of the Japanese species (Bednarczyk, 1993; Daoud, 1993; Kawamura, 1989).

Stratigraphy	Types				N	Species
	M <sup>1</sup>	1	2	3		
Loc.						
Recent	REC	58	—	2	60	<i>M.avellanarius</i>
Pleistoc.	LQ	3	—	—	3	
	KG	16	7	—	23	
Pliocene	RK1A	2	1	—	3	<i>M.pliocaenicus</i>
	WE1	—	1	—	1	
	PN	—	2	—	2	
	PO	1	16	—	17	

Fig. 4 – Variation of M<sup>1</sup> in the *Muscardinus pliocaenicus* - *avellanarius* lineage from the Early Pliocene to Recent in Central Europe. Important change in the frequency of morphotypes occurs probably in Late Pliocene or during Early Pleistocene (RK1A - KG) which indicates replacement of *M. pliocaenicus* by *M. avellanarius*. For abbreviations of names of localities see Fig. 1 (for details see Daoud, 1993).

MOUSE-TAILED DORMICE (*Myomimus*)

The only European species belonging to the subfamily Myomiminae - *Myomimus roachi* is a member of a group of glirids, which were very diverse in the Miocene. The genus *Myomimus* is probably a descendant of *Peridyromys* Stehlin et Schaub, 1951 and appeared in the Middle Miocene (Daams, 1981). *Myomimus* becomes more widely distributed in Late Miocene sediments, but is only known from Spain and the eastern Mediterranean region. In the Pliocene the mouse-tailed dormice were represented by the *M. maritsensis* de Bruijn, Dawson

et Mein, 1970 - *M. roachi* lineage (de Bruijn et al., 1970); the distribution of which seems to have been then restricted to the Balkan Peninsula, Asia Minor and Israel. This lineage shows a distinct tendency towards simplification of the dental pattern and size increase of molars. The extant species occurred in SW-Europe since the Middle Pleistocene.

## DISCUSSION

Myoxids are one of the oldest families of rodents. Various anatomical studies (cf. Koenigswald, 1993; Wahler et al., 1993) confirmed the point of view that the various genera show greater taxonomic distances than are normally observed between genera in other rodent families. This is probably connected with the very long independent evolution of the particular lineages. The basic dental morphology of the genera discussed above was already present during Early and Middle Miocene times, and has not changed significantly ever since in each particular lineage. The morphological patterns of cheek teeth of Myoxidae show a variation which can be expressed in terms of morphotype variability as was done by Daams (1981). These morphotypes are distinguished on the basis of (1) the shape of enamel ridges visible on the occlusal surface, (2) the manner of interconnection between them and (3) the occurrence of extra ridges. Most often, only one morphotype predominates in each population studied and others occur only occasionally. In a few cases (e.g.  $M^2$  of *Myoxus*), in particular populations, different morphotypes prevail (Daoud, 1993), which suggests the hereditary background of these changes.

The general morphological dental patterns of Myoxidae do not change so gradually with time as is seen in other groups of Neogene and Quaternary rodents. Various taxonomic studies have shown that particular genera or groups of species are characterized by a combination of features and not by the exclusion of features. In spite of the great intrapopulation variability preserved in some genera, the morphological directional changes, especially during the Pliocene and Quaternary, were slight and even negligible in most species. Particular morphotypes of glirid cheek teeth have no adaptive value and are not subject to linear selection.

Generally, in most lineages, evolution is only expressed by size increase of the cheek teeth. In most cases, these tendencies seem to be gradual processes. The size increase of the molar surface may suggest an increase in the whole body size of these dormice from the Pliocene to recent times.

However, especially in the *Myoxus* lineage, animals from the Early Pliocene are significantly larger than the Late Pliocene samples. The same tendency is observed in the *Muscardinus* lineage, although it is not so distinctly expressed (Daoud, 1993).

Various explanations of this phenomenon can be offered. The first arises from possible climatic changes during the Pliocene. In this case the body size changes according to Berginann's rule, which states that the size of homoiothermic vertebrates is larger in a cool climate. The second explanation is based on the possible competition occurring between myoxids and species belonging to very expansive, new families of rodents (e.g. Muridae, Arvicolidae) which have

undergone important development during the Pliocene. Changes in body size can be accounted for as an adaptation to new arrangements within ecological niches.

It is known that Myoxidae are very rare members of recent vertebrate communities. However, it is interesting to note, that the frequency of myoxids found in some fossil assemblages, especially those from uppermost Early Pleistocene sediments, may be very high. Such a situation is observed, for instance, in the Early Pleistocene locality Kielniki 1 (Poland) where 90% of the fossil remains belong to *Myoxus sackdillingensis*, while in Kozi Grzbiet (Poland) this species occurs with a frequency of almost 35% (Daoud, 1993). In most Pliocene and Early Pleistocene localities from Europe the frequency of *Myoxus* fluctuates between 3% and 15%. Late Quaternary and Holocene assemblages are characterized by a very low frequency, which, in most cases, does not exceed 1%. These distinct differences may originate in different taphonomic processes which lead to accumulation of fossil assemblages. However, we cannot exclude the possibility that the Myoxidae were more numerous during the Early Pleistocene in Central Europe than they are now.

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