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Cranial Anatomy and Relationships of Dormice (Rodentia, Myoxidae)¹

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ABSTRACT

Cranial, mandibular, and dental morphology of living dormice (rodent family Myoxidae) are described. Forty three osteological and 11 dental characters served as the basis for PAUP analysis. The data support the hypothesis that the Myoxoidea is monophyletic and the sister taxon to the combined Muroidea plus Dipodoidea; these three superfamilies constitute the rodent suborder Myomorpha. *Graphiurus*, which retains the condition of hystricomorphy in the masseter muscle, represents the earliest branch of the Myoxidae, the subfamily Graphiurinae. The remaining taxa are myomorphous and cluster into two groups. The Leithiinae, consisting of the tribes Leithiini (*Elio-*

mys and *Dryomys*) and Seleviniini (*Myomimus* and *Selevinia*), share the presence of a fenestra in the mandibular angle, low inclination of the anterior edge of the coronoid process, and a complete transverse valley in m2. The Myoxinae (*Myoxus*, *Muscardinus*, and *Glirulus*) have lost the sphenofrontal and stapedial foramina, accessory crests are prominent features of the nearly flat molar crowns, and the coronoid process arises in an anterior position. Structures of the middle ear chamber of *Graphiurus* are described in detail, and problems of homology and character polarity are discussed.

¹ Dedicated to the memory of Marie Adelaide Lawrence, our colleague, mentor and friend.

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INTRODUCTION

SCOPE OF THE PAPER

Brandt (1855) described the characteristics of dormouse skulls, family Myoxidae, following the dipodoid and muroid section of his work, because he felt that this sequence was necessary for understanding myoxid morphology. However, he said (*ibid.*, p. 152, fn.) that in systematics the myoxids must be placed before these rodents and next to the Sciuroidea, since dormice are intermediate between the two major groups. The question of how myoxids are related to other rodents has been debated to the present day. Reasons for this instability are easily found in the interpretation of morphology and the consideration of the fossil record. Living myoxids resemble dipodoid and muroid rodents in two chief features: the infraorbital foramen is larger than in protrogomorphous rodents, and the entrance to the lacrimal canal is anteromedial to that foramen instead of being situated in the anterodorsal part of the orbit. Relatively large eyes, arboreal ability, bushy tails, and cranial arterial circulation are sciuridlike. This paper, a comparative study of cranial and dental morphology, is a further attempt to elucidate relationships among myoxid genera and of myoxids as a whole to other rodents.

TEMPORAL AND GEOGRAPHIC RANGE
AND BIOLOGY

The family Myoxidae is an Old World rodent group that includes eight or nine living genera and numerous extinct taxa. The fossil record of the family extends back approximately 50 million years into the late early Eocene in France. The following data on dormouse biology are summarized from Ognev (1947), Masuda (1987), and Nowak (1991). The living dormice are comparable in weight to the range from house mouse to squirrel. The tails are bushy except for *Myomimus*. The animals are crepuscular and nocturnal. Most genera are chiefly arboreal, and forests and thickets are common habitats. Some *Eliomys*, *Dryomys*, and *Graphiurus* are terrestrial and live in rocky or other open habitats; *Myomimus* is reported to be mouselike and terrestrial. The dormice are omnivores;

Graphiurus, *Myoxus*, *Muscardinus*, and *Glirulus* prefer fruits, nuts, and berries supplemented with insects, whereas *Eliomys* and *Dryomys* favor insects, birds, and small mammals (Ognev, 1947). In all cases the diet is rich in proteins and fats and low in cellulose. All dormouse genera hibernate or experience dormancy in at least some part of their range (information is lacking for *Myomimus* and *Chaetocauda*).

Little is known about *Selevinia*. It lives in the desert of the Kirghiz Steppes, ambles or moves in small jumps on its hind legs, and can climb with agility. The tail is covered with short hairs. According to Ognev (1947: 486) it is crepuscular. The stomach contents, stated in the original description, were unchewed leaves of the desert bush *Salsola laricifolia* (Bashanov and Belosludov, 1941). Ognev noted that a captive specimen ate only insects.

Dormice are characterized by low-crowned cheek teeth in which cusps are largely subsumed into the connecting crests; these and the accessory crests are nearly equal in prominence. The dental formula includes P4-M3 and p4-m3; the adult *Selevinia* has no premolars. Tullberg (1899) proposed that the absence of the cecum and the lack of a definite boundary between the small and large intestines is associated with a diet low in cellulose and high in fats, proteins, and carbohydrates. The consistent absence of a cecum suggests that the ancestor of the lineage indulged in the same energy-rich foods. Vorontsov's (1967: 143) proposal that "the specialization of molar teeth of Myoxidae to the cellulose type of nutrition in the series from *Myomimus*, *Eliomys* and *Dryomys* to *Glis* and *Muscardinus* is marked by an increase in the number of transverse enamel columns from 4-5 to 7-8" is not supported by dietary information. The diet of *Muscardinus* (Storch, 1978) is consistent with that of other dormice.

NOMENCLATURE HISTORY

The genera of dormice have been gathered under three different familial names: Gliridae Muirhead, 1819; Myoxidae Gray, 1821; and

Muscardinidae Palmer, 1899. The oldest name was originally presented as the family Glirini (Muirhead, 1819: 433); it included three genera—*Dipus*, *Gerbillus*, and *Myoxus*. No explanation was given for the choice of the family name; we assume it was based on the specific name of *Myoxus glis*. According to the International Code of Zoological Nomenclature, Third Edition (1985), Article 11: "(f) Family-group names.—(i) A family-group name must, when first published, (1) be a noun in the nominative plural based on the generic name then used as valid for a genus contained in the family-group taxon [Articles 63, 64] either by express reference or by inference in content from the formation of the family-group name . . ." Muirhead's name Glirini does not satisfy this criterion. The next available name, Myoxidae Gray, 1821 (emended by Waterhouse, 1839, from the original spelling Myosidae), which included the genera *Echimy*s and *Myoxus*, is valid (see also Holden, 1993). The name Muscardinidae is a junior synonym of Myoxidae.

Although Gliridae is now the name applied most commonly to the family of dormice, Myoxidae and Muscardinidae continue to be used in published works. Preference for the name Gliridae arose with Simpson's (1945) classification of mammals. This work was cited in the Zoological Record for the year 1945, and the change from Myoxidae to Gliridae occurred in that volume. The switch was made in the Bibliography of Fossil Vertebrates 1939–1943 (Camp et al., 1949); the editors stated that their classification was based on Simpson's work.

Instability in the family name reflects continuing uncertainty over the validity of the generic names *Myoxus* and *Glis*. Holden (1993) commented, "... the oldest available name to replace *Glis* Brisson is *Myoxus* Zimmermann, valid in Linnaeus (1788) for dormice, and the correct family name for dormice is Myoxidae." Brisson's (1762) names are invalid because his work does not satisfy the Principle of Binomial Nomenclature as stated the International Code of Zoological Nomenclature, 1985, Article 5(a) and its application, Article 11(c). Both text and index of Brisson contain a mixture of names that are uninomial, binomial, and trinomial. The same generic name, e.g., *Mus*, may ap-

pear under two or more genera. The work does contain a uninomial key to the genera, but this does not satisfy the criteria for validity in Article 11(c). Trouessart (1898–1899: 453, fn. 1) and Schulze et al. (1929: 1375) rejected *Glis* on the same ground, that Brisson's work is not binomial. We disagree with Merriam (1895) that the uninomial generic key of Brisson (1762) validates the name *Glis*. Zimmermann (1780: 351) proposed the genus *Myoxus* in a work that is wholly binomial. The first species listed, which may be considered the type species, is *Myoxus glis*. The specific name, here as elsewhere in the work, is enclosed in parentheses that set it apart from the following description in Latin; parentheses are omitted in some instances where there is no further description. The name *Myoxus* is the oldest available generic name for the species *Myoxus glis* (see also discussion in Holden, 1993).

The sequence in which valid generic names were given to dormice is as follows:

Myoxus Zimmermann, 1780: 351
Muscardinus Kaup, 1829: 134, 139
Graphiurus Smuts, 1832: 32–33
Eliomys Wagner, 1840: 176–185
Glirulus Thomas, 1906: 347–348
Dryomys Thomas, 1906: 348
Myomimus Ognev, 1924: 115–116
Chaetocauda, Wang, 1985: 67–75.

Brandt (1855) and Reuvens (1890) summarized the early taxonomic history of the family and its genera. Dormice were first described under the generic names *Glis*, *Myoxus*, *Sciurus*, and *Mus*. The four Eurasian taxa were commonly, but not always, included in the same genus; for example Linnaeus (1766) spoke of *Mus avellanarius* and *Mus quercinus*, but of *Sciurus glis*. Brandt (1855: 177) recognized Oken (1838) as the first to show myoxids as a specific group that is separate from mice and squirrels. However, Oken's larger category, "Klettermause," also included sciurids and hystricognathous genera. More biologically sensible classifications to modern eyes antedate Oken's publication. Brisson (1762) placed the genus *Gliris* between the genera *Sciurus* and *Muris*. Zimmermann (1780) divided the gnawing animals into eleven genera, four of which are not rodents. He presented the relevant genera in the fol-

lowing order: *Sciurus*, *Myoxus*, *Dipus*, *Mus*; his species of dormice are now split among the genera *Myoxus*, *Dryomys*, *Eliomys*, and *Muscardinus*. Gmelin placed *Myoxus* similarly between *Sciurus* and *Dipus* in his edition of Linnaeus' *Systema Naturae* (1788). The recognition of taxa that constitute the core of the Myoxidae has remained stable for nearly two centuries.

Wagner (1840: 185; 1843: 263–274) divided the genus *Myoxus* into four subgenera—*Graphiurus*, *Eliomys*, *Glis*, and *Muscardinus*—and a small group of species “sedis incertae.” After the middle of the 19th century the use of the four names as genera became common practice. Two different dates, 1840 and 1843, have been cited for Wagner's naming of the genus *Eliomys*. Both refer to the same article, and with either date the name is valid. The year 1840 is given by Sherborn (1925–26), Neave (1939), and Holden (1993); 1843 is given by Palmer (1904), Trouessart (1898–99), Schulze et al. (1929), and Simpson (1945). We have examined the bound copy of volume 2 of the *Abhandlungen der mathematisch-physikalischen Classe der königlich bayerischen Akademie der Wissenschaften* that is held by the Library of the American Museum of Natural History, and we conclude that 1840 is the correct date. The first *Abteilung*, which contains Wagner's paper, is for the years 1837 to 1840 and bears the date 1840. The third *Abteilung* begins with a volume title page for the entire span from 1837 to 1843 and is dated 1843; this is followed by a list of the contents of the entire volume. Placement of the volume's contents at the beginning of the third section indicates that publication of the *Abteilungen* was sequential and not simultaneous; thus, there is no reason to doubt the date of 1840 on the first section. Further confirmation of the 1840 date was given by Wagner (1841a, b) who cited this particular article as from the past two years.

Thomas (1906) created the generic name *Glirulus* for the Japanese dormouse, originally considered a species of *Myoxus*. He created the subgenus *Dryomys* for the species *Eliomys nitedulus* to which he believed *Glirulus* was most nearly allied. *Myomimus* and *Chaetocauda* were added as full genera to the family. *Chaetocauda* Wang, 1985, was con-

sidered a synonym of *Dryomys* by Holden (1993). Another genus, *Selevinia*, was described by Belosludov and Bashanov (1939) as a murid. In 1941 they (Bashanov and Belosludov) placed the genus in a new family Seleviniidae and remarked on cranial resemblance to the myoxoids. The genus is generally considered to be a close relative of the myoxoids; Holden (1993) placed it in the Myoxidae.

PRIOR VIEWS ON PHYLOGENY

Reuven's (1890) annotated chronology of the classification of myoxoids reveals the instability of their placement with regard to the rest of the sciurognathous rodents. This controversy has continued to the present day. Ellerman (1940) considered the Muscardinidae (= Myoxidae) to be a family of the Muroidea, whereas the Dipodoidea stood as a separate superfamily. Simpson (1945), Wilson (1949), and Wood (1955) [with reservations], Wahlert (1978), and Chaline and Mein (1979) placed the Gliroidea (= Myoxoidea) in the suborder Myomorpha which also included Muroidea, Dipodoidea, and, excepting Simpson, the Geomyoidea. Meng (1990) placed the Myoxidae in a clade with the sciurids, apodontids, and extinct reithroparamyines based on comparative analysis of auditory features. Stehlin and Schaub (1951), Thaler (1966), Parent (1980), Hartenberger (1985), and Vianey-Liaud (1985) treated the group as independent of other rodent taxa. Grassé and Dekeyser (1955) and Schaub (1958) placed the Gliroidea in a suborder Non-Pentalophodonta but treated them as an independent group.

Bugge (1971a, b, 1974) examined the cephalic arterial system in rodents and drew conclusions about the relationship of myoxoids. He found that in the Cricetini and certain of the New World mice “the stapedia artery supplies the dura, eyeball and orbit, and upper and lower jaws, while the internal carotid artery (*ci*) supplies the brain with the assistance of the vertebral artery . . .” (1974: 44). He interpreted this as primitive, presumably for rodents and for these muroids in particular. “In all the sciuroids examined, the internal carotid artery (*ci*) atrophies immediately after the departure of the stapedia artery

(*st*) and the brain is supplied by the vertebral artery" (p. 49). "The stapedia artery . . . is persistent, but its area of supply is annexed to a varying extent by the external carotid artery system (*ce*) . . ." (p. 51). Bugge concluded that myoxids have closer affinity to the Sciuromorpha than to the Myomorpha because the internal carotid artery is likewise obliterated after the departure of the stapedia.

Treatment of the Myoxoidea as an independent group stems chiefly from the great antiquity of the earliest fossil representative—late early Eocene. The oldest muroids are of late Eocene age, sciuroids of early Oligocene. If the myoxid fossils are correctly identified, then the lineage is among the oldest known in rodents, and common ancestry with either of these later groups must have occurred at the protrogomorphous grade of evolution. Vianey-Liaud (1985: 293) presented morphological evidence in support of independent treatment of myoxoids; she stated that myomorphy in the group had a different origin from myomorphy in muroids because "it did not exist in at least two protrogomorphous lower Oligocene glirid lineages." She termed the supposed convergent condition "pseudo-myomorphy." The two protrogomorphous species are *Gliravus majori* and a new primitive species from the middle Oligocene of Itardies, Quercy (ibid., fig. 4a, b).

The myoxid genera have been grouped in a variety of ways. Winge (1941), Ellerman (1940), and Simpson (1945) set *Graphiurus* apart in its own subfamily on account of the primitive arrangement of the masseter muscle. Bruijn (1967) recognized five subfamilies based on dental characters:

- Graphiurinae: *Graphiurus*
- Glirinae: *Glis*, *Muscardinus*
- Dryomyinae: *Dryomys*, *Eliomys*, *Myomimus*
- Glirulinae: *Glirulus*
- Gliravinae: extinct genera only.

Daams (1981) proposed a similar classification into five subfamilies:

- Gliravinae: extinct genera only
- Glirinae: *Glis*, *Muscardinus*
- Dryomyinae: *Dryomys*, *Glirulus*, *Eliomys*
- Myomiminae: *Myomimus*
- Graphiurinae: *Graphiurus*.

Lydekker (1896) named the family Leithiidae to separate the giant Pleistocene dormouse of Malta, *Leithia*, from other myoxids. Both Bruijn (1966, 1967) and Daams included *Leithia* in the Dryomyinae Bruijn, 1966; Leithiinae thus is the oldest familial name for this group and Dryomyinae is its synonym (Holden, 1993).

Bugge (1971a, 1974) described the variety of cranial arterial patterns found in *Myoxus glis*, *Muscardinus avellanarius*, *Eliomys quercinus*, and *Graphiurus murinus*. The primitive condition in which the stapedia artery is well developed and all three branches—the supraorbital, infraorbital, and mandibular rami—are present occurs in *Eliomys* and *Graphiurus*. In *Myoxus* the stapedia stem is thin, the supraorbital ramus is obliterated proximally, and anastomoses connect the rami to the external carotid blood supply. The stapedia artery stem is completely obliterated in *Muscardinus*, and anastomoses connect the rami to the external carotid system.

Kratochvil (1973) compared the anatomy of male sexual organs in *Eliomys quercinus*, *Dryomys nitedula*, *Myoxus glis*, and *Muscardinus avellanarius*; other taxa included *Marmota* and *Spalax*. Based on detailed dissection, he divided the myoxids into two subfamilies, Muscardininae and Glirinae. Within the Glirinae, *Eliomys* and *Dryomys* are the most similar, and *Myoxus* stands apart. He emphasized the "unity of morphological, anatomical, ecological and zoogeographical criteria supporting the above taxonomic conclusions" (p. 50).

Van der Meulen and Bruijn (1982) correlated molar pattern with ecology in living taxa. Rossolimo and Pavlinov (1985) characterized genital morphology in *Myomimus* as the most primitive and in *Glirulus* as the most derived among dormice. Wahlert and Sawitzke (1988) noted basicranial muscle insertions in *Eliomys* that appear derived relative to muroids.

Koenigswald (in press) examined the incisor enamel microstructure in all living myoxids, except *Chaetocauda*, and in some fossil taxa. All have uniserial Hunter-Schreger bands in the portio interna of enamel in upper and lower incisors; the portio externa consists primitively of radial enamel. Ko-

enigswald divided the taxa into three groups based on differences in schmelzmuster—the three dimensional arrangements of one or more enamel types—in lower incisors. *Glirolulus japonicus* and *Myoxus glis* of Group 1 share primitive, transversely oriented Hunter-Schreger bands in the portio interna of the enamel and have a thick (derived) prism-free outer zone of the portio externa. *Dryomys* and *Eliomys* plus extinct taxa comprise Group 2 in which the Hunter-Schreger bands are tilted relative to a transverse plane and rise at 45° toward the mesial side of the tooth. Group 3 contains *Graphiurus*, *Muscardinus*, *Myomimus*, and *Selevinia*, plus extinct taxa. The Hunter-Schreger bands are oriented longitudinally in the portio interna. Interprismatic enamel is parallel to the prisms in the portio interna of members of Groups 1 and 2, whereas it is at an angle to the prisms in the inner zone of the portio interna in some members of Group 3. In all myoxids the angular relationship of prisms between the Hunter-Schreger bands and portio externa is preserved so that the portio externa in Group 3 consists of tangential rather than radial enamel; in non-myoxid rodents with rotated or longitudinal Hunter-Schreger bands this angular relationship is changed. Koenigswald pointed out the similarity of these groups based on schmelzmuster with those of Kratochvil. He unequivocally placed *Selevinia*, based on its schmelzmuster, in Group 3 and stated that *Selevinia* is neither a separate family nor the sister group to the myoxids.

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MATERIALS AND METHODS

Measurements were taken with a Helios dial caliper calibrated to 1/20 mm. Condylolobasilar length is a direct line from a tangent to the back of the incisors to one touching the posterior margin of the occipital condyles. Diastemal length is taken from the back of an incisor to the front of the first cheek tooth on the same side. Palatal width is the minimum dimension between M1's.

Cranial data were recorded and character polarities assessed using *Paramys copei* as the standard for primitive states. Other outgroups included the sciurid genus *Sciurus*, the dipodoid *Sicista*, and the muroid *Cricetulus*. These three genera were selected because they represent the rodent groups to which myoxids may be closely related, and because their crania appear to lack extreme specialization. This assessment is based on Wahlert's (1972) analysis of sciurid skulls and on two unpublished studies by Wahlert that examine the

range of cranial characters in a variety of muroids, and that reassess paramyid cranial anatomy in comparison with *Cocomys* from the early Eocene of China and with other mammals. We follow Tullberg's (1899: 62–63) system of nomenclature for the divisions of the masseter muscle but have anglicized his terms. The list of character states is given in Appendix 1 and the data matrix in Appendix 2.

Parameters of the PAUP analysis (Swoford, 1989) were as follows: characters unordered, multistate taxa treated as uncertainty; "branch-and-bound" method used to identify all optimal trees; unrooted trees rooted using outgroup method; character-state optimization by delayed transformation (DELTRAN).

Illustrations of crania were prepared by the senior author with a Nikon microscope with camera lucida attachment. The occlusal plane (an average) was aligned parallel to the page plane in ventral and dorsal views and perpendicular to the page plane in anterior and posterior views. Mandibles were oriented as in life and not laid flat on the medial surface.

SPECIMENS EXAMINED

Specimens were examined in the mammalogy collections of the American Museum of Natural History (AMNH), Carnegie Museum (CM), Muséum National d'Histoire Naturelle, Paris (MNHN), and Natural History Museum of the Smithsonian Institution (USNM). Identifications follow those given on the specimen labels at these institutions. If an emendation in species has been made in Corbet (1980), the label name is given in parentheses. For the purposes of this paper changes in species limits within genera would not alter our results. Place names used are those of the Comprehensive Edition of The Times Atlas of the World (1983); not all localities, however, appear on these maps. The specimens figured in this paper are so noted.

Dryomys nitedula. *D. n. intermedius*: USNM 174695, Italy, NE Belluno Prov., Padola tributary of Cadore River. *D. n. nitedula*: AMNH 206584, Russia, Checheno Ingushskaya A.S.S.R., Ishcherskaya area. *D. n. phrygius*: USNM 327716, USNM 327717, USNM 327718, Turkey, Ulu Dag Mountain. *D. n. pictus*: AMNH 176248, Azerbaydzhan,

Zakataly distr.; USNM 369886, Iran, Tehran reg., 11 km ENE Fasham; AMNH 217346 (figured), Pakistan, Quetta-Pishin reg., Urak. *D. n. ssp.*: USNM 413717, USNM 413718, USNM 413719, Pakistan, Dir reg., 26 km N Dir; USNM 413720, Swat reg., 10 km SW Utrot.

Eliomys quercinus. *E. q. cyrenaicus*: USNM 302274, Libya, Darnah. *E. q. dichrurus*: USNM 152771 (= *E. q. pallidus*), Sicily, Palermo Prov., Castelbuono; AMNH 160902, Italy, Abruzzo Prov., Valle del Sangro. *E. q. lusitanicus*: USNM 152766, Spain, Sevilla Prov., Sevilla. *E. q. munbyanus*: USNM 483103, Morocco, 5 km NE Essaouira. *E. q. quercinus*: AMNH 42505, France, Côte d'Or Dept., Aignay-le-Duc; USNM 152777, France, Gard Dept., near Nîmes; MNHN CG1988-279 (in alcohol), France; AMNH 150118 (figured), AMNH 150127, AMNH 150129, Federal Republic of Germany, Bayern, Waldmünchen.

Glirulus japonicus: AMNH 164112, Japan; USNM 299317, USNM 299318 (figured), Japan, Honshu, Shizuoka Prefecture.

Graphiurus. *G. crassicaudatus*: USNM 429506, Togo, Atakpamé reg., Ezimé; CM 2973, Cameroon, Centre-Sud reg., Lolodorf. *G. hueti nagtglasii*: CM 10334, Cameroon, Centre-Sud reg., Sangmelima. *G. h. ssp.*: CM 6123, Cameroon, Centre-Sud reg., Lolodorf; CM 10332, CM 10337, Cameroon, Centre-Sud reg., Sangmelima. *G. lorraineus*: AMNH 49888, Zaire, Haut-Zaïre Prov., Bafwabaka; CM 59461, CM 59463, Cameroon, Ouest reg., 11 km S, 1 km E Bamenda. *G. murinus caunzensis*: AMNH 88200, Angola, Northernmost Bie Distr., Chitau. *G. m. ssp.*: AMNH 180986, Zaire, Kivu Prov., SW Lake Kivu, Falls of Lwiro River; MNHN CG1988-280 (in alcohol), Centrafrique. *G. olga*: CM 59484, Cameroon, Est reg., 23 km S, 8 km E Garoua. *G. parvus parvus*: USNM 182876, Kenya, N Nyiro River (= Ewaso Ng'iro). *G. playtops rupicola*: USNM 256924, Namibia, Mt. Brukkaros. *G. p. ssp.*: AMNH 116668 (figured), Zambia, Northwestern Prov., Zambezi.

Muscardinus avellanarius avellanarius: USNM 152788, England, Essex, Colchester; AMNH 149416 (figured), Austria, Nieder-Osterreich, Waldviertel Distr.; USNM 17243, Switzerland, Vaud Canton, Lausanne; USNM 152785, Italy, Roma Prov., Roma; USNM 112908 (= *M. a. "sylvaticus"*), Poland, Silesia, Wolfshau (old name, place not found).

Myomimus. *M. personatus*: USNM 354835, Iran, Khorasan reg., 90 km W Quchan. *M. setzeri*: USNM 350725 (figured), Iran, Luristan reg., 50 km SW Borujerd.

Myoxus glis. *M. g. glis*: AMNH 181979, AMNH 181978, Federal Republic of Germany, Baden-Württemberg, Radolfzell; AMNH 160904 (figured), Italy, Novara Prov., Verbainia; USNM

145171, Switzerland, Appenzell Canton, Wolfthalen. *M. g. orientalis*: USNM 327714, USNM 327715 (= *M. g. "persicus"*), Turkey, Trabzon. *M. g. persicus*: USNM 341580, Iran 25 km E Gorgán; USNM 341581, Iran 20 km E Gorgán; AMNH 88752, AMNH 88754, Iran, near Gorgán, Dar Koleh. *M. g. ssp.*: USNM 240437 (= *M. g. "braueri"*), formerly Yugoslavia, Crna Goa Republ., Cetinje.

Paramys copei: AMNH 4755, AMNH 4756, Lost Cabin Member, Wind River Formation, USA, Wyoming, Wind River (Department of Vertebrate Paleontology).

Sciurus. S. aberti: AMNH 146948, Mexico, Durango. *S. alleni*: AMNH 147988, Mexico, Tamaulipas. *S. arizonensis*: AMNH 5415, USA, Arizona. *S. aureogaster*: AMNH 26051, Mexico, Jalisco. *S. carolinensis*: AMNH 1145, USA, Florida. *S. deppei*: AMNH 126128, Honduras. *S. griseus*: AMNH 138514, USA, California. *S. nay-aritensis*: AMNH 1253, Mexico, Jalisco. *S. variegatoides*: AMNH 68535, Guatemala. *S. yucatanensis*: AMNH 79358, Guatemala.

Sicista. S. betulina: AMNH 178814, Russia, Krasnoyarsk Terr.; AMNH 206585, Russia, Ryazan Prov.; AMNH 206586, Russia, Yaroslavl Prov. *S. concolor flava*: AMNH 37837, Kashmir. *S. nappaea*: AMNH 206587, Russia, Altai Reg. *S. subtilis subtilis*: AMNH 20658, Russia, Orenburg Prov.

Cricetulus. C. barabensis: AMNH 57902, Mongolia. *C. curtatus*: AMNH 57858, Mongolia. *C. griseus*: AMNH 57938, China, Hebei. *C. longicaudatus*: AMNH 56312, China, 100 mi NE of Beijing; AMNH 57724, Mongolia. *C. migratorius*: AMNH 88829, Iran, Astarabad; AMNH 176254, SW Turkmeniya. *C. triton*, AMNH 33094, China, North China; AMNH 56724, China, Fujian.

RESULTS

CRANIAL ANATOMY

Diagrams of the skulls and mandibles of each genus examined are presented in figures 1 through 5 to facilitate comparison.

In dorsal view the premaxillary bones extend about as far posteriorly as the nasals. They extend as far or farther than the maxillae in all genera except *Myoxus*. The nasal bones narrow posteriorly. A median suture extends between the anterior third to half of the frontal bones up to the internal torus that separates the olfactory bulbs from the cerebral hemispheres. The suture between the parietals is usually entire. The interparietal bone is wide and may just touch the squamosals.

Temporal muscles are restricted laterally, and myoxids lack both temporal and supraorbital crests.

In profile the rostrum is deep, and the premaxilla extends high above the anterior end of the incisor alveolus. The arch of the diastema is highest near its midpoint. In two genera, *Myoxus* and *Graphiurus*, the jugal bone extends anteriorly along the mediodorsal edge of the maxillary zygomatic root, and its tip touches the tiny lacrimal bone. The jugal is short in other taxa; it appears to be slightly longer in *Muscardinus* and *Myomimus* but does not approach the lacrimal bone.

The anteroventral tip of the alisphenoid meets the posterior tip of the maxilla; a wedge of the palatine may be seen ventral to their union. *Myoxus* is the only genus in which the dorsal edge of the alisphenoid bone meets a descending lamina of the parietal; their union is dorsal to the zygomatic root. The suture between these two bones is broader on the inside than on the outside of the skull; externally the junction is partly obscured by the overlapping edge of the squamosal. The anterior part of the parietal overlies the posterior portion of the frontal bone. In all other genera the parietal has no descending lamina, and the squamosal directly overlaps the frontal.

The anterior portion of the medial masseter in all myoxids extends through the large infraorbital foramen and arises on the rostrum, the hystricomorphous condition. In *Graphiurus* the lateral masseter is restricted to the ventral and lateral surface of the zygomatic arch; the genus is hystricomorphous. In the other six genera the origin of the anterior part of the deep lateral masseter extends dorsally alongside and dorsal to the infraorbital foramen, the sciuromorphic condition. The combined anterior extension of both medial and lateral divisions of the masseter defines the myomorphous condition that is seen in all myoxids but *Graphiurus*. There is no separate tubercle or area for origin of the superficial division of the lateral masseter in *Graphiurus*; Tullberg (1899: 174) stated that the superficial and deep portions of the lateral masseter are only slightly separated from each other at the front. He noted that the superficial portion is well separated in the other myoxid genera in which the deep

division arises anteriorly on the rostrum. The origin of the superficial division is indicated by a rough area just anteroventral to the infraorbital foramen in *Muscardinus*. In *Myoxus* the origin varies from a rough area to a tubercle ventrolateral to the foramen. The tubercle is clearly defined in this location in the other genera. Radtke (1989) presented a detailed description of the masseteric musculature in *Eliomys*.

In ventral view the maxillary roots of the zygomatic arches arise alongside the anterior part of the dentition. If one holds the cheek teeth horizontal and draws a tangent to the anteriormost curves of the posterior edge of the root on each side, the line passes through some part of P4, except in *Graphiurus*, where this line falls either anterior to P4 or passes through that tooth.

The anteriormost end of the palatine bones is medial to the M1M2 junction in *Myoxus*, *Muscardinus*, *Graphiurus*, and *Dryomys*. It is medial to M2 in *Glirulus*, *Eliomys*, and *Myomimus*. The ratio of palatal width between the first molars to condylobasilar length is low to moderate in all but *Glirulus* and many *Dryomys*, where it is higher than .15. The posteromedial edge of the palate bears a weak posteriorly projecting spine in *Myoxus*, *Myomimus* and some species of *Graphiurus*; the spine is lacking in other genera.

The pterygoid region is triangular with a lateral flange that terminates posteriorly at or anterior to the foramen ovale. The flange is low and thick in *Myoxus* and lacking in *Muscardinus*. The length of the pterygoid region is measured from the posterior edge of M3 to the anterior end of the foramen ovale. The ratio of this dimension to condylobasilar length permits comparison of taxa. The ratio is between .10 and .20 in all taxa except *Muscardinus*, where it is less. The pterygoid region is longest in *Myoxus* in which the additional length is posterior to the foramen ovale.

The ratio of maximum articular width of the occipital condyles to condylobasilar length is between .14 and .20 except in *Muscardinus*, where it is .11.

The anterior end of the masseteric fossa on the lateral side of the mandible is approximately ventral to the p4m1 junction; it is slightly posterior in *Myoxus*. The mental fo-

ramen is above the middle of the ramus and anterior to the end of the fossa. In lateral view the leading edge of the coronoid process slopes posteriorly at an angle of less than 60° relative to the occlusal plane of the cheek teeth in *Graphiurus*, *Eliomys*, *Dryomys*, and *Myomimus*. The inclination is steeper in *Myoxus*, *Muscardinus*, and *Glirulus*. The coronoid process conceals the posterior part of m3 in *Myomimus*, the anterior part of m3 in *Myoxus* and *Glirulus*, and some of m2 in *Muscardinus*. It does not conceal any molar teeth in *Graphiurus*, *Eliomys*, and *Dryomys*.

The most ventral part of the angle bends medially; the superior angular process turns laterally, and the angle thus has the appearance of being twisted. *Myoxus* shows this to the least degree; it is best displayed in *Muscardinus*. The bone at the ventral edge of the angle is thick and surrounds a region where bone is thin or a fenestra is present. With the occlusal plane of the cheek teeth horizontal and the jaw resting on its medial side, the posterior end of the angle is directly below or slightly anterior to the posterior tip of the condyloid process.

CRANIAL FORAMINA

A tiny pair of interpremaxillary foramina is usually present in the diastemal palate between the incisors and the incisive foramina. There is considerable variation in their symmetry and in their number which ranges from 0 to 4. The incisive foramina vary in shape from oval to one in which the posterior part is expanded laterally; this latter condition is more common. The foramina usually occupy somewhat more than 50 percent of the diastemal length. This ratio has considerable range; it is greatest in *Graphiurus*, from 33 to 61 percent. It is consistently low in *Myoxus*, from 32 to 42 percent, and very high in the two specimens of *Myomimus*, 80 to 88 (a juvenile) percent. The maxillary-premaxillary suture meets the foramina a short distance posterior to the middle except in *Myomimus* and some species of *Graphiurus* where it is at the middle. There is proportionally more space between the back of the incisors and the anterior ends of the foramina in *Myoxus* than in other genera, except for one specimen of *Glirulus*.

The posterior palatine foramina are entirely within the palatine bone except in *Muscardinus*, where they are intersected by the maxillary-palatine suture. In *Myomimus*, *Glirulus*, and some *Graphiurus* they are medial to M3; in *Myoxus*, *Eliomys*, and *Dryomys*, and some *Graphiurus* most commonly to the posterior part of M2 and to the anterior part of M3; and in *Muscardinus* to the anterior and middle parts of M2. The foramina are large except in *Glirulus* and *Myomimus*. The posterior palatine foramina appear to be lacking in some specimens of *Graphiurus*; they are probably combined with the posterior maxillary foramina from which a channel leads anteriorly onto each side of the palate. The posterior edge of the palate is medial to some part of M3 except in *Muscardinus* where it ends medial to the middle or posterior part of M2.

In *Myoxus*, *Graphiurus*, *Glirulus*, and *Dryomys* the posterior maxillary foramen is enclosed medial to the posterior point of the maxilla just posterior to M3. The palatine forms the medial and posterior edges of the foramen. The posterior tip of the maxilla meets the palatine and the anteroventral edge of the alisphenoid just posterior and lateral to the foramen. The posterior maxillary foramen is absent in *Eliomys* and *Myomimus*, and the maxillary point has a medial suture with the palatine. A foramen that appears to serve the same function of transmitting the descending maxillary vein is present within the palatine near this region in a few specimens of *Eliomys*. The posterior maxillary foramen is very large in *Muscardinus*, and some or all of its ventral aperture is medial to M3; the pterygoid forms a very small portion of its posterolateral border, and the maxillary-alisphenoid junction is broad lateral to the foramen.

The infraorbital foramen is moderately tall and nearly oval; the greatest breadth is above the middle. *Myomimus* differs in that the foramen does not extend as far dorsally and is widest below the middle. The bony entrance to the lacrimal canal is medial or antero-medial to the infraorbital foramen and lateral to the incisor alveolus. The maxilla forms the lateral border of the canal. The lacrimal bone, which has a small process overhanging the anterodorsal part of the orbit, is minute and

does not appear to participate in the lateral or medial margins of this aperture. The lacrimal bone is not firmly sutured to the skull and is often lost from dried specimens. A nonossification is usually present medial to the infraorbital foramen and posterodorsal to the lacrimal opening; in life it is covered by connective tissue. It may be equivalent to the nonossification at the junction of lacrimal, maxillary, and frontal bones that is seen in various rodent groups including members of the Sciuridae and Muroidea. The incisor alveolus is sometimes exposed by this unossified area of the rostral wall.

The sphenopalatine foramen is dorsal to a zone that ranges from the anterior part of M2 to the posterior part of M3; *Muscardinus* is exceptional in that the foramen is dorsal to the posterior part of M1. The orbitosphenoid bone is excluded from the margin of the foramen. The maxilla, palatine, and frontal participate in its margin; rarely the palatine is excluded. Exposure of the ethmoid bone excludes the frontal from the dorsal edge in *Graphiurus*; this condition also occurs in some specimens of *Eliomys*.

The ethmoid foramen is either in the frontal bone very close to the frontal-orbitosphenoid suture, or it is combined with an unossified area dorsal to the orbitosphenoid bone. The nonossification is usually present, but of variable size. The ethmoid foramen is dorsal to some part of M3 in most *Graphiurus* (in others it is just posterior to M3); it is dorsal to M3 or to the M2M3 junction in *Eliomys*, *Dryomys*, and *Myomimus*, to the M2M3 junction in *Glirulus*, to a part of the posterior half of M2 in *Myoxus*, and to the posterior part of M1 in *Muscardinus*.

The optic foramen, which is within the orbitosphenoid bone, is about 1.0 mm in diameter in all genera except *Graphiurus*, *Glirulus*, and *Myomimus* in which it is somewhat smaller. The foramen is dorsal and entirely posterior to M3 in *Graphiurus*, *Eliomys*, *Dryomys*, and *Myomimus*. It is just posterior in *Glirulus*, dorsal to M3 in *Myoxus*, and dorsal to a zone from the anterior part of M2 to the anterior part of M3 in *Muscardinus*. The foramen is medial or slightly anterior to the edge of the anterior alar fissure except in *Myoxus* and *Muscardinus* where it is quite far anterior; *Glirulus* appears to be interme-

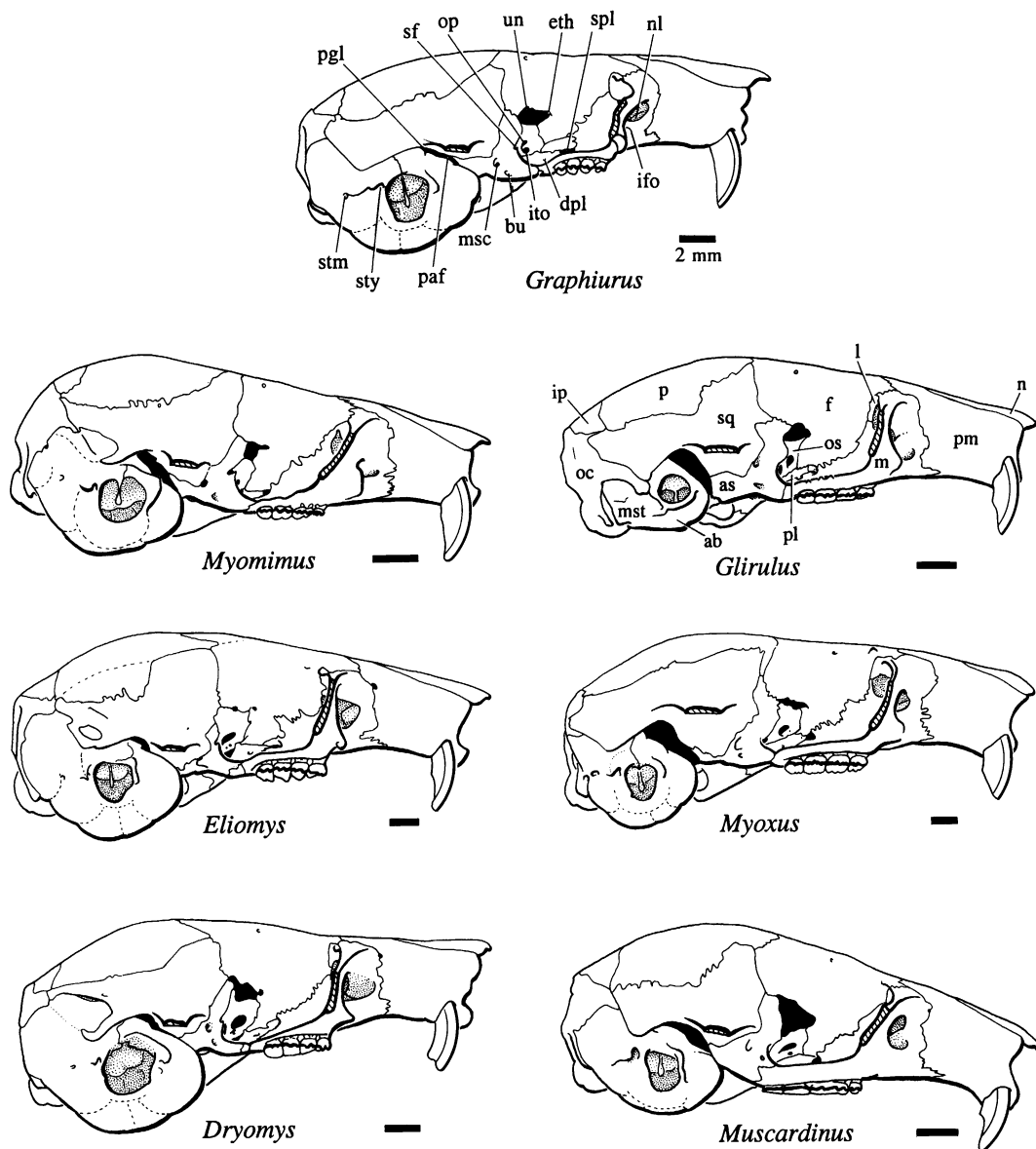


Fig. 1. Myoxid skulls, lateral views. Scale bars are approximately 2 mm long. See text list of specimens examined for specimen numbers and localities.

Abbreviations for foramina and other apertures: **ac**, alisphenoid canal, posterior end; **bu**, buccinator; **dpl**, dorsal palatine; **eth**, ethmoid; **fo**, foramen ovale; **hy**, hypoglossal; **ifo**, infraorbital; **in**, incisive; **ito**, interorbital; **ju**, jugular; **mlf**, middle lacerate; **msc**, masticatory; **nl**, nasolacrimal; **op**, optic; **paf**, posterior alar fissure; **pgl**, postglenoid; **pom**, posterior maxillary; **ppl**, posterior palatine; **sf**, sphenofrontal; **spl**, sphenopalatine; **spv**, sphenopalatine vacuity; **stm**, stapedius muscle canal; **sty**, stylomastoid; **trc**, transverse canal; **un**, unossified area. Mastoid foramen absent in this *Graphiurus* specimen and stapedial foramen not exposed to view.

Abbreviations for bones and their processes: **as**, alisphenoid; **ab**, auditory bulla; **bo**, basioccipital; **bs**, basisphenoid; **f**, frontal; **ip**, interparietal; **j**, jugal; **l**, lacrimal; **m**, maxilla; **mst**, mastoid region; **n**, nasal; **oc**, occipital; **os**, orbitosphenoid; **p**, parietal; **pl**, palatine; **pm**, premaxilla; **ps**, presphenoid (continuous with orbitosphenoid); **sq**, squamosal.

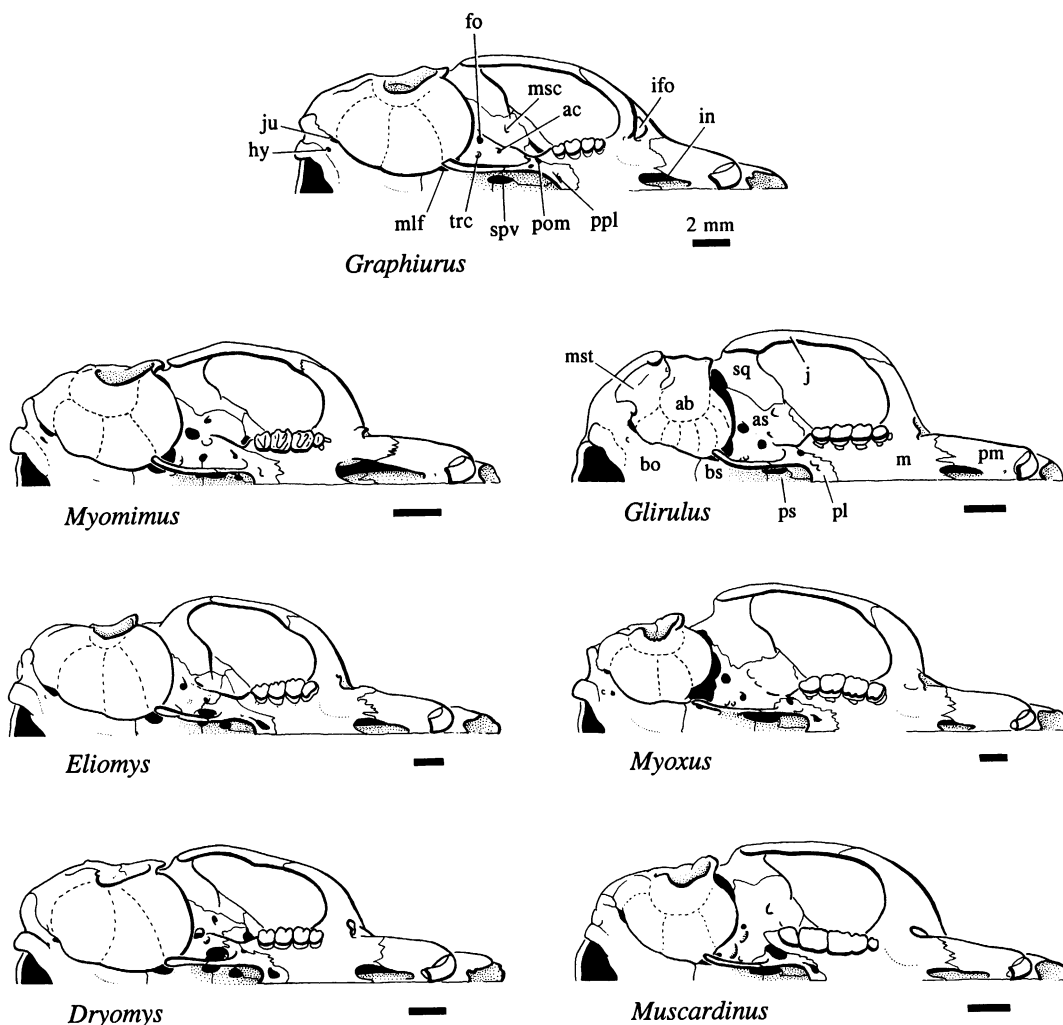


Fig. 2. Myoxid skulls, ventral views. See fig. 1 for abbreviations; scale approximate.

diate. An interorbital foramen is commonly present in the orbitosphenoid bone ventral to the optic foramen.

The dorsal palatine foramen is in the maxillary-palatine suture or more commonly within the palatine bone close to this suture. It is a short distance posterodorsal to M3 except in *Myoxus* and *Glirulus* where it is dorsal to the posterior part of M3 and in *Muscardinus* where it is dorsal to the posterior part of M2. In some specimens of *Graphiurus* the foramen appears to be combined with the posterior maxillary foramen. It is far from the sphenopalatine foramen in all genera.

The sphenofrontal foramen is situated between the orbitosphenoid and alisphenoid bones just dorsal to the anterior alar fissure; the frontal is excluded from its margin in myoxids. The foramen is moderately large in *Graphiurus*, *Eliomys*, *Dryomys*, and *Myomimus*. In some specimens a groove on the inside of the cranium for the superior ramus of the stapedia artery leads anteriorly to it from just lateral to the foramen ovale; the groove may continue externally across the orbital wall to the ethmoid foramen. The sphenofrontal foramen is tiny in some specimens of *Myoxus* and is lacking in others. No trace of the sphenofrontal foramen was found

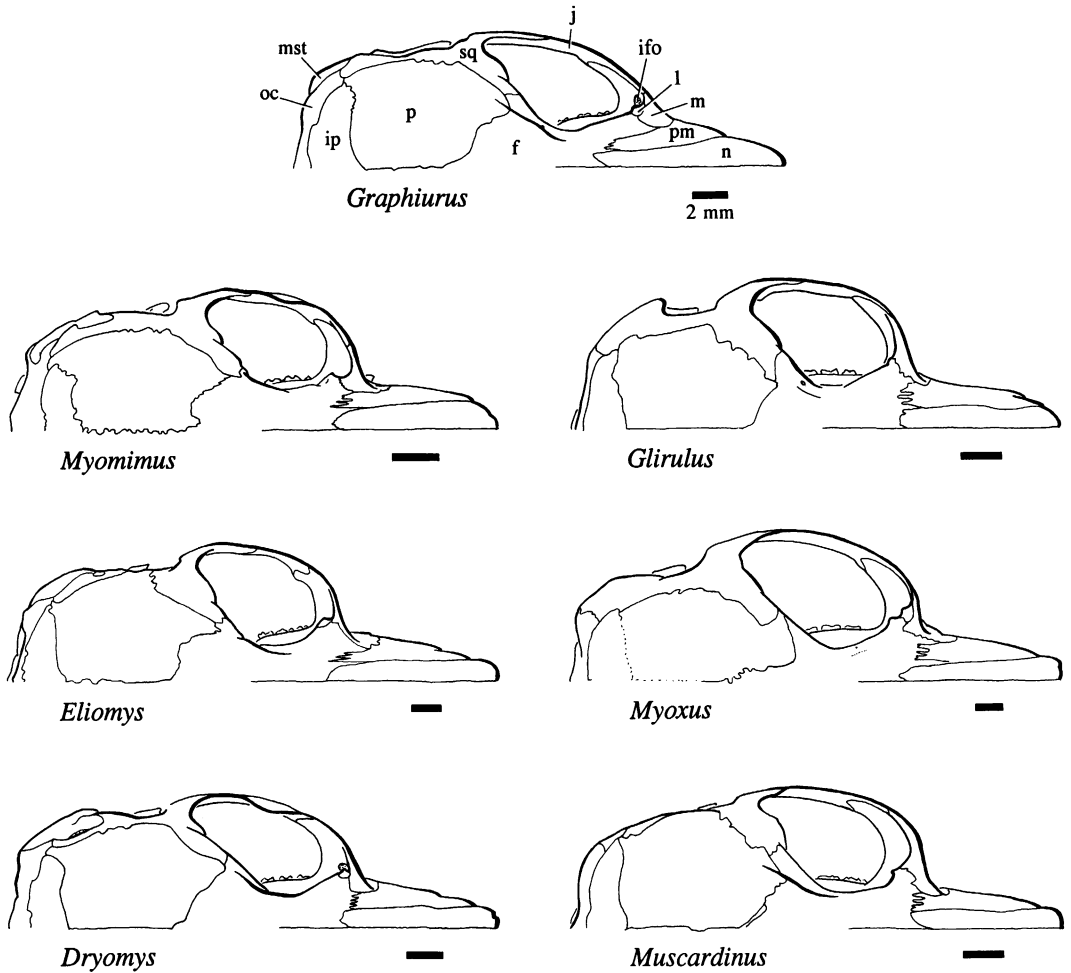


Fig. 3. Myoxid skulls, dorsal views. See fig. 1 for abbreviations; scale approximate.

in *Muscardinus* and *Glirulus*. This is associated with the loss of the superior ramus of the stapedia artery which Bugge (1971a) said was lacking in *Myoxus* and *Muscardinus*.

The anterior alar fissure is above M3 in *Muscardinus* and posterior to M3 in all other taxa. The sphenopalatine vacuities extend up to the level of the anterior alar fissure in most genera. They extend farther and are visible in the orbit in *Eliomys* and some *Dryomys*.

Masticatory and buccinator foramina are usually separated, and the bony strut between them varies in width. The two foramina are united in many specimens of *Myoxus* and in some specimens of *Graphiurus*. The masseteric and buccinator nerve canals are short and rarely share a common posterior portion.

A fenestra in the alisphenoid, anterodorsal to the masticatory foramen, occurs in *Graphiurus*, *Dryomys*, *Myomimus*, and in some *Muscardinus* and *Eliomys*. In many but not all taxa it occurs where the external depression accommodating the masseteric nerve crosses an internal channel excavated by the superior ramus of the stapedia artery.

The foramen ovale is surrounded by bone in the posterolateral part of the pterygoid fossa. The accessory foramen ovale is lacking. The entrance to the alisphenoid canal is anteromedial to the foramen ovale; it is closest to that foramen in *Muscardinus*. The alisphenoid canal is not confluent with the beginning of the channels for masseteric and buccinator nerves, and it appears to be open

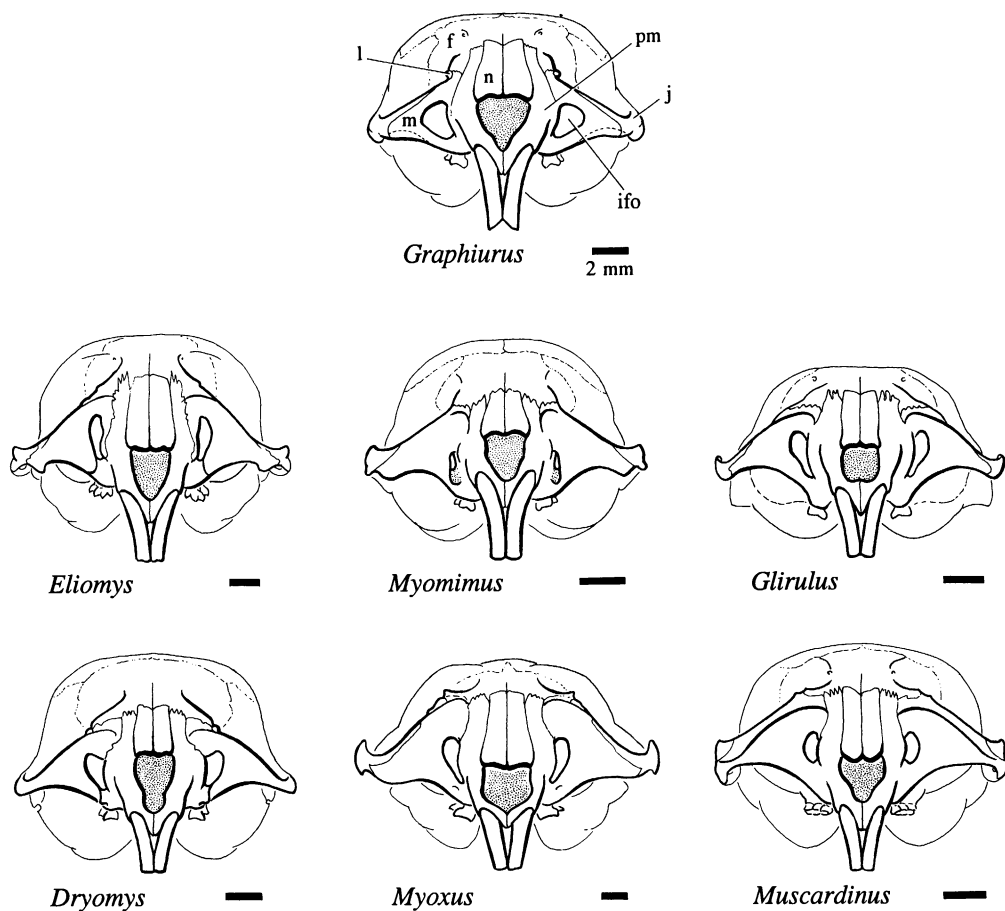


Fig. 4. Myoxid skulls, anterior views. See fig. 1 for abbreviations; scale approximate.

internally into the cranial cavity. The transverse canal is moderately large and enters the basisphenoid bone near the base of the hamular process medial to the foramen ovale. The roof of the pterygoid fossa is completely ossified, and there is no sphenopterygoid canal. An opening is present at the anterior apex of the fossa in *Eliomys*, some *Dryomys*, and some *Graphiurus*; the palatine-ptyergoid suture intersects its margin. This opening is lacking in *Myoxus*, *Myomimus*, and *Glirulus*. The large posterior maxillary foramen in *Muscardinus* may be a combination of the foramen with this aperture; the fact that the anterior part of the pterygoid participates in its margin supports this view. Other small foramina adjacent to the medial flange of the fossa occur variably in most taxa. Oval sphenopalatine vacuities flank the basisphe-

noid-orbitosphenoid (= presphenoid) suture in the roof of the choana in all genera.

The middle lacerate foramen is prominent anteromedial to the auditory bulla in all taxa. In *Myoxus* it extends laterally and produces a gap between the pterygoid fossa and the bulla. The postglenoid foramen is situated between the squamosal bone and the auditory bulla. It extends ventrally as a short, narrow posterior alar fissure in *Graphiurus*, *Eliomys*, and *Dryomys*. The fissure is broader and extends farther ventrally in *Myoxus*, *Muscardinus*, *Myomimus*, and *Glirulus*, and there is variation in the continuity and combinations of continuity between the postglenoid foramen, posterior alar fissure, and middle lacerate foramen; complete continuity is common in *Myoxus*.

The stapedial/internal carotid foramen is

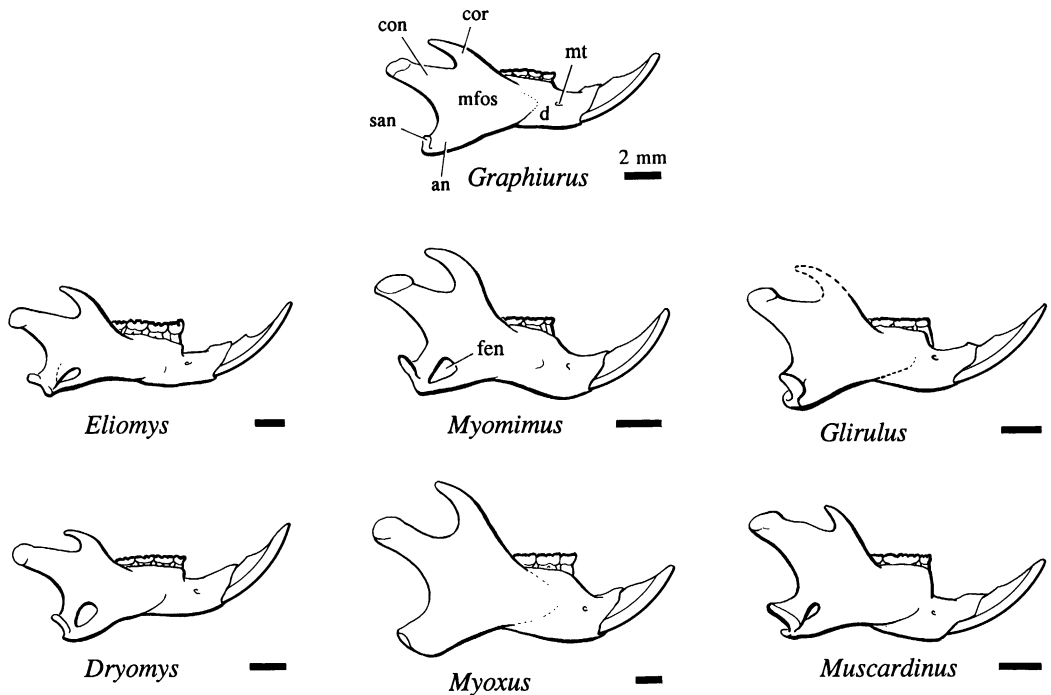


Fig. 5. Myoxid mandibles. Abbreviations: an, angle; con, condyloid process; cor, coronoid process; d, dentary bone; fen fenestra; mfos, masseteric fossa; mt, mental foramen; san, superior angular process. Scale approximate.

present in the posteromedial curvature of the bulla deep within the aperture of the jugular foramen in *Graphiurus*, *Myomimus*, *Dryomys*, and *Eliomys*. It is very tiny or absent in *Myoxus*, and it is lacking in *Glirulus* and *Muscardinus*. The tiny hypoglossal foramen (or foramina) is between the condyle and the jugular foramen. The stylomastoid foramen points ventrally and is situated posterior to the bony auditory meatus. A small foramen in the mastoid bone is the end of the tube in which the stapedius muscle takes its origin; the aperture is a short distance posterior to the stylomastoid foramen. The foramen was not observed in *Glirulus*. The posterior edge of the meatus is flush with the bulla except in *Glirulus* where it protrudes slightly, and the entire circumference forms a short tube. Dissection revealed the chorda tympani nerve emerging from the canal of Huguier in the wall of the bulla anterior to the bony meatus. The tiny mastoid foramen is situated dorsomedially in the mastoid-occipital suture; the foramen could not be found in many specimens of *Graphiurus*.

Temporal foramina are lacking. The occipital end of the squamosal is solid in *Graphiurus*, *Myoxus*, *Glirulus*, and *Muscardinus*; it is posteriorly emarginate in *Myomimus*. *Dryomys* and *Eliomys* show a variety of conditions. The bone is emarginate in most specimens; in others one side is emarginate, and the other has a group of small holes within the bone; a single large hole within the bone may characterize the posterior emargination on the opposite side. There is no squamosomastoid foramen.

The mental foramen of the mandible is anteroventral to p4. The mandibular foramen on the medial side of the jaw is posterior to the cheek teeth and ventral to the anterior end of the mandibular notch (between coronoid and condyloid processes) in all taxa except *Muscardinus* and *Eliomys*. In *Muscardinus* it is farther dorsal relative to the teeth and posterior with regard to the end of the notch. In *Eliomys* it is farther anterior, thus closer to the third molar. In *Dryomys*, *Eliomys*, and *Myomimus* a prominent fenestra is present in the ventral part of the angle

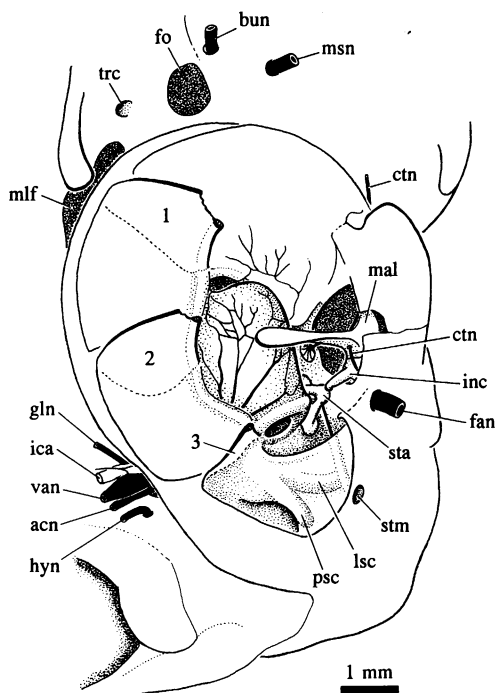


Fig. 6. Auditory region, left side, of *Graphiurus* in slightly oblique view, anterior is at top. See text for description. Abbreviations: 1, 2, 3 tympanic septa; acn, accessory nerve; bun, buccinator nerve; ctn, chorda tympani nerve; fan, facial nerve; fo, foramen ovale; gln, glossopharyngeal nerve; hyn, hypoglossal nerve; ica, internal carotid artery; inc, incus; lsc, lateral semicircular canal; mal, malleus; mlf, middle lacerate foramen; msn, masseteric nerve; psc, posterior semicircular canal; sta, stapes; stm, foramen at end of stapedius muscle canal; trc, transverse canal; van, vagus nerve. Important structures without labels: stapedial artery canal crosses promontorium in the base of the tympanic septum 3; cochlear fenestra faces posterolaterally; nerve branches on promontorium. Scale is approximate; distance from medial side of bulla to lateral edge of bony auditory meatus approximately 5.7 mm.

that is bent medially. The region in *Muscardinus* may be entire or perforate. The aperture is covered with connective tissue in life. In *Graphiurus*, *Glirulus*, and *Myoxus* the bone here is usually entire but thin and translucent, though in a very few specimens perforate.

AUDITORY REGION

We have dissected the middle ear region in *Eliomys* and *Graphiurus* (fig. 6) and have examined it in the skull of *Myoxus*. The ec-

totympanic bullae are moderately large and rounded. In all genera except *Glirulus* three complete radial septa project from the bulla wall; the free edge of each extends from the crista tympanica medially to the part of the ectotympanic that overlaps the promontorium. In *Glirulus* the septa are more numerous, and interconnecting partitions are present.

Lateral to the jugular foramen an aperture in the bulla marks the passage of the internal carotid/stapedial artery into the middle ear in *Graphiurus*, *Myomimus*, *Dryomys*, and *Eliomys*. It is tiny or absent in *Myoxus*. The artery runs anterolaterally within the base of the third and posteriormost septum. It emerges from the septum and passes laterally inside a bony tube that shows considerable relief from the surface of the promontorium. The tube skirts the ventral margin of the cochlear fenestra (= fenestra rotundum) in *Graphiurus*, *Myomimus*, and *Dryomys*. The bone of the promontorium is thin and nearly transparent just anteroventral to the tube in *Eliomys*; Parent (1980: 112) stated that the artery crosses the fenestra rotundum at mid height. The ventral side of the bony tube is open where the now exposed stapedial artery passes through the obturator foramen of the stapes; the artery then enters a foramen in the medial side of the fallopian canal, and turns anteriorly within the bone. It can be traced inside the skull to the foramen ovale, where the superior ramus branches off and ascends to the sphenofrontal foramen (Bugge, 1974: 64A). The stapedial artery is absent in adult specimens of *Myoxus*, but its embryonic course is indicated by an open groove that runs laterally across the promontorium just anteroventral to the foramen rotundum. In a dry specimen a tiny thread of tissue stretches from the lateral end of the groove, through the stapes, to a minute tubular opening in the fallopian canal. There is no trace of the stapedial artery in *Muscardinus* and *Glirulus*. These data for *Myoxus* and *Muscardinus* confirm the observations of Bugge (1971a). In all genera the fallopian canal for the facial nerve is a completely closed tube that forms the medial side of the epitympanic recess.

Dissection of *Graphiurus* and *Eliomys* revealed that the cranial cervical ganglion is situated ventromedial to the bulla, alongside

the internal carotid artery. In *Eliomys* a tiny branch from the nerve runs anteriorly with the vessels of the external carotid system. In both taxa the main trunk of the nerve follows the internal carotid artery into the carotid/stapedial foramen. We believe that some of the nerves seen on the promontorium are continuations of the carotid nerve.

In a dissected specimen of *Graphiurus* four nerve branches emerge in this region from under the edge of the ectotympanic, near the point where the arterial tube leaves the posterior septum. We have located one foramen in this position in dry specimens of *Eliomys* and *Myoxus*. The nerves follow anterolateral courses across the promontorium where they ramify and anastomose. Parent (1980: 113) called this the nerve of Jacobson (= tympanic nerve). Wible (1984: 180) suggested that this is the internal carotid nerve. A third possibility is that both of these nerves enter the middle ear in approximately the same position. We believe the third to be the most likely.

The chorda tympani nerve diverges from the facial nerve close to the stylomastoid foramen. In *Graphiurus* it runs anteriorly, crosses below the incus, and passes through a tiny foramen in the manubrium of the malleus. This foramen is lateral to the insertion of the tensor tympani muscle. The nerve continues along the medial edge of the anterior process of the malleus and leaves the ectotympanic recess. It emerges from the canal of Huguier anterior to the bony auditory meatus. The tensor tympani muscle appears as a thread that ascends from the manubrium of the malleus to a small, circular mass of muscle that arises on the petrosal anterolateral to the vestibular fenestra.

The cochlea is bent, with the posterior part directed slightly laterally and the cochlear fenestra facing posterolaterally; its lateral end is ventral to the posterior part of the vestibular fenestra. The vestibular fenestra and the base of the stapes are elongated ovals that are slightly concave on the promontorial side. The fenestra is somewhat oblique to the vertical plane and approximately parallel to the tympanic membrane. The crura of the stapes point ventrolaterally; the stapes also has a slight posterior slant except in *Myoxus*. In ventral view the anterior end of the vestibular fenestra is more medial than the posterior.

The cochlear fenestra faces posterolaterally except in *Glirulus* and *Myomimus* where it appears to open posteriorly.

The mastoid portion of the petrosal is pneumatized, and a large chamber opens behind the cochlear fenestra. Its walls and nearly horizontal floor are formed by a partition that extends forward from the posterior wall of the mastoid. The floor ends in a concave edge posterior to and facing the fenestra; the lateral semicircular canal describes an arch in the floor posterior to this edge. The posterior semicircular canal courses through the medial part of the floor and then turns dorsally. Parent (1980: 113) observed that the origin of the stapedius muscle is within a bony tube that runs posterolaterally and opens externally on the surface of the mastoid behind the stylomastoid foramen. The tube passes through the floor of the mastoid chamber; we suspect that the muscle origin is enclosed because the floor appears to be a two-part structure—a mastoid partition that is overlapped on the ventral side by the ectotympanic. The external opening of the canal for the stapedius muscle was observed in all taxa except *Glirulus*. Externally the dorsal part of the mastoid region is slightly inflated in *Myoxus* and substantially inflated in the other genera.

DENTITION

Figures 7 through 13 present stereoscopic photographs of dentitions of the seven genera examined. All myoxids except the adult *Selevinia* have a fourth premolar and three molars in the upper and lower dentitions. The premolar, although it is the smallest tooth, is molariform in all but *Muscardinus*, *Myomimus*, and *Graphiurus ocularis*, in which it is reduced. Bashanov (1951) observed that very young *Selevinia* possesses five upper cheek teeth—the anterior two are lost and the alveoli quickly heal over; it is not known whether these teeth are part of the deciduous or permanent series. The genus has three cheek teeth in the lower dentition. The ratio of crown length of the cheek teeth to condylobasilar length is greater than .20 in *Myoxus*, *Muscardinus*, and *Glirulus*; the ratio is less in the other genera. In all but *Myoxus* and *Muscardinus* the occlusal surface of the upper cheek teeth is strongly helical, with the posterior teeth pointing laterally and the anterior teeth medially. In *Myoxus* the sur-



Fig. 7. *Graphiurus lorraineus*, AMNH 49888, stereo pair of upper right and lower left dentition. Rostral end is up, buccal is to the left. Crown length upper dentition, 3.3 mm, lower, 3.2 mm. Scale bar approximately 1 mm.

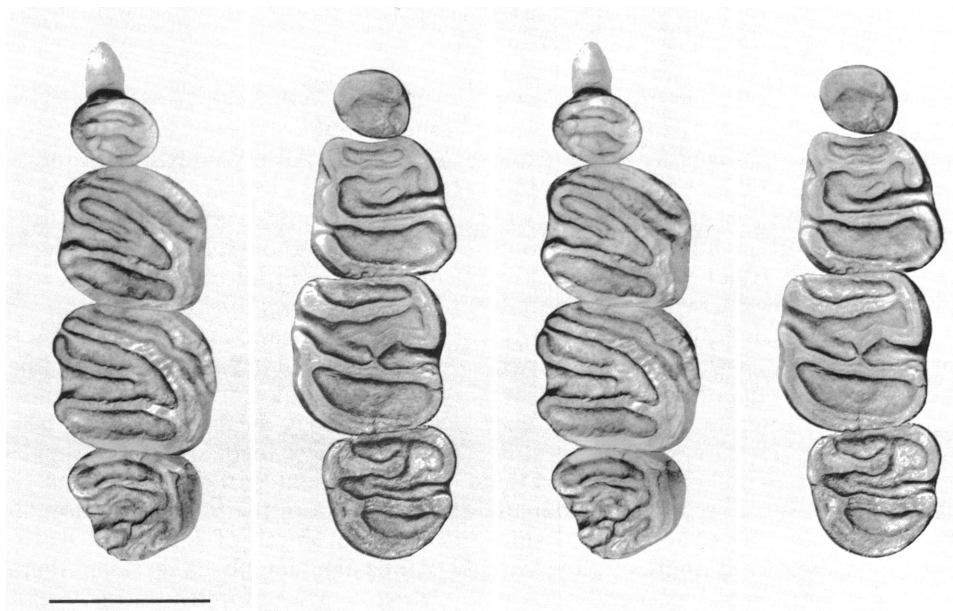


Fig. 8. *Myomimus setzeri*, USNM 350725, stereo pair of upper right and lower left dentition. Rostral end is up, buccal is to the left. Crown length upper dentition, 3.0 mm, lower, 2.9 mm. Scale bar approximately 1 mm.

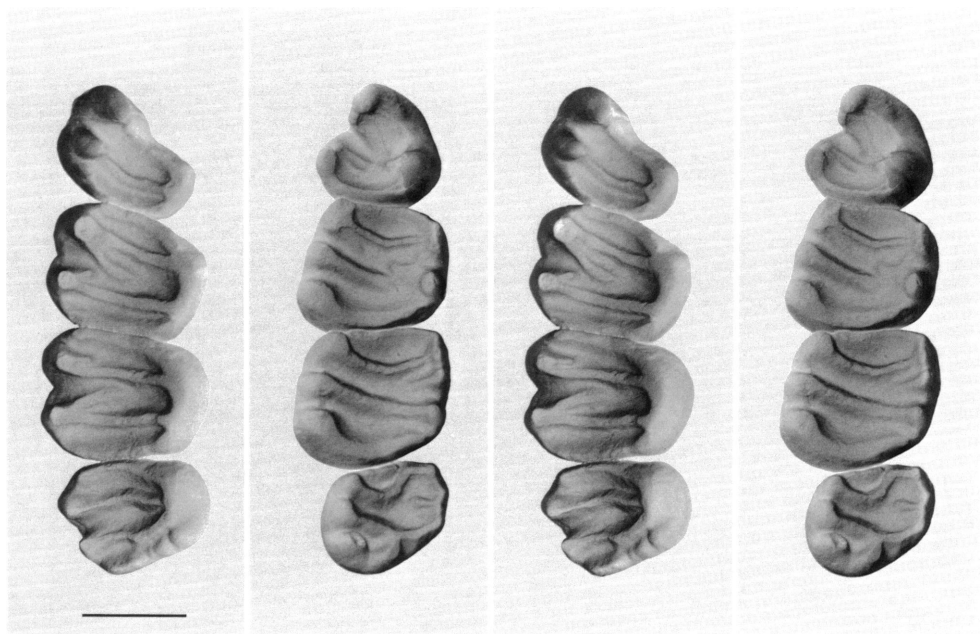


Fig. 9. *Eliomys quercinus*, AMNH 150129, stereo pair of upper right and lower left dentition. Rostral end is up, buccal is to the left. Crown length upper dentition, 4.8 mm, lower, 4.8 mm. Scale bar approximately 1 mm.

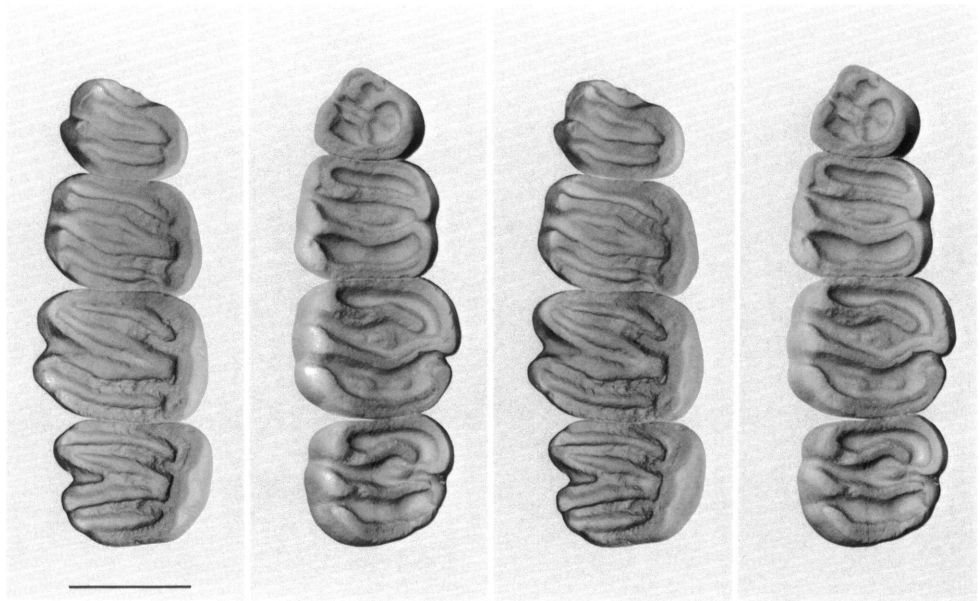


Fig. 10. *Dryomys nitedula*, AMNH 217346, stereo pair of upper right and lower left dentition. Rostral end is up, buccal is to the left. Crown length upper dentition, 3.9 mm, lower, 4.0 mm. Scale bar approximately 1 mm.

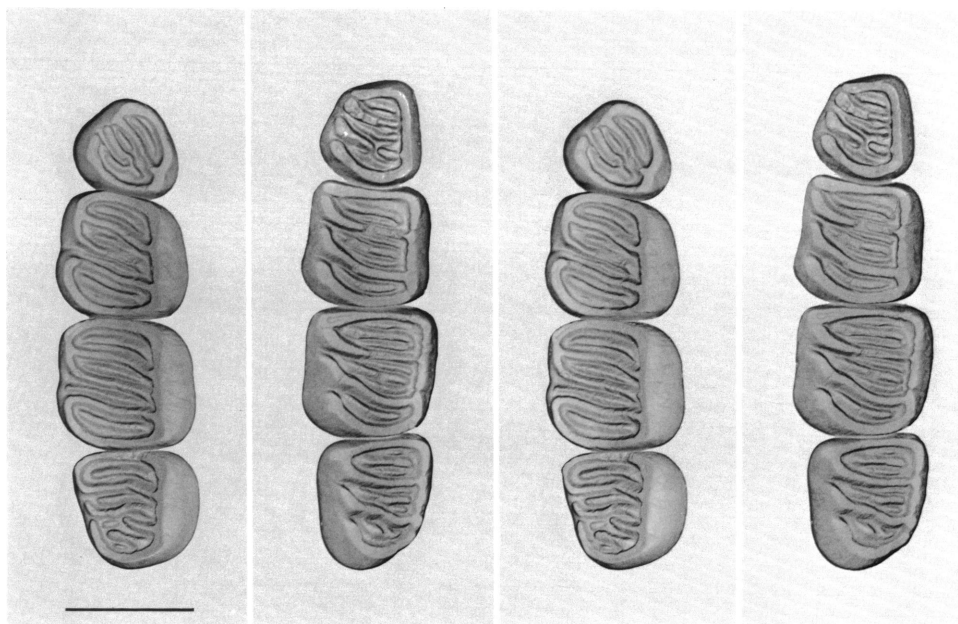


Fig. 11. *Glirulus japonicus*, AMNH 164112, stereo pair of upper right and lower left dentition. Rostral end is up, buccal is to the left. Crown length upper dentition, 3.6 mm, lower, 3.8 mm. Scale bar approximately 1 mm.

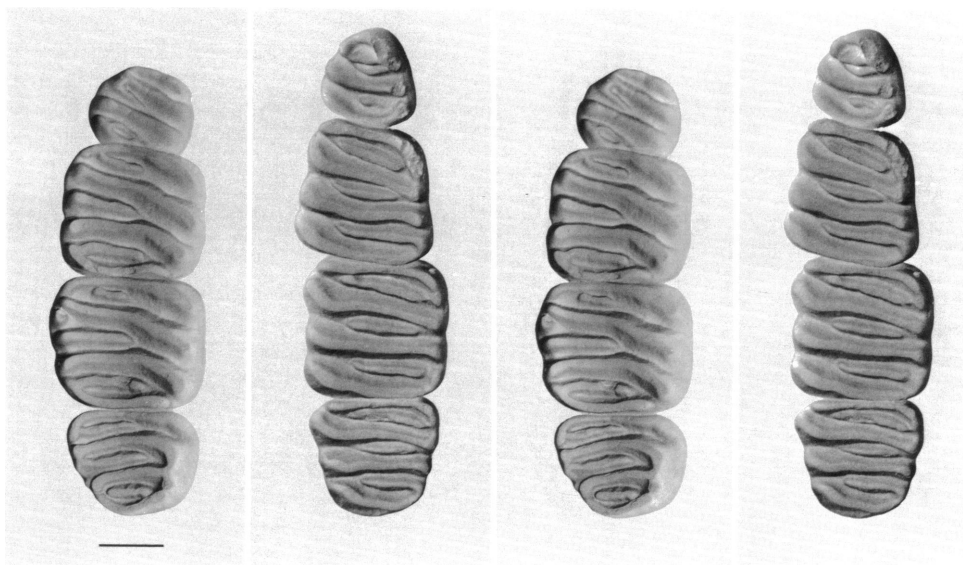


Fig. 12. *Myoxus glis*, AMNH 88752, stereo pair of upper right and lower left dentition. Rostral end is up, buccal is to the left. Crown length upper dentition, 7.0 mm, lower, 7.6 mm. Scale bar approximately 1 mm.

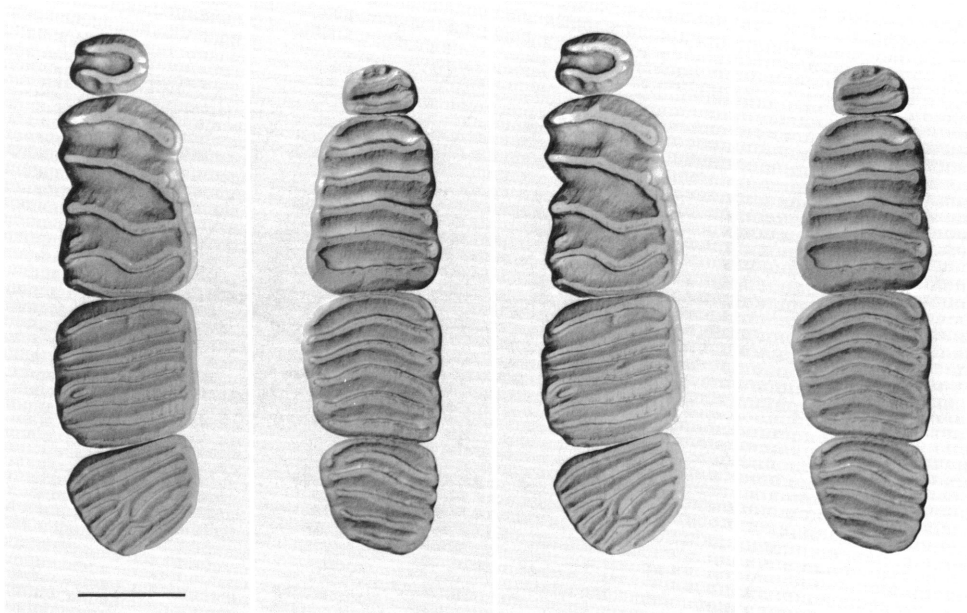


Fig. 13. *Muscardinus avellanarius*, AMNH 149416, stereo pair of upper right and lower left dentition. Rostral end is up, buccal is to the left. Crown length upper dentition, 4.9 mm, lower, 4.6 mm. Scale bar approximately 1 mm.

face is nearly flat; in *Muscardinus* it is either flat or with the helix reversed and posterior teeth pointing more medially than the anterior. Dentitions of the European genera were figured by Storch (1978).

Tooth cusps are mostly subsumed in ridges. The lateral and medial ends of the ridges, which represent the cusps, are of substantially different heights in *Eliomys* and *Dryomys*. The difference appears less in *Myoxus*, *Graphiurus*, *Glirulus*, and *Myomimus*. The crowns are flat in *Muscardinus*.

Upper and lower tooth crown patterns are based on a series of four transverse lophs with accessory crests interposed. In the upper dentition the four are anteroloph, protoloph, metaloph, and posteroloph; in the lower dentition, anterolophid, metalophid, hypolophid or mesolophid, and posterolophid (Thenius, 1989: 190). Anterior and posterior lophs are also termed cingula. Accessory crests do not span the entire width of the crown except in *Muscardinus*. The number of accessory crests in M2 is one in *Myomimus*, one or two in *Graphiurus*, *Eliomys*, and *Dryomys*, three in *Myoxus* and *Muscardinus*, and four or more

in *Glirulus*. The number in m2 is one in *Eliomys* and *Myomimus*, one or two in *Graphiurus*, two or three in *Dryomys*, three in *Myoxus*, and four or more in *Glirulus*. In *Graphiurus* the peripheral crests are prominent and the internal ones low and variable so that the crowns often appear as basins.

In addition to the transverse loph, the teeth are divided by transverse valleys. The number of complete transverse valleys in m2 is one in *Eliomys*, *Dryomys*, and *Myomimus*, two in *Myoxus*, and three in *Muscardinus*. In both *Graphiurus* and *Glirulus* there is no complete valley because the lophs are united by a longitudinal crest on the lingual side of the tooth, an unusual difference from the primitive buccal continuity. Buccal connections in m2 are common between the tips of the anterolophid and metalophid and the hypolophid and posterolophid. One or both connections occur in *Graphiurus*; one connection occurs in *Glirulus*, *Eliomys*, *Dryomys*, and *Myomimus*. The lophs are not joined buccally in *Myoxus* and *Muscardinus*.

The upper incisors of *Eliomys* and *Dryomys* are unusual in that the enamel appears

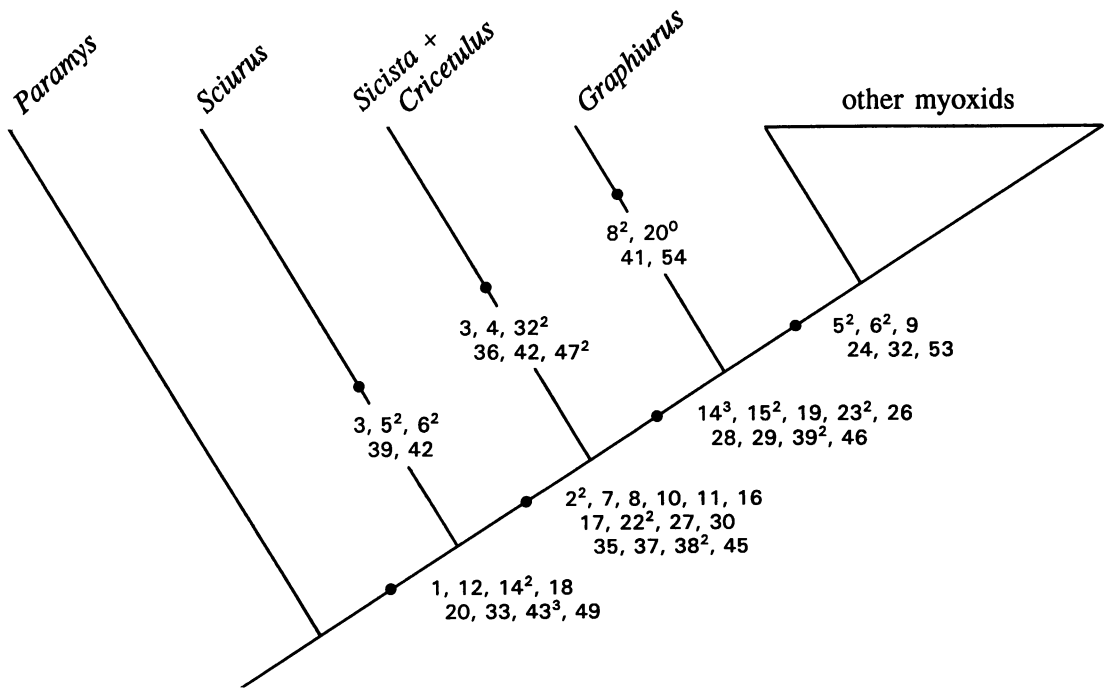


Fig. 14. Shortest tree showing relationship of myoxids and *Graphiurus* to outgroups. Numbers refer to characters and character states in Appendix 1. All characters are at state 0 in *Paramys*. Listing of a number by itself indicates change to state 1; a number followed by a superscript indicates change to that higher state, except superscripts of 0 or number followed by minus sign are reversals to the state indicated.

to extend farther onto the lateral side than in other myoxids; the lateral sides are broadly grooved at the edge of the enamel cover in a majority of *Eliomys* and all *Dryomys* specimens examined. Interdental wear often sharpens the lower incisors of myoxids to narrow but rounded points.

DISCUSSION

Analysis of the data matrix by PAUP yielded one shortest tree (fig. 14) of 139 steps, consistency index excluding uninformative characters 0.652, and retention index 0.548. The consistency index is slightly less than the expected value of 0.683, calculated according to the formula of Sanderson and Donoghue (1989, fig. 1).

There were five trees of 140 steps, 19 of 141 steps, and 40 of 142 steps. In all of these *Sicista*, *Cricetulus*, and the Myoxidae constitute a clade with *Sciurus* as the sister group. *Sicista* and *Cricetulus* form a unique clade in

about half of the trees; alternatively, one or the other is the sister taxon to the myoxids. The association of *Glirulus*, *Myoxus*, and *Muscardinus* as a clade occurs in most trees; *Eliomys* and *Dryomys* are usually associated, and *Myomimus* commonly groups together with them. *Graphiurus* exhibits great mobility and appears as the first myoxid branch or as a sister taxon either to the *Myoxus* cluster or to *Eliomys* plus *Dryomys*. *Myomimus* also occupies a basal position in some of the trees.

In the shortest tree (fig. 14) eight forward transformations set the recent taxa apart from *Paramys*; 14 additional forward transformations distinguish the Myomorpha, *Sicista*, *Cricetulus*, and the myoxids from *Sciurus*. Chief among these characters are anterior portion of medial masseter hystricomorphous, posterior edge of anterior root of zygoma lateral to some part of P4, premaxillary-maxillary suture meeting incisive foramina near the middle, incisive foramina longer than half of diastemal length, entrance

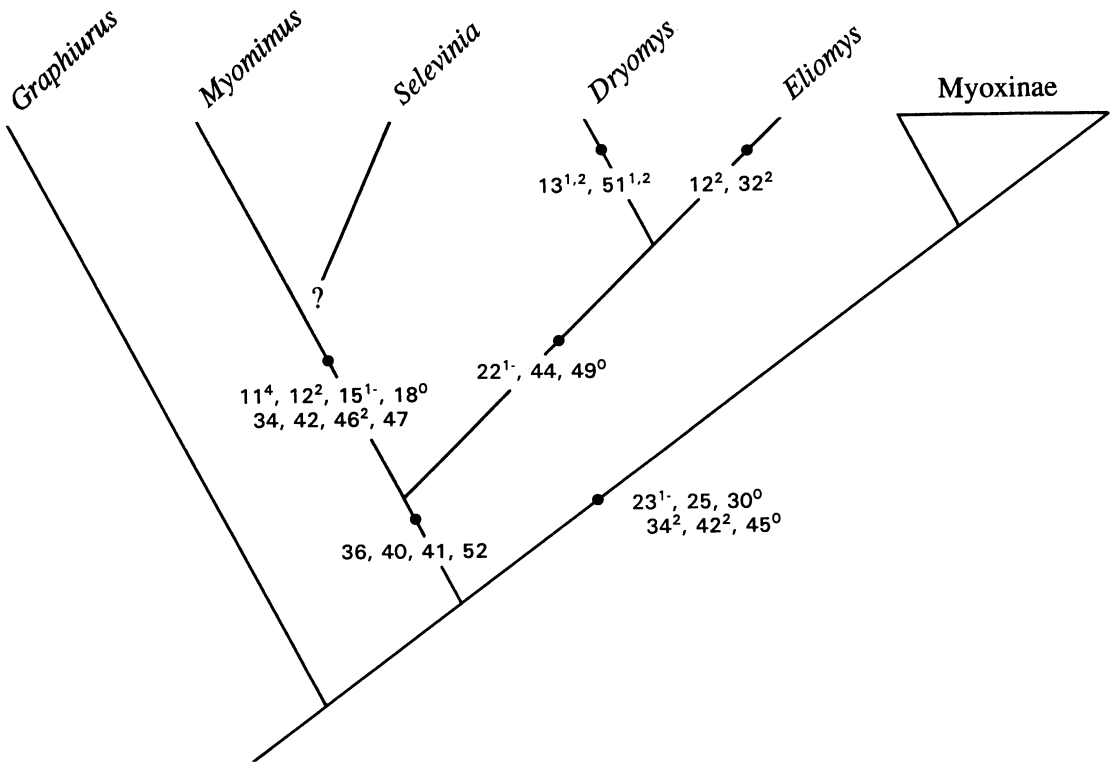


Fig. 15. Portion of shortest tree showing relationships among myoxids and within Leithiinae. See fig. 14 for explanation of numbers.

to lacrimal canal low and medial to infra-orbital foramen, optic foramen 1.0 mm or smaller, temporal foramina absent, and dorsal part of mastoid somewhat inflated.

The Myoxoidea are distinguished from other Myomorpha by the following three derived characters: back edge of posterior palatine foramen medial to some part of M3; bullae with three primary septa; and P4 as first upper cheek tooth. To this list can be added the absence of a cecum and the lack of a definite boundary between the small and large intestines (Tullberg, 1899), obliteration of the internal carotid artery immediately after branching of the stapedia artery (Bugge, 1974), and crown pattern of cheek teeth based on four transverse lophs into which cusps are subsumed. Other characters of our study offer equivocal support because they exhibit homoplasy within the myoxids. Many *Graphiurus* specimens are distinguished from other myoxids by the forward position of the

maxillary zygomatic root despite primitiveness of the lateral masseter, the lingual connecting crest in the lower cheek teeth, and the low relief of internal features of the tooth crowns.

Myoxids other than *Graphiurus* show certain advances: deep division of lateral masseter sciuromorphic; its superficial division with separate origin, usually in the form of a tubercle; and jugal failing to reach lacrimal bone (except in *Myoxus*). *Eliomys*, *Dryomys*, and *Myomimus*, the Leithiinae (fig. 15), are characterized by squamosal bone containing a fenestra or emarginate posteriorly, fenestra present in mandibular angle, inclination of anterior edge of coronoid process low, complete transverse valley present in m2. *Eliomys* and *Dryomys* are similar in the peculiar cross-sectional shape of the upper incisors, 45° tilt of the Hunter-Schreger bands in the portio interna of the middle of the enamel in lower incisors (Koenigswald, in press), and

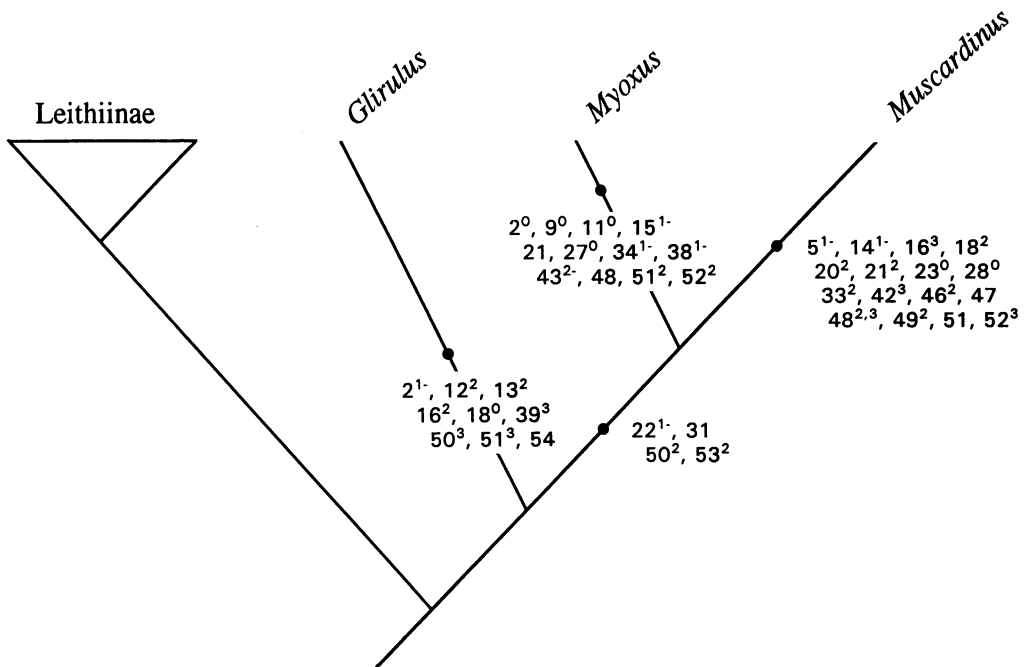


Fig. 16. Portion of shortest tree showing relationships among Myoxinae. See fig. 14 for explanation of numbers.

in primitive dental crown pattern. *Myomimus* has elongated incisive foramina and premolars of reduced size.

The descriptions and figures of *Selevinia* presented by Bashanov and Belosludov (1941) and Ognev (1947) include derived character states that suggest placement of the genus in the cladogram. However, without the opportunity to examine specimens first hand, the limited number and mixture of described characters make such placement uncertain. *Selevinia* exhibits reduction of the cecum and torsion of the mandibular angle that are typical of the Myoxoidea. The anterior portion of the deep lateral masseter arises on the anterior part of the zygoma and perhaps on the rostrum as in myoxids, excluding *Graphiurus*. *Selevinia* shares with the Leithiinae the presence of a fenestra in the angle of the mandible and low angle of ascent of the coronoid process relative to the occlusal plane of the cheek teeth. The relatively long incisive foramina, rather small infraorbital foramen, and tail covered with short hairs are characters found also in *Myomimus*. Autapomorphic characters of *Selevinia* include grooved upper

incisors, absence of premolars in the adult, small molar size with simple basined crown and single root, and very large auditory bullae. The premolars in *Myomimus* are somewhat reduced. The particular suite of derived characters leads us to associate *Selevinia* with *Myomimus* as Ognev (1947: 485) suggested.

Myoxus, *Muscardinus*, and *Glirulus*, the Myoxinae (fig. 16), are distinguished by small or absent sphenofrontal and stapedia foramina, prominent accessory crests parallel to primary crests on molar crowns, occlusal surface of cheek teeth nearly flat, and coronoid process concealing most or all of m3 in lateral view of the mandible. Primitive character states shared within this group include the anterior position of the dorsal palatine foramen, lack of a fenestra anterodorsal to the masticatory foramen, and moderately great length of the cheek tooth dentition relative to condylobasilar length. *Glirulus* and *Muscardinus* are defined primarily by characters transformed in the forward direction. In *Glirulus* the bullae contain multiple interconnected septa, M2 and m2 have four or more accessory crests, and a lingual connecting crest

occurs in the lower cheek teeth. *Muscardinus* has a host of uniquely derived characters: posterior maxillary notch enclosed by stout maxillary-alisphenoid bridge; anterior end of sphenopalatine foramen far anterior, dorsal to M1; ethmoid and optic foramina anterior relative to upper cheek teeth; pterygoid region short (distance from M3 to anterior end of foramen ovale); stapedia artery stem completely obliterated (Bugge, 1971a); coronoid process concealing part of m2; premolars reduced; occlusal surface of cheek teeth flat; and three transverse valleys present on m2. *Myoxus* and *Muscardinus* share the rudimentary lateral pterygoid flange, reduction or absence of the stapedia artery (Bugge, 1971a), and presence of more than one entire transverse valley in m2. *Myoxus*, however, retains several primitive characteristics that require evolutionary reversal in this hypothetical tree: premaxilla short dorsally; jugal touching lacrimal bone; incisive foramina relatively short; parietal and alisphenoid bones meeting; and dorsal part of mastoid only slightly inflated.

Vianey-Liaud (1985) has correctly called the masseteric condition of the Myoxidae "pseudo-myomorphy" and pointed out that the lower Oligocene species *Gliravus majori* was protrogomorphous. *Graphiurus* apparently retains the hystricomorphous condition, which may be the first step in the origin of both myomorphy and "pseudo-myomorphy." Other derived characters, however, associate the Myoxidae with the Dipodoidea and Muroidea in a suborder Myomorpha.

Parent (1980) described the middle ear regions of fossil and recent rodents. He selected *Eliomys* instead of *Graphiurus* as the morphological standard for the Myoxidae because Jaeger (1977: 121) had proposed that the dentition of the latter is simplified (derived) with respect to those of other myoxids. Parent found several features that myoxids share with sciurids but not with myomorphs. These include: bent cochlea; stapedia artery crossing cochlear fenestra at mid-height; retention of stapedia and loss of internal carotid artery; and nerve of Jacobson (= tympanic nerve) departing from ectotympanic with stapedia artery and ramifying on cochlea (seen in *Eliomys*). He noted a unique external opening in the mastoid, posterior to the stylomastoid foramen, that is the end of

the tubelike fossa for the origin of the stapedius muscle. Lavocat and Parent (1985: 338) stated that this tube is a specialization of a fundamentally primitive character; they hypothesized that the stapedius muscle extended out of the tympanic cavity onto the posterior surface of the skull in *Sciuravus* and the Theridomorpha as in recent myomorphs and some archaic insectivores and *Tupaia*.

The stapedia artery, encased in a bony tube, appears to cross an elongated cochlear fenestra in some *Eliomys*. In *Graphiurus* and *Myoxus*, however, the tube is immediately anteroventral to a normal fenestra; we judge this to be close to the primitive position and, in contrast to Parent and to Meng (1990), consider the peculiar condition in *Eliomys* to be derived.

The emergence of the internal carotid nerve from the bony arterial tube onto the promontorium in myoxids indicates that the embryonic branching point of the stapedia from the internal carotid artery was within the middle ear, the primitive position which is known in *Sciuravus* and *Leptotomus* (Wahlert, 1974). The anterior continuation of the internal carotid artery has been lost, but the nerve indicates its earlier presence. The anterior part of the carotid artery has apparently atrophied as in sciurids (Bugge, 1974; Wible, 1984: 184). Bugge (1974) considered retention of the internal carotid artery beyond the branching point of the stapedia in Myomorpha and obliteration of the artery beyond this point in Sciuromorpha to be of primary phylogenetic significance in differentiating the suborders. Wible (1984: 203) stated that "these similarities seem insufficient to include the Gliroidea in the Sciuromorpha." In the Myomorpha (ibid.: 201) "the internal carotid is 'shifted' medially out of the tympanic cavity from the primitive 'indifferent' position on the promontorium." He stated (ibid.: 202) that "the absence of these derived features in the Gliroidea confirms the acknowledgedly (e.g., by Simpson, 1945; Wood, 1955) isolated position of that superfamily within Myomorpha, and does not by itself support Bugge's (1974) exclusion of that group from the suborder." If one looks at other characters described by Bugge, such as the primitive lack of anastomoses between the intracranial and stapedia rami, then the

myoxids are equally similar to the Sciurini and the Cricetini.

Koenigswald's (in press) analysis of incisor enamel schmelzmuster revealed that all myoxids share tilted Hunter-Schreger bands in the lower incisors. The tilt ranges from very slight in the middle of the tooth (Group 1) to fully longitudinal orientation (Group 3). Koenigswald's results agree with ours in uniting *Myoxus* with *Glirulus* and *Eliomys* with *Dryomys*, and in placing *Selevinia* together with *Myomimus*. He showed that there are distinct differences in the design of myoxid enamels and those of other rodents in which the Hunter-Schreger bands are longitudinal. However, he did not discuss the possibility of homoplasy of derived schmelzmusters within the Myoxidae. The unity of his Group 3 is questionable, and the enamels of *Graphiurus*, *Muscardinus*, *Myomimus*, and *Selevinia* show differences in detail that might indicate separate origins from more primitive myoxid schmelzmusters.

Based on the analysis of cranial and dental characters we arrange the extant dormice as shown below.

This classification is nearly identical to that of Bruijn (1967); the only differences are inclusion of *Glirulus* in the Myoxinae, creation of tribes for the Leithiinae, and placement of

Selevinia together with *Myomimus*. The family group name Seleviniini Bashanov and Belosludov, 1939, takes precedence over Myomimini Daams, 1981. The genital morphology described by Rossolimo and Pavlinov (1985) can be accounted for because both *Glirulus*, which is unique, and *Myomimus* which is plesiomorphous, stand farthest apart from the other members of their respective subfamilies. The other differences of *Glirulus* from both *Myoxus* and *Muscardinus* may be the result of the early divergence of these groups.

Order Rodentia

Suborder Myomorpha

Superfamily Dipodoidea

Superfamily Muroidea

Superfamily Myoxoidea Gray, 1821

Family Myoxidae Gray, 1821

Subfamily Graphiurinae Winge, 1887

Genus: *Graphiurus*

Subfamily Leithiinae Lydekker, 1896

Tribe Leithiini Lydekker, 1896

Genera: *Eliomys*, *Dryomys*

Tribe Seleviniini Bashanov and

Belosludov, 1939

Genera: *Myomimus*, *Selevinia*

Subfamily Myoxinae Gray, 1821

Genera: *Myoxus*, *Muscardinus*,

Glirulus

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APPENDIX 1

Cranial and Dental Character States

1. Posterior extent of nasals relative to premaxillae
 0. farther posterior
 1. about equal
 2. not as far
2. Posterior extent of premaxillae relative to maxillae
 0. not as far
 1. about equal
 2. farther
3. Anterior end of premaxillae
 0. tall
 1. not tall
4. Side view of diastemal palate
 0. flat or gentle arch
 1. ascends anteriorly, then abruptly descends at incisor
5. Indication of origin of superficial masseter
 0. no mark
 1. rough spot
 2. tubercle or flange
6. Lateral masseter
 0. protrogomorphous
 1. sciurumorphous—origin not on rostrum
 2. sciurumorphous—origin reaches rostrum
7. Anterior part of medial masseter

0. protrogomorphous
1. hystricomorphous (infraorbital canal enlarged)
8. Posterior edge of anterior root of zygoma lateral to
 0. P4M1 junction
 1. some part of P4
 2. anterior to first cheek tooth
 - ? some part of M1
9. Jugal bone
 0. touches lacrimal
 1. does not touch lacrimal
10. Premaxillary-maxillary suture meets incisive foramina
 0. near the back
 1. near the middle
11. Ratio of lengths of incisive foramina to diastema
 0. 30 to 49%
 1. 50 to 59%
 2. 60 to 69%
 3. 70 to 79%
 4. 80% or > 80%
 - ? most specimens < 30%
12. Anteriormost part of palatine bone medial to
 0. anterior part of M1
 1. M1M2 junction or close to it
 2. M2
13. Palatal width between M1's / condylobasilar length
 0. < .14
 1. .14 to .15
 2. > .15
14. Back edge of posterior palatine foramina medial to
 0. M1M2 junction
 1. M2 anterior and middle
 2. M2 posterior and M2M3 junction
 3. M3
15. Posteriorly projecting medial spine at back of palate
 0. present and strong
 1. weak
 2. absent
16. Posterior maxillary notch or foramen
 0. wide open laterally
 1. just enclosed by tip of maxillary prong
 2. well enclosed
 3. enclosed by stout maxillary-alisphenoid bridge
 - ? no trace of foramen
17. Entrance to lacrimal canal
 0. anterodorsal in medial wall of orbit
 1. low and medial or anterior to infraorbital foramen
18. Anterior end of sphenopalatine foramen dorsal to
 0. M2 posterior and M3
 1. M1M2 junction to M2 middle
 2. M1 middle and posterior
19. Nonossification usually between orbitosphenoid and frontal
 0. none
 1. slight to moderate
20. Ethmoid foramen dorsal to
 0. some part of M3
 1. M2 and M2M3 junction
 2. M1
21. Optic foramen dorsal to and
 0. entirely posterior to M3
 1. some part over M3
 2. entirely anterior to M3
22. Shorter diameter of optic foramen
 0. 1.5 mm and larger
 1. about 1.0 mm
 2. < 1.0 mm
23. Dorsal palatine foramen dorsal to
 0. M2 posterior
 1. M3
 2. and entirely posterior to M3
24. Dorsal palatine foramen
 0. very close to sphenopalatine foramen
 1. distant from sphenopalatine foramen
 - ? possibly combined with posterior maxillary foramen
25. Sphenofrontal foramen
 0. present
 1. absent
26. Frontal bone relative to sphenofrontal foramen
 0. reaches foramen
 1. does not reach foramen
 - ? sphenofrontal foramen absent
27. Parietal bone relative to alisphenoid
 0. reaches alisphenoid
 1. does not reach alisphenoid
28. Posterior entrance to alisphenoid canal
 0. close to foramen ovale
 1. distant from foramen ovale
 - ? not visible
29. Accessory foramen ovale
 0. present
 1. absent
30. Fenestra anterodorsal to masticatory foramen
 0. absent
 1. present
31. Lateral pterygoid flange
 0. generally weak
 1. only lateral to muscle
 2. strong up to foramen ovale
 3. strong up to auditory bulla
32. Sphenopalatine vacuity relative to anterior alar fissure
 0. does not extend as far anteriorly
 1. extends anteriorly up to edge of fissure
 2. is visible in orbit

33. Distance from the posterior edge of M3 to the anterior end of the foramen ovale / condylobasilar length
 0. > .20
 1. < .20, > .10
 2. < .10
34. Stapedial artery
 0. present and large
 1. present and small
 2. absent
35. Postglenoid foramen
 0. within squamosal bone
 1. between squamosal and auditory bulla
36. Posterior part of squamosal bone
 0. entire
 1. with foramen or posterior emargination
37. Temporal foramen (in or near squamosal-parietal suture)
 0. present
 1. absent
38. Dorsal part of mastoid region
 0. not inflated
 1. somewhat inflated
 2. greatly inflated and margin rounded
39. Primary septae in auditory bullae
 0. none
 1. two
 2. three
 3. many
40. Fenestra in angle of mandible
 0. absent
 1. present
41. Inclination of coronoid process relative to occlusal surface of cheek teeth
 0. > or = 60°
 1. < 60°
42. Lower teeth concealed by coronoid process in lateral view
 0. none
 1. posterior part of m3
 2. anterior part of m3
 3. part of m2
43. Anteriormost part of masseteric fossa ventral to
 0. posterior part of m2
 1. m1m2 junction or posterior m1
 2. m1 middle or m1 anterior
 3. p4m1 junction or posterior p4
44. Enamel cap of upper incisor
 0. grades into lateral surface
 1. indents lateral surface
45. Crown length of upper cheek teeth / condylobasilar length
 0. > or = .20
 1. < .20
46. First tooth in upper dentition
 0. P3
 1. P4
 2. reduced P4
 3. M1
47. First tooth in lower dentition
 0. p4
 1. reduced p4
 2. m1
48. Upper cheek tooth occlusal surface
 0. strongly helical
 1. weakly helical
 2. flat
 3. reverse helical
49. Upper cheek teeth with buccal cusps
 0. much higher than lingual cusps
 1. slightly higher than lingual cusps
 2. equal in height to lingual cusps
50. Number of accessory crests or cusps in M2
 0. one
 1. two
 2. three
 3. four or more
51. Number of accessory crests or cusps in m2
 0. one
 1. two
 2. three
 3. four or more
52. Number of complete transverse valleys on m2
 0. none (longitudinal crest is buccal)
 1. one
 2. two
 3. three
 - ? longitudinal crest is lingual
53. Buccal cusp connections in m2 (anterolophid-protolophid, hypolophid-posterolophid)
 0. both pairs connected
 1. one pair connected
 2. no connections
54. Lingual connecting crest in lower cheek teeth
 0. absent

APPENDIX 2

Data Matrix of Cranial and Dental Character States

| Taxon | Character states | | | | | |
|--------------------|------------------|----------|--------------------|----------------|----------|-------|
| <i>Paramys</i> | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 |
| <i>Sciurus</i> | 1(01)102 | 20?00 | ?(12)(012)(12)(01) | (01)0101 | (01)0000 | |
| <i>Sicista</i> | 12110 | 011(01)1 | 42(01)20 | 11(12)(01)(01) | 02001 | |
| <i>Cricetulus</i> | 22111 | 11211 | (123)10(23)1 | ?1101 | 11110 | |
| <i>Myoxus</i> | 1000(12) | 21101 | 01031 | (12)11(01)1 | 1111(01) | |
| <i>Muscardinus</i> | 1(12)001 | 21111 | (12)1012 | 31212 | 21011 | |
| <i>Graphiurus</i> | 12000 | 01201 | (012)1(012)32 | 11(01)10 | 022?0 | |
| <i>Glirulus</i> | 11002 | 21111 | (01)2232 | 21011 | 02111 | |
| <i>Eliomys</i> | 1(12)002 | 21111 | (123)2(01)32 | ?111(01) | 01210 | |
| <i>Dryomys</i> | 1(12)002 | 21411 | (012)1(12)32 | (12)1(01)1(01) | 01210 | |
| <i>Myomimus</i> | 12002 | 21111 | 42(01)31 | ?101(01) | 02210 | |

| Taxon | Character states (continued) | | | | | |
|--------------------|------------------------------|----------|----------|----------|----------|------------|
| <i>Paramys</i> | 00000 | 00000 | 00000 | 00000 | 00000 | 0000 |
| <i>Sciurus</i> | 000(01)0 | 00100 | 00010 | 01300 | 00010 | 0000 |
| <i>Sicista</i> | ?1?1(01) | 02101 | 11200 | 01101 | 22010 | 10?0 |
| <i>Cricetulus</i> | (01)1001 | 0(12)101 | 11100 | 0(12)201 | 32110 | 0000 |
| <i>Myoxus</i> | ?0110 | 11111 | 01120 | 02200 | 10112 | 2220 |
| <i>Muscardinus</i> | ?101(01) | 11221 | 0122(01) | 03300 | 21(23)22 | 1320 |
| <i>Graphiurus</i> | 11111 | 0(01)101 | 01220 | 10301 | 1001(01) | (01)?(01)1 |
| <i>Glirulus</i> | ?1110 | 01121 | 01230 | 02300 | 10013 | 3?11 |
| <i>Eliomys</i> | 1111(01) | 02101 | 11221 | 10311 | 1000(01) | 0110 |
| <i>Dryomys</i> | 11(01)11 | 0(12)101 | 11221 | 10311 | 1000(01) | (12)110 |
| <i>Myomimus</i> | 11(01)11 | 01111 | 11221 | 11301 | 21010 | 0110 |

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