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# AFFINITIES AMONG LIVING DORMOUSE GENERA

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ABSTRACT – This paper focuses on relationships among the living Palaearctic myoxid genera, excluding the African hystricomorphous graphiurines. Features of the dental occlusal pattern, skull, enamel ultrastructure of the lower incisors, muscles of mastication (in particular, the ptergoids), external male genital morphology, and auditory region are reviewed. A working hypothesis of possible evolutionary relationships among myoxids and a new classification of Seleviniinae (including *Selevinia*, *Chaetocauda*, and *Myomimus*) are proposed. Most characters closely group *Eliomys* with *Dryomys* (= Dryoinyinae) and *Myoxus* with *Glirulus* (= members of Glirinae). The Seleviniinae are considered most primitive and *Muscardinus* most advanced among living dormice.

Key words: Myoxidae, Evolution, Systematics, Taxonomy, Morphology.

RIASSUNTO – *Affinità tra i generi viventi di Mioxidi* – Questo lavoro è incentrato sulle relazioni esistenti tra i generi paleartici viventi di Mioxidi, con esclusione dei Grafiurini Istricomorfi africani. Vengono riesarninati caratteri quali: pattern di occlusione dentale, cranio, ultrastruttura dello smalto degli incisivi inferiori, muscoli della masticazione (in particolare gli pterigoidei), morfologia genitale estema inaschile e regione auditiva. Vengono proposte una ipotesi di lavoro delle possibili relazioni evolutive tra i Mioxidi ed una nuova classificazione dei Seleviniinae (che includono *Selevinia, Chaetocauda e Myomimus*). Molti caratteri raggruppano *Eliomys* con *Dryomys* (= Dryomyinae) e *Myoxus* con *Glirulus* (= Glirinae). I Seleviniinae sono considerati i piu primitivi e *Muscardinus* il piu avanzato tra i Mioxidi viventi.

Parole chiave: Myoxidae, Evoluzione, Sistematica, Tassonomia, Morfologia.

## INTRODUCTION

Extant myoxoids (= gliroids) are a small and apparently well-defined group of Old World rodents. Synapomorphies of the Palaearctic genera include brachyodont cheek-teeth with transverse crests, the acquisition of a "pseudomyomorphous" zygomasseteric structure, and the lack of a caecum and of a definite boundary between colon and small gut. However, the African genus *Graphiurus* does not fit such diagnoses, Graphiurines show a primitive configuration of the lateral masseter muscle: Its origin is confined to the ventral and lateral surface of the zygomatic arch and its superficial and deep portions are only slightly separated anteriorly (Tullberg, 1899). The genus is hystricomorphous and thus departs from the myomorphous condition of the other myoxids. The fossil record of *Graphiurus* extends back only to the African Plio/Pleistocene. This is inconsistent with the view of retained primitive characters by which *Graphiurus* would represent a very early branch of the European Paleogene myoxids. Quite recently, Vinney-Liaud &

Jaeger (1993) presented a new and intriguing hypothesis, supported by new data and new fossils. It suggests that the family Graphiuridae originated from the African fossil family Zegdoumyidae (and not from an European myoxid stemgroup) and is closely related to the anomalurids. Further discussions must await detailed description and interpretation by Vianey-Liaud and Jaeger.

I will restrict this report to features of the extant Palaearctic myoxid species. It should be noted, however, that comparisons based only on the living members of a particular group do not cover all characteristics and all biological adaptations which occurred during its evolutionary history. For example, fossil dormice are known which possessed gliding membranes (Mein & Romaggi, 1991), others had decidedly hypsodont cheek-teeth (Daams, 1990), and some Paleogene taxa showed a primitive protrogomorphous infraorbital foramen (Vianey-Liaud, 1989).

As previously understood, myoxoids comprise the families Myoxidae (= Gliridae) and Seleviniidae. Platacanthomyids, an alleged myoxoid subfamily or family in Ellerman's (1940) and Simpson's (1945) classifications, are assigned to Muroidea by dental and cranial evidence (Stehlin & Schaub, 1951). Myoxoids have a very long and independant fossil history, dating back in Europe to the late Early Eocene (Hartenberger, 1971; Vianey-Liaud, 1989), and supposedly they have acquired a myomorphous zygomasseteric structure independently from other major rodent clades. Hence myoxoids are best classified as a suborder of their own, Glirimorpha Thaler, 1966. A suite of additional dormouse characters corroborates this view. However, the subdivision of the Glirimorpha and the phylogenetic relationships among their various genera are still a matter of dispute.

This paper focuses on the grouping and affinities of the living Palaearctic glirimorph genera. It reviews recent relevant papers on features of the dentition, skull, enamel ultrastructure, muscles of mastication, external genital morphology, and auditory region. Finally, I present my current understanding of affinities among dormouse genera and propose a new classification of the Seleviniinae.

## DENTAL PATTERN

The occlusal pattern is the major feature on which paleontologists base their classifications. Systematic groupings rely on characters like the degree of concavity and cusp development; the number and relative length and height of main- and extra-ridges; the formation of a trigon and central basin; the position of the protocone (or actually the place where protoloph and metaloph meet lingually); and the presence or absence of an endoloph. The assessment of character polarity - primitive or derived states - usually refers to a basic pattern of geologically early taxa, in particular of *Gliravus*. (In *Gliravus*, the molars are concave and show prominent main-cusps and relatively poorly developed ridges; anteroloph and posteroloph are lower than the V-shaped proto- and metaloph; there is a central basin; and the protocone is situated halfway along the crown length). Even so, some higher taxa were essentially based on symplesiomorphic dental characters, for instance the subfamily Graphiurinae as defined by Kretzoi (1943).

Evolutionary changes of dental patterns which become obvious from the fossil record, are used to reconstruct phylogenetic lineages and phylogenetic trees up to the living genera. Results are exemplified by Chaline & Mein's (1979) and Daams' (1981) views. Myoxid subfamilies, including the fossil taxa, were diagnosed by Daams (1981) and the extant genera were grouped by him as follows:

1) Glirinae *(Myoxus, Muscardinus):* Molars flat or slightly concave, main cusps weak or absent, extra ridges tend to be situated labially in the upper and lingually in the lower molars, occlusal pattern usually complicated.

2) Dryomyinae (*Dryomys*, *Eliomys*, *Glirulus):* Molars concave, extra ridges generally narrower than main ridges, generally with endoloph on M1-2/, occlusal pattern usually complicated.

3) Myomiminae (*Myomimus*): Molars concave, main cusps fairly well-developed, extra ridges narrower than main ridges, generally no endoloph on M1-2/, simple occlusal pattern.

There is consensus from most classifications that the occlusal pattern closely groups *Eliomys* with *Dryomys*. In more recent studies, *Myomimus* takes a rather remote position as does *Myoxus*. The classification of *Glirulus* and *Muscardinus* is somewhat controversial, *Glirulus* being either assigned to the Dryomyinae (Daams, 1981) or taking an isolated position (subfamily Glirulinae; de Bruijn, 1967), and *Muscardinus* being either referred to Glirinae (= Myoxinae) (de Bruijn, 1967; Daams, 1981) or representing a rather independant lineage (Kretzoi, 1943; Thenius, 1969). The Chinese dormouse *Chaetocauda* was described recently by Wang Youzhi (1985). Wang obviously accepted Daams' classification. He included *Chaetocauda* in Myomiminae.

Future work on dormouse teeth should stress the functional and constructional arguments in order to assess character polarity. I think that more significant than numbers of crests and valleys could be their cross-sectional views or the relationships between the widths of ridges and valleys. Van der Meulen & de Bruijn (1982) demonstrated that flatness is a derived character and most probably related to the acquisition of a more longitudinally directed power stroke during mastication.

## PAUP ANALYSIS OF CRANIAL AND DENTAL CHARACTERS

Wahlert, Sawitzke & Holden (1993) selected 43 osteological and 11 dental characters of living dormice which served as the basis for a "Phylogenetic analyis using parsimony." Cranial foramina played an important role among these characteristics. They reached the following conclusions: The living myomorphous genera cluster into two groups of subfamily rank, their Leithiinae and Myoxinae. Leithiinae consists of two tribes, the Leithiini (with *Eliomys* and *Dryomys*) and the Myomimini (with *Myomimus* and *Selevinia*). Myoxinae includes *Myoxus*, *Glirulus,* and *Muscardinus*. Leithiinae share among other features a perforated angular process and low inclination of the coronoid process of the mandible, a squamosal containing a fenestra or emarginate posteriorly, and a complete transverse valley in M/2. Myoxinae have lost or largely reduced the sphenofrontal and stapedial foramina, the occlusal surface of the molars is nearly flat and marked by prominent accessory ridges, and the coronoid process arises in an anterior position, thus concealing most or all of M/3 in lateral view.

In most PAUP generated trees, *Myoxus, Glirulus,* and *Muscardinus* occur as a clade and *Eliomys* is usually associated with *Dryomys.*

*Myomimus* commonly groups with *Eliomys* and *Dryomys*, and takes a basal position in some of the trees. The authors stressed various apomorphous dental characters: *Eliomys* and *Dryomys* share the peculiar cross-sectional shape of the upper incisors and a primitive molar pattern; *Myomimus* has premolars of reduced size; *Selevinia* has no premolars in adults and small molars with simple basined crowns: *Myoxus* and *Muscardinus* share the presence of more than one entire transverse valley in M/2; *Glirulus* has lower cheek teeth with a lingual connecting crest and upper and lower second molars with 4 or more accessory crests; and *Muscardinus* has reduced premolars, flat crowns, and 3 transverse valleys on M/2.

Wahlert et al. (1993) also considered and supplemented Bugge's (1974, 1985) observations on the cranial arterial patterns. In the more primitive condition of *Eliomys*, *Dryomys*, and *Myomimus* the stapedial artery system is well developed. In the more derived patterns of *Myoxus, Glirulus,* and *Muscardinus* the stapedial artery system is reduced in favor of the external carotid system. The stapedial artery is absent in adult specimens of *Myoxus,* and the stapedial artery stem is completely obliterated in *Glirulus* and *Muscardinus.*

## ENAMEL MICROSTRUCTURE OF LOWER INCISORS AND SIZE OF AUDITORY REGION

The enamel on the labial surface of rodent incisors is composed of two layers. The enamel microstructure of the inner layer shows some variation which is widely used in the classification of major rodent clades such as suborders but which can also be distinctive at family level. W. von Koenigswald's (1993) recent studies revealed that the enamel pattern of living and fossil dormice is more diverse than in most other rodent groups. **All** myoxoids have uniserial Hunter-Schreger bands in the portio interna of the incisors i.e. alternating prism layers, which are usually one prism thick, have a similar orientation. Koenigswald observed in the lower incisors of dormice an increasing tilt of the Hunter-Schreger bands relative to a transverse plane of the tooth, which ranges from almost transverse to longitudinal. Tranversely arranged Hunter-Schreger bands were considered primitive and the shared derived character of longitudinally oriented bands was supposed to have evolved by parallelism to other rodent groups. Koenigswald stated that the rearrangement of the Hunter-Schreger bands is hard to explain biomechanically. On the basis of the observed schmelzmuster of the portio interna on the lower incisors he referred the living dormouse genera to three different groups, without giving these formal taxonomic ranks:

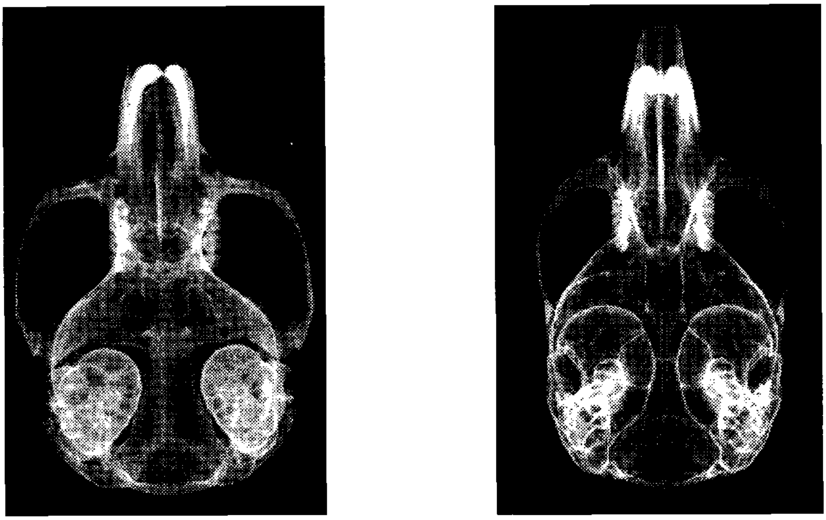
Group 1) *Myoxus* and *Glirulus* have transverse, only slightly tilted Hunter-Schreger bands. **A** thick prism-free outer layer of the portio externa on the lower incisors is a synapomorphous character of the two genera.

Group 2) *Dryomys* and *Eliomys* are more derived in having diagonally oriented Hunter-Schreger bands. The bands rise at an angle of maximally 45" from the lateral toward the mesial side of the incisor.

Group 3) *Myomimus*, *Selevinia* and *Muscardinus* show longitudinally arranged Hunter-Schreger bands.

Koenigswald's grouping of *Myoxus* with *Glirulus, Dryomys* with *Eliomys*, and *Myomimus* with *Selevinia* is in agreement with other current classifications (e.g. Wahlert et al., 1993; Holden, 1993; Storch, this paper). The advanced position of *Muscardinus*, too, fits these views. However, Wahlert et al. (1993) questioned the unity of Koenigswald's group 3. Koenigswald's polarity assessment of the tilt of the Hunter-Schreger bands is derived from a general evolutionary trend among rodents but in my understanding it is not corroborated by most other characters within the family Myoxidae. In particular, the supposedly most advanced status of *Selevinia* and *Myomimus* is strongly contradicted by various morphological features.

The relative size of the middle and inner ear, however, seems to support Koenigswald's systematic view of *Myoxus* and *Glirulus*. We prepared radiographs of skulls (Figs. 1-2) and then related the basicranial width (= distance between the outermost bony margin of the semicircular canals) to the width of the cochlea and the width and length of the bulla (Habersetzer & Storch, in preparation). *Myoxus* and *Glirulus* show relatively smaller inner and middle ears than the remainder (Figs. 1-2), thus suggesting a plesiomorphous character state. We also have to consider, however, relationships between ecology and morphology across taxa. The majority of morphological characters of the auditory region, corroborates a rather advanced status for *Myoxus* and *Glirulus* among Myoxidae (Habersetzer & Storch, in preparation).



Figs. 1-2 – Radiographs of the **skulls** of 1 = *Glirulusjaponicus* and *2* = *Dryomys laniger*. Note the different relative size of the cochlea and bulla. Radiographs J. Habersetzer.

## MUSCLES OF MASTICATION

The muscles of mastication play an important role in rodent classification following Waterhouse, Brandt, Tullberg, and other 19th century authorities. Major clades among rodents are essentially based on this functional complex and relationships within particular groups are also discussed on the basis of muscle arrangement (e.g. Vorontsov, 1982).

The zygomasseteric structure of Palaearctic myoxoids looks moderately myomorphous. The zygomatic plate is broadened and tilted upwards, and it gives origin to part of the lateral masseter. The tendinous anterior head of the pars superficialis and the anterior pars profunda of the lateral masseter are well separated. The lateral masseter forms a small pars reflexa on the medial face of the laterally bent angular process. The infraorbital foramen is of moderate size and it is penetrated by a small portion of the anterior medial masseter (Tullberg, 1899; Radtke, 1989). The subdivision of the masseter complex and its areas of origin and insertion on the skull show only slight differences among extant dormice. The fossae pterygoideae, however, which give origin to the pterygoideus medialis muscles are markedly different (Storch, 1978). The pterygoideus medialis acts antagonistically to the masseter with regard to lateral jaw movements and these differences thus suggest particular chewing specializations. We can distinguish 4 groups (Fig. 3):

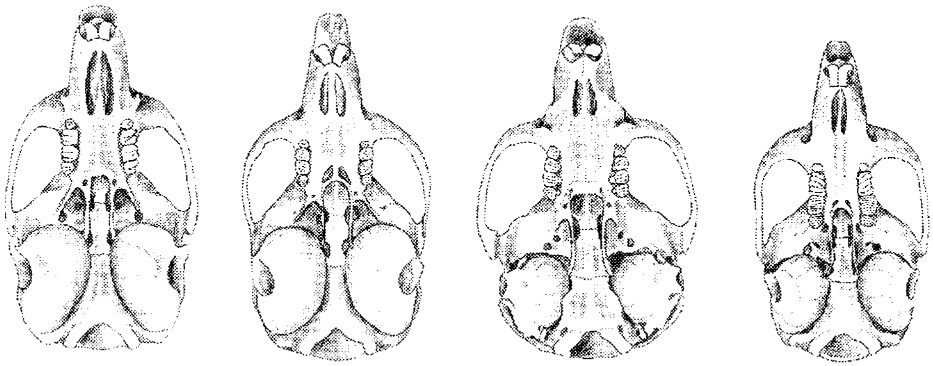
1) In *Myomimus roachi* the fossa pterygoidea forms anteriorly an excavation of the palatine; this is an unique feature among extant myoxids.

2) The lamina lateralis of the pterygoid fossa is well-developed and hence the fossa is deep in *Myomimus roachi, Eliomys*, and *Dryomys nitedula.* In *Dryomys laniger*, there is overall correspondence morphologically but the pterygoid fossa is somewhat shallower.

3) The lateral pterygoid process is low and short posteriorly and thus the pterygoid fossa is reduced in *Myoxus* and *Glirulus*.

4) **A** lateral pterygoid process and thus a delimited fossa pterygoidea are lacking in *Muscardinus*.

It is impossible to judge details of the pterygoid region in *Selevinia* and *Chaetocauda* from available illustrations.



Myomimus roachi Dryomys laniger Glirulus japonicus Muscardinus avellanarius

Fig. 3 – Ventral aspect of the **skulls** of four dormouse species. Note the different configuration of the pterygoid fossae. Drawings A. Helfricht.

A deep fossa pterygoidea provides more space for muscle attachment and it allows a more differentiated mode of muscle insertion; both increase the efficiency of the pterygoideus medialis muscle. In *Eliomys*, for example, the strong pterygoideus medialis takes its origin by two distinct tendinous heads from the lateral and the medial pterygoid processes of the expanded fossa (Radtke, 1989). A strong bifurcate medial pterygoid muscle suggests an improved control of laterally directed jaw movements which are caused by the masseter and zygomatico-mandibularis. The well-developed pterygoideus medialis, masseter, and zygomatico-mandibularis thus indicate a distinct lateral component in the power stroke of the chewing cycle. The antagonistic activity of the pterygoideus medialis is essential to mastication on a single side of the jaws.

I consider the configuration of a deep pterygoid fossa (*Myomimus*, *Elionzys*, *Dryomys*) primitive for myoxids and geologically early taxa supposedly showed an even greater laterally directed component of the power stroke than living species. More advanced is the condition in *Myoxus* and *Glirulus*. Their reduced pterygoid fossa suggests an increase of the longitudinal (= propalinal) component of the power stroke. Most derived is *Muscardinus*. The lateral pterygoid process is lacking and this suggests antero-posterior mastication without noticeable lateral movements.

## EXTERNAL GENITAL MORPHOLOGY

The importance of male genital morphology in myoxid systematics was demonstrated by Kratochvil (1973) and Rossolimo & Pavlinov (1985). Kratochvil described in detail the glans penis of *Dryomys*, *Elionzys*, *Myoxus*, and *Muscardinus*. The surface of the corpus of the glans penis is subdivided into distinct pad-like structures covered with horny spines and segments or pads without such spines (Fig. 4).

The os penis extends beneath the dorsal segment of the glans. *Muscardinus* differs from the other genera in some penile features on which Kratochvil based his new subfamily Muscardininae. When sexually inactive, the glans penis of *Muscardinus* includes only the distal half of the baculum while in *Myoxus*, *Dryomys*, and *Eliomys* (= Kratochvil's Glirinae) its whole length is enclosed. The os penis is flattened in the latter and cylindrical in *Muscardinus*. The penile character state of *Muscardinus* is certainly derived and the isolated position of this genus is supported in Kratochvil's view by its complex stomach, including a glandular bulbus oesophageus. Kratochvil subdivided his Glirinae further into the tribes Glirini (Myoxus) and Dryomyini (*Dryomys*, *Eliomys*) by penile features.

Rossolimo & Pavlinov studied the morphology of the glans in *Myomimus* and *Glirulus* and concluded that *Myomimus* is characterized by the most primitive and *Glirulus* by the most advanced penile structure among extant myoxids (Fig. 4). Both genera have no features in common with the above mentioned genera. In *Myomimus*, the glans penis is stout, its surface is plain and unstructured except for short wrinkles distally, and most of its body is covered by short spines. The os penis is also peculiar (Ognev, 1947, Fig. 255). In *Glirulus*, the elongated body of the glans is marked by many small irregular wrinkles, two deep sublateral fissures, two elongated pad-like structures ventrally, and a long bulge dorsally; there are no spines at all. Accordingly, Rossolimo & Pavlinov advocated two monotypic subfamilies, Myomiminae and Glirulinae.

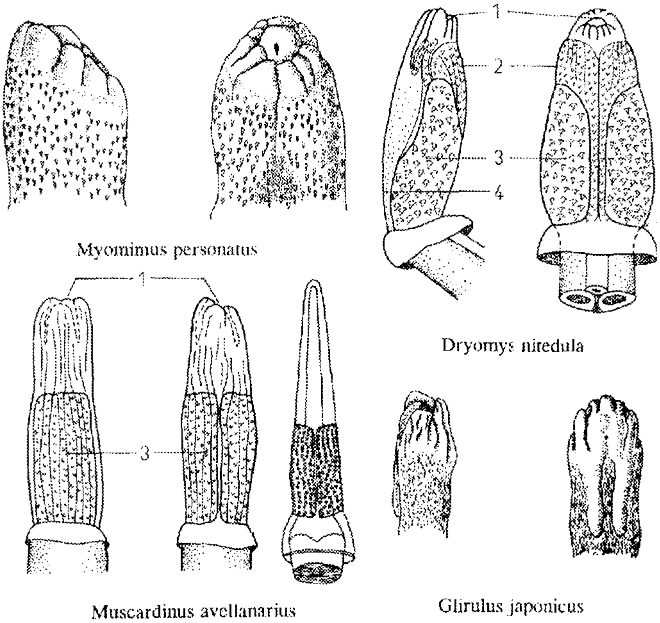


Fig. 4 – Glans penis of four dormouse species in lateral (left) and ventral (right) views. After Kratochvil 1973 *(D.n., M.a.)* and Rossolimo & Pavlinov 1985 *(M.p., G.j.)*. 1 = Ostium urethrae; 2 = ventral. 3 = lateral, and 4 = dorsal pads.

Our knowledge of penile morphology in *Chaetocauda* and *Selevinia* is very limited. The os penis of *Chaetocauda* (Wang, 1985, Fig. 2) looks peculiar and the glans penis of *Selevinia* (Belosludov & Bashanov, 1938, Fig. 2; Ognev, 1947, Fig. 259), too, is not reminiscent of that in other dormice. The drawings, however, do not allow judging characters in further detail. The baculum of *Selevinia* may be similar to that of *Chaetocauda* but obviously most of its proximal part seems to be broken off in the illustration by Belosludov & Baslianov (1938, Fig. 2).

## DISCUSSION

### Possible relationships among living dormouse genera

Figure 5 depicts my current understanding of affinities among living dormouse genera, resulting from conclusions by other students and from my own data. Numbers in Fig. 5 refer among other features to the following presumably non-primitive characters:

1.- Myomorphous zygomasseteric structure. (Well separated origin of anterior pars superficialis and pars profunda of lateral masseter on the broadened and inclined zygomatic plate, part of the anterior medial masseter penetrates infraorbital foramen).- Brachyodont molars with transverse ridges. - Lack of caecum and macroscopic boundary between colon and small gut.

2.- Simple dental pattern. - Foramina incisiva very long posteriorly. - Tail covered with short hairs.

3.- Deeply grooved upper incisors. - Reduced dental pattern. - Very large auditory bullae.

4.- Anteroloph usually free on M1-2/. - Fossa pterygoidea deeply excavated. - Glans penis unstructured and covered with spines.

5.- Small single-rooted molars. - Premolars absent in adult animals.

6.- Upper molars with V-shaped protoloph and metaloph and markedly weaker anteroloph and posteroloph. - Lower molars with highly reduced or lacking mesolophid and without extra-ridges.

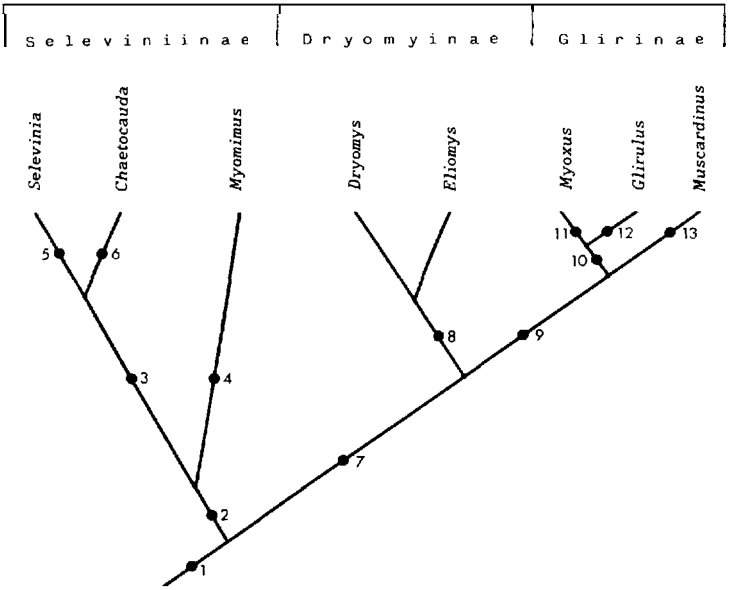


Fig. 5 – Possible relationships among living dormouse genera

7.- Occlusal pattern complicated. - Glans penis subdivided into pad-like structures.

8.- Molars concave, main cusps well-developed, and generally with an endoloph on M1-2/. - Enamel cover of upper incisors indents lateral surface. - Diagonally oriented (= 45" tilt) Hunter-Schreger bands in the portio interna of the enamel in lower incisors. - Lamina lateralis of the fossa pterygoidea well-developed and fossa pterygoidea deep. - Glans penis with lateral spiny pads.

9.- Main cusps of cheek teeth weak or absent. - Reduction or absence of stapedial artery. - Reduction or absence of lateral pterygoid process. - Coronoid process arises in anterior position, conceiling M/3 in lateral view.

10.- Transverse Hunter-Schreger bands in the portio interna of the enamel in lower molars. - Thick prism-free outer layer of the portio externa of the enamel in lower incisors.- Lateral pterygoid process short and fossa pterygoidea reduced. - Angular process of lower jaw without perforation.

11.- Molars only slightly concave and main cusps weak. - **All** ridges of M1-2/ free lingually, protoloph separated from metaloph. - Glans penis without spines on lateral pads.
12.- Entolophid of lower cheek teeth usually complete. - Auditory bullae with many primary partition walls. - Glans penis with wrinkles, pads, and bulges; spines are absent.
13.- Occlusal surface flat and ridges without terminal cusps. -Premolars reduced. - Lateral pterygoid process and fossa pterygoidea absent. - Glans penis includes only distal half of baculum at state of rest. - Stomach with bulbus oesophageus.

## CLASSIFICATION OF SELEVINIINAE

*Selevinia* was referred to myoxoids on the basis of shared characters of the bulla, auditory ossicles, lower jaw, mesopterygoid fossa, pads on hands and feet, and the lack of a caecum. Ognev (1947) and Ellerman (1949) attributed to *Selevinia* the rank of a subfamily, Seleviniinae, among Myoxidae, while current classifications usually prefer a family status, Seleviniidae, among Myoxoidea (Chaline & Mein, 1979; Honacki et al., 1982; Klingener, 1984; Pavlinov & Rossolimo, 1987: Thenius, 1989; etc.). *Selevinia* shows striking adaptations to its desert habitat in Kazakhstan (e.g., enormous bullae) and its arthropod diet (e.g., reduced dentition), and this divergence from a familiar dormouse morphology obviously stiinulated the current view of its isolated position. Ognev (1947), on the other hand, emphasized the resemblance of *Seleviniu* to *Myomimus* in many characters. Judging from rather limited available information, *Selevinia* shares myoxid characters with other living dormice and I can see no compelling arguments for its exclusion from this family. This view is corroborated by cranial anatomy (Wahlert et al., 1993) and enamel ultrastructure (Koenigswald, 1993).

*Chaetocauda* from northern Sichuan, China, was originally closely compared with *Myomimus* and assigned to the subfamily Myomiminae (Wang, 1985). Recently, Holden (1993) considered *Chaetocauda* a synonym of *Dryomys* and she even questioned the specific status of the single species, *C. sichuanensis*. *Chaetocauda* remains enigmatic in several respects owing above all to the rather brief original description and the inaccessibility of actual specimens. Nevertheless, illustrations and descriptions of *Selevinia* (Argyropulo & Vinogradov, 1939; Ognev, 1947; Bashanov & Belosludov, 1941) and *Chaetocauda* (Wang, 1985) present a suite of highly diagnostic shared characters and I consider both genera close relatives. These synapomorphic characters include:

Upper incisors large and deeply grooved on their labial enamel surface; their cutting edges with V-shaped notch the apex of which meets the longitudinal groove - Molars with extremely simple occlusal pattern. Upper molars of *Chaetocauda* are concave, with V-shaped protoloph and metaloph, markedly shorter and apparently narrower and lower anteroloph and posteroloph, and with prominent protocone, paracone, and metacone. In *Selevinia* the occlusal pattern is reduced but occlusal outlines still have two lingual lobes as in *Chaetocauda* (cf. Ognev, 1947; Fig. 259-2). Lower molars of *Chaetocauda* are without (M/1, M/3) or with short and faint (M/2) mesolophid, without extra ridges, and with prominent metaconid and protoconid. The foramina incisiva are wide and very long posteriorly, extending to middle of P4/ in *Chaetocauda*. A particular combination of cranial features is found, e.g. wide interorbital region and hard palate, short rostrum, and very large auditory bullae. The outlines of the skull and lower jaw of *Selevinia* and *Chaetocauda* are virtually identical in lateral view.

I place *Selevinia* together with *Chaetocauda* in one suprageneric taxon. Next to it is *Myomimus*; it shares among other characters the long foramina incisiva. Synapomorphic features of *Selevinia* and *Chaetocauda* which are lacking in *Myomimus* - such as grooved incisors - suggest two distinct lineages within this group. They may be ranked as tribes Seleviniini and Myomimini within Seleviniinae. Grouping *Selevinia* together with *Myomimus* was also favoured by Ognev (1947), Koenigswald (1993), and Wahlert et al. (1993). I regard Seleviniini as the most primitive group of living inyoxids because of the decidedly plesiomorphic dentition of *Chaetocauda*, which is strongly suggestive of a basic sciurid pattern.

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