Early Eocene mimotonids of Kyrgyzstan and the problem of Mixodontia

ALEXANDER O. AVERIANOV

The Mimotonidae is a sister group for Lagomorpha that lacks important lagomorphs synapomorphy in the structure of p3. The family consists of six genera (*Mimotona, Gomphos, Zagmys, Mimolagus*, and two newly described genera). Together with Eurymylidae they form an evolutionary grade of ancient Glires and it is argued that the concept of Mixodontia is valid. Two new mimotonids, *Anatolmylus rozhdestvenskii* gen. n., sp. n. and *Aktashmys montealbus* gen. n., sp. n. from the latest Early Eocene (late Ypresian) of Andarak 2 locality (Kyrgyzstan) are described.

K e y w o r d s: Mammalia, Glires, Mixodontia, Early Eocene, Central Asia.

Alexander Averianov, Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, 199034 St. Petersburg, Russia.

Introduction

The order Mixodontia was established by Sych in 1971 for a single genus and species *Eurymylus laticeps* Matthew & Granger 1925, from the Paleocene of Mongolia (Matthew & Granger 1925; Matthew *et al.* 1929), which Sych could not assign either to the Lagomorpha or Rodentia. Since Sych's paper the range of Mixodontia increased, it includes now two families: the Eurymylidae and the Mimotonidae with a dozen genera and about 20 species [Wilson (1989) cited three families, adding Rhombomylidae], all from the Paleocene or Eocene of Asia, except *Mimolagus* which is most probably of Oligocene age. However, if one reads the general papers and the text-books on the systematics of eutherian mammals, the Mixodontia is either non-existing, or is not accepted (e.g., McKenna 1975, 1982; Butler 1985; Novacek 1986; Carroll 1988). On the other hand, the specialists working on the Early Tertiary Asian mammalian faunas have difficulties in assigning Early Tertiary Glires to Lagomorpha or Rodentia (as Sych had)

and they assign them to the order Mixodontia (e.g., Shevyreva & Gabunia 1986; Russell & Zhai 1987; Dashzeveg & Russell 1988; Dashzeveg *et al.* 1987; Averianov 1991). However, even among the specialists working on Asian Early Tertiary faunas there is no general consensus concerning the Mixodontia, as e.g. recently, Li & Ting (1993) assign the representatives of mixodontians of other authors either to Lagomorpha or to Rodentia. But this conclusion was based on the morphological features of a few taxa which are represented by most complete material, e.g., skull fragments (*Mimotona* for Mimotonidae and *Heomys* or *Rhombomylus* for Eurymylidae). In the present paper an attempt to reevaluate some of these morphological features and to involve all the diversity of Early Paleogene mixodontians in the phylogenetic reconstructions is done.

A diverse fauna of Mixodontia was described recently from the Paleocene and Eocene of Mongolia, including several subfamilies of Eurymylidae (Dashzeveg & Russell 1988). In contrast to eurymylids, mimotonids are a more coherent and better delimited group (Li & Ting 1985, 1993). Here the two new genera (*Anatolmylus* gen. n. and *Aktashmys* gen. n.) of Mimotonidae from the latest Early Eocene of the locality Andarak 2 in Kyrgyzstan are described. The tarsal elements of mimotonids from this locality were described previously (Averianov 1991).

The studied specimens are housed at the Czernyshev Central Museum of Geological Exploration, St. Petersburg (abbreviated CCMGE) and Zoological Institute, Russian Academy of Sciences, St. Petersburg (ZIN).

Capital and lower-case letters: I/i (incisor), P/p (premolar) and M/m (molar), refer to upper and lower teeth.

Relationships of the Mimotonidae and the problem of Mixodontia

The Mixodontia is commonly considered to be important for understanding the origin of mammalian orders Rodentia and Lagomorpha (Wood 1942; Van Valen 1964; Hartenberger 1977, 1980, 1985; Li 1977; Dawson *et al.* 1984; Wilson 1989; Li & Ting 1985, 1993). It is usually believed that one family of mixodontians, the Eurymylidae, is closely related to the Rodentia, while another family, the Mimotonidae, was close to, if not the ancestor of the Lagomorpha.

The idea about relationships of Eurymylidae with Rodentia is based primarily on the similarities in the morphology of the upper cheek teeth in the Late Paleocene eurymylid *Heomys* and the oldest ctenodactyloid rodents, e.g. *Cocomys* (Li 1977; Li & Ting 1985). But the main of these common features: the nonmolariform P4 and large metaconules on the upper cheek teeth, are considered now to be symplesiomorphic, and it is accepted that *Heomys* is too late in time and too advanced in various morphological details to be the rodents ancestor (Dawson *et al.* 1984; Li *et al.* 1989; Averianov 1993). Curiously, the type genus of the Eurymylidae,

Eurymylus, in dental morphology is much closer to lagomorphs than to rodents, especially concerning reduction of the cusp pattern, that was emphasised by Wood (1942), Li (1977), and Wilson (1989). But *Eurymylus* is more specialized than lagomorphs in lacking I3 and P2. The best known eurymylid, the *Rhombomylus*, which is represented by about 20 complete skulls and 150 jaws, differs markedly from the oldest rodents by unique specialisations in the ear region, including great inflation of the mastoid process (Ting & Li 1984). In fact, eurymylids and early ctenodactyloid rodents share many plesiomorhic features, but few, if any, uncontested synapomorphic features (Li *et al.* 1989), so even sister-group relationship between these two groups was questioned (Patterson & Wood 1982). Therefore there are no reasons up to date to include the family Eurymylidae in the order Rodentia, as was done by Li & Ting (1985, 1993). But it seems likely that eurymylids were close to the stock out of which the rodents originated.

There are different points of view on the content of the Mimotonidae. According to Li & Ting (1985, 1993) the family consists of four genera (*Mimotona*, *Mimolagus*, *Gomphos*, and *Hypsimylus*). Dashzeveg & Russell (1988) restricted it to two genera (*Mimotona* and *Gomphos*) and placed *Hypsimylus* into a monotypic subfamily within the Eurymylidae. Following Bleefeld & McKenna (1985), Dashzeveg & Russell (1988) considered *Mimolagus* as a true lagomorph. Because of the absence of the calcaneofibular facet on the calcaneus of *Mimolagus* and the rodent-like shape (unusual for lagomorphs) of its first upper incisors (I2), without any notch on the anterior surface, it seems more reasonable to not include *Mimolagus* into the order Lagomorpha. By the structure of I2, mentioned above, *Mimolagus* differs clearly also from *Mimotona*, but possibly not from unnamed mimotonids from the Early Eocene of Mongolia which lack a notch on this incisor (McKenna 1993). So it is possible to assign *Mimolagus* to the Mimotonidae.

The monotypic genus *Hypsimylus* is known only from the holotype of its type species, *H. beijingensis* (Dashzeveg & Russell 1988: Fig. 11), from the Late Eocene of China. It is a mandibular fragment with just erupted, unworn p4, and with m1 worn to the degree usual for this ontogenetic stage. If the anterior tooth is a dp4, as proposed by Zhai (1977), it ought to be worn at least as much if not more than m1. The peculiar structure of the talonids of p4 and m1 of *H. beijingensis,* with the distinct 'conid'-like hypoconulids forming a separate column, indicates that this is a true lagomorph and therefore I exclude it from the Mimotonidae. This opinion was expressed earlier by Wilson (1989).

A poorly known mixodontian *Zagmys insolitus*, presented by one mandible fragment with one and a half anterior cheek teeth from the Early Eocene of Mongolia (Dashzeveg *et al.* 1987), was assigned to Mixodontia *incertae sedis* in the original description and subsequently to a new monotypic subfamily within Eurymylidae (Dashzeveg & Russell 1988). It shares some characters with *Gomphos* and the new mimotonid genus

described here (see remarks after description of *Anatolmylus rozhdestven-skii* gen. et sp. n.). Therefore, *Zagmys* is placed here in the Mimotonidae.

Thus, the family Mimotonidae includes six genera: *Mimotona, Gomphos, Zagmys, Mimolagus*, and the two new genera proposed in this paper.

In their latest publication, Li & Ting (1993) have completely broken up the concept of Mixodontia, assigning the Mimotonidae to Lagomorpha and the Eurymylidae to Rodentia. They found the following derived characters which *Mimotona* shares with lagomorphs (Li & Ting 1993, p. 153): (1) a dental formula of 2.0. 3.3 / 2.0.2–3.3; (2) large incisive foramen; (3) malar extending forward to anterior margin of orbit, zygomatic arch plate oriented vertically, having a distinct fossa on the lateral side of the zygoma for the masseter lateralis; (4) a ventral hook present on the zygomatic process of the maxilla; (5) upper cheek teeth unihypsodont, roots located within orbit; (6) I2 rootless, enlarged, limited to premaxilla; (7) enamel of I2 restricted to anterior surface of tooth, notched and having one layer; (8) I3 behind I2 and much smaller than I2; (9) movement of lower jaw mainly transverse; (10) symphysis long, with a small accessory symphysis appearing behind it; (11) lower diastema long, not curved; (12) paraconid reduced, trigonid compressed anteroposteriorly; (13) talonid of preceding tooth at the same height of occlusal surface as the trigonid of the succeeding tooth.

It seems, however, that not all of the cited above features could be considered as unquestionable synapomorphies of *Mimotona* and Lagomorpha. The dental formula of *Mimotona* (character 1) reflects the stage of teeth reduction which must be possessed by the common ancestor of all Glires in any case. So, this is a symplesiomorphy of *Mimotona* and Lagomorpha relative to the more derived dental formula of other Glires (Eurymylidae and Rodentia).

The unilateral hypsodonty (character 5) is shared also by some eurymylids (*Eomylus, Nikolomylus*) and some rodents. The rootless enlarged I2 (character 6) is a common feature for all Glires, and is limited to the premaxilla in most mammals (primitive feature). The condition of *Mimotona* (character 8) when I3 is behind and smaller than I2 (but not much smaller, as indicated by Li & Ting) is much closer to the condition of *Zalambdalestes* (Kielan-Jaworowska 1984) than to true lagomorphs with a peg-like minute I3 attached to the posterior wall of I2. So, the condition of *Mimotona* is clearly plesiomorhic and reflects an intermediate stage of upper incisor reduction towards the lagomorph condition. Additionally, the shape of the cross section of I2 in *M. wana* (Li & Ting 1993: Fig. 11.1) and in the specimen described here (Fig. 6A–B) is not the same as in ochotonids, or leporids, or even in primitive Paleogene lagomorphs which share some characters of both families.

The mainly transverse movement of the lower jaw (character 9) is characteristic for all primitive mammals and therefore is plesiomorphic for Glires. It was retained not only in mimotonids and lagomorphs, but also in eurymylids and to some extend in the earliest rodents. The relatively

long lower diastema (character 11) is common for all Glires; it is not much curved also in some eurymylids (*Khaychina*). The reduction of the para-conid and the antero-posterior compression of the trigonid (character 12) is the common trend for all Glires, not only for mimotonids and lago-morphs, and for other herbivorous mammals as well (primates, majority of ungulates).

Despite the mentioned above differences, character states 2, 3(?), 4, 7, 10, and 13 cited by Li & Ting (1993) indicate that the Mimotonidae is a sister group of the Lagomorpha. This situation, when one group of Mixo-dontia, the Eurymylidae, seems to be the sister group for Rodentia, while another, the Mimotonidae, is the sister group for the other order, the Lagomorpha, is a good example of Romer's (1933) schemes of 'vertical' and 'horizontal' classifications (Fig. 1A–B). Romer advanced the 'horizontal' cleavage, the erection of a stem group including the base from which the long-lived later groups have been derived, as the best solution to the problem of such a kind. The concept of Mixodontia fits this solution and from this point of view is quite acceptable.

From the point of view of phylogenetic systematics (e.g. Hennig 1966; Eldredge & Cracraft 1980), the Mixodontia is a paraphyletic taxon, be-cause it does not include all clades nested within it (Rodentia and Lago-morpha, Fig. 1E), and therefore this taxon is not acceptable. In this example the following monophyletic groups only could be considered as natural taxa: Glires, Rodentia, and Lagomorpha (Fig. 1C–D). So, the problem of Mixodontia lies entirely in the field of the theory of Biological Systematics. There are two possible solutions to this problem and classi-fication of Glires: (1) only two monophyletic groups are accepted: Rodentia + Eurymylidae and Lagomorpha + Mimotonidae, taxon Mixodontia is not valid (e.g. Li & Ting 1993), 'vertical' cleavage of Romer; and (2) three groups are accepted, two monophyletic, Rodentia and Lagomorpha, and one paraphyletic, Mixodontia (e.g. Dashzeveg & Russell 1988), 'horizontal' cleavage of Romer.

Which solution gives a more natural classification? It depends how strongly the monophyly of the proposed groups is proved. As was dis-cussed above, there is weak evidence for uniting rodents and eurymylids into one natural group, because most of the similar features between them are symplesiomorhies and there are no clear synapomorphies. On the other hand, there are some synapomorphies between *Mimotona* and Lago-morpha that show sister-group relationship between these taxa. But in any case, the solution 1, in fact, really can give only the groups Rodentia + *Heomys* and Lagomorpha + *Mimotona*, while the remaining 10 genera of primitive Glires, which take the intermediate position between *Heomys* and *Mimotona*, have no place in the classification.

This situation is caused not only by the incompleteness of the data, but mostly by the nature of divergent evolution, when taxa were evolving in many different directions, not only in two leading to the modern orders. An attempt to reconstruct the phylogenetical relationships of these 'waste
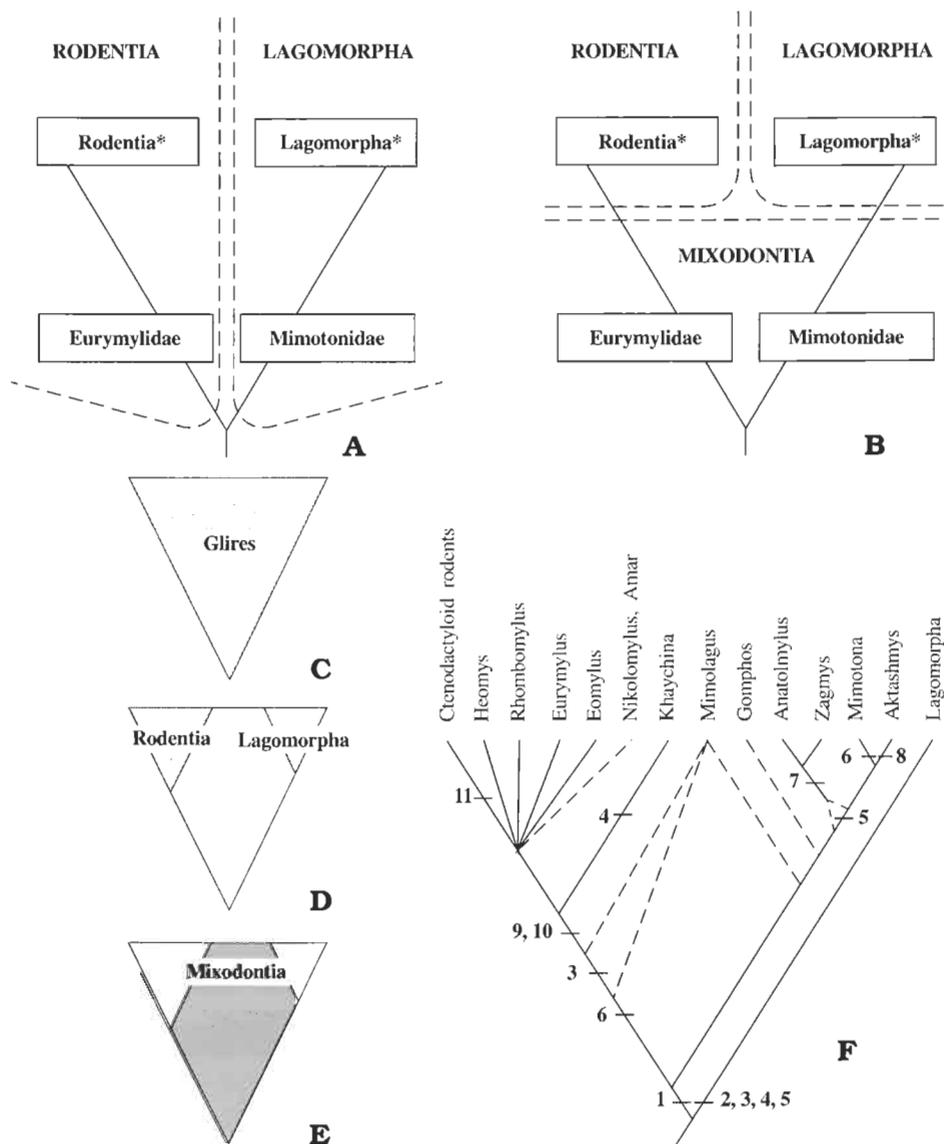
Fig. 1. Various phylogenetic trees depicting the problem of Mixodontia. ❑A. 'Horizontal' classification (*sensu* Romer 1933); taxon Mixodontia not valid. ❑B. 'Vertical' classification, taxon Mixodontia valid. Asterisk denotes the Rodentia and the Lagomorpha of modern type, without Eurymylidae or Mimotonidae. ❑C–E. Different types of groups in cladistic classification: monophyletic (C and D) and paraphyletic (E). ❑F. Phylogenetic relationships of the mixodontian taxa, Lagomorpha, and Ctenodactyloid rodents. Characters: 1 — p3 greatly reduced, m3 largest tooth among lower cheek teeth; 2 — tooth germs of p2 and p3 fused, composite p3 large with the tendency to increase in size during evolution, m3 decreased in size; 3 — i3 lost; 4 — diastema between i2 and p3 increased; 5–12 with the groove on the anterior surface; 6 — p3 one rooted; 7 — deep dentary; 8 — great degree of unilateral hypsodonty of upper cheek teeth, which wasn't reached by Eocene lagomorphs; 9–13 lost; 10 — P2 lost; 11 — p3 lost.

basket' mixodontians is represented on the Fig. 1F. This cladogram, even being preliminary due to lacking more complete data, shows the complex pattern of the inter- Lagomorpha-Rodentia radiation of mixodontians.

Although the sister-group relationships of *Mimotona* and Lagomorpha is unquestioned, it seems that the taxon Lagomorpha + *Mimotona* would not be a natural group, because *Mimotona*, firstly, lacks some important synapomorphies of later lagomorphs, and, secondly, it shows an evolutionary tendency in one important character opposite to those of lagomorphs.

The most important autapomorphy of lagomorphs which *Mimotona* and other mimotonids lack is the peculiar and complex p3, possibly of composite origin (Sych & Sych 1977). Other important features which are too characteristic for lagomorphs, but not too derived in mimotonids, are the reduced cusp pattern on the cheek teeth and the presence of the calcaneofibular facet on the calcaneus (Averianov 1991).

The different evolutionary trends are the following: the lower teeth increase in size from p3 to m3 in mimotonids and in the opposite direction in true lagomorphs. This may indicate rather unsimilar anatomy of jaw muscles and different masticatory movements in mimotonids and lagomorphs.

If all the considerations mentioned above are taken into account, the solution 2 of the Mixodontia problem would seem more attractive and the taxon Mixodontia would be a good natural group. In this I follow Dashzeveg & Russell (1988) and other authors, who have considered the Mixodontia as an evolutionary grade. This case may serve as an additional example supporting Charig's conclusion (1982) that, while the cladistic (=Hennigian) procedure for *phylogeny reconstruction* is preferable, the preferred *classification* is the conventional (=Simpsonian), because it allows paraphyletic taxa.

Geological setting of the locality Andarak 2

The Eocene vertebrate bearing locality Andarak 2 is situated about 3 km northeast of Andarak Village, Lyailyak District, Osh Region of Kyrgyzstan (Fig. 2). The Paleogene deposits in this area have a limited distribution, and are restricted to the northern slope of the local range (Aktash mountain), formed by Paleozoic rocks, which is one of the foothills of the Turkestan Range. The Paleogene deposits on the Aktash Range are badly exposed, they can be observed only in three outcrops, separated by short distances about 1–2 km. Despite of their close position, the Paleogene deposits in these outcrops are varied greatly in composition and thickness of layers. The first two outcrops (sections I and II, within the Village Andarak and about 1 km northeast of the village) were described in detail by Gekker *et al.* (1962). The section I is the mammal and other vertebrate bearing locality Andarak 1 (Russell & Zhai 1987). It is composed of pebble
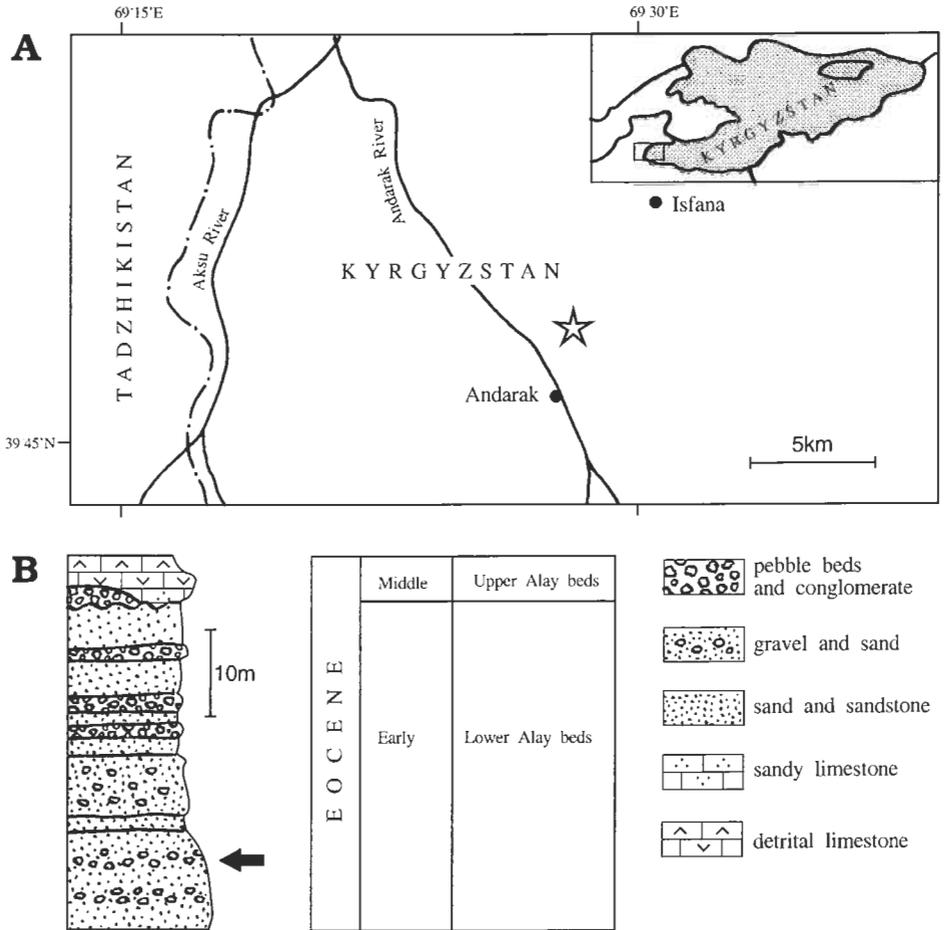
Fig. 2. ❑A. Sketch map of the south-western part of Kyrgyzstan showing the location of Andarak 2 locality (asterisk). Modified from Russell & Zhai (1987). ❑B. Geological section of Andarak 2 locality. The mammal bearing level indicated by arrow.

beds and conglomerates of the Suzak Formation (1.7 m), silts and silt-stones of the Lower Alay Formation (5.0 m), and the oyster-bearing limestones of the Upper Alay Formation (2–3 m exposed). In the base of the Upper Alay beds there is a layer of conglomerate which produces a number of marine vertebrates, but a few terrestrial vertebrates inculding mammals. The section II is more complete and has a greater thickness, but produces a few shark teeth only. The third Paleogene section, where the mammal bearing locality Andarak 2 is located, has a much greater thickness of sands of the Lower Alay Formation (more than 25 m of visible thickness) with some horizons of oyster-bearing conglomerates (Fig. 2). Each of these horizons has produced abundant remains of marine verte-brates and, at a lesser extent, remains of mammals. Most numerous

samples of mammals were made during screen-washing of matrix from the lowermost horizon. All remains of mimotonids described here come from this level.

The geological age of the Andarak 2 locality was considered previously as Middle Eocene (Reshetov *et al.* 1978; Russell & Zhai 1987). This conclusion was based on the presence of oysters *Ostrea (Turkostrea) turkestanensis* Romanovsky 1879, which is the characteristic species of the Alay Formation, and because it was simpler for geologists to correlate the Suzak-Alay boundary with the Lower-Middle Eocene boundary. However, the rich and diverse fauna of elasmobranch fishes (at least 40 species) from the mammal bearing layer of the Andarak 2 locality, which was recently redeterminated (Averianov & Udovichenko 1993), is most similar to the shark assemblage from the Paniselian beds of Belgium (Late Ypresian, Cuisan), which corresponds to the upper half of the nannoplancton NP 12 zone (Steurbaut & Nolf 1986). So, the Early Eocene (Late Ypresian) age for the Andarak 2 locality is accepted here.

Among the mammals from the Andarak 2 locality varied tapiroids, one species of the oldest amynodonts, a chalicothere, a hyaenodontid, a large mesonychid and others are represented. But the remains of diverse Glires are most abundant: Ctenodactyloid rodents (Tamquammyidae and Yuomyidae), the most ancient lagomorphs (at least two taxa), and the mimotonids described here. Only four taxa from this mammal assemblage, the tapiroids *Rhodopagus minutissimus* Reshetov 1979 and *Pataecops microdon* Reshetov 1979, the tamquammyid rodent *Alaymys ctenodactylus* Averianov 1993 and the palaeoryctoid 'insectivore' *Sarcodon udovichenkoi* Averianov 1994, have been described (Reshetov 1979; Averianov 1993, 1994).

Taxonomic descriptions

Cohort Glires Linnaeus 1758
Order Mixodontia Sych 1971
Family Mimotonidae Li 1977
Genus *Anatolmylus* gen. n.

Type species: *Anatolmylus rozhdestvenskii* sp. n.

Etymology: The genus and species named in the memory of Dr. Anatolyi K. Rozhdestvenski, who discovered the locality Andarak 2 in 1969.

Diagnosis. — A relatively large mimotonid. Differs from *Mimotona* and *Gomphos* by extremely deep and relatively short horizontal ramus of mandible with distinctly more curved tooth row and incisor (i2). Diastema is short, shorter than in *Mimotona*. The lower and upper cheek teeth with unilateral hypsodonty; p4 molariform. Paraconid on the lower molars virtually absent. On the upper molars paraconule and metaconule absent, the mesostyl small.
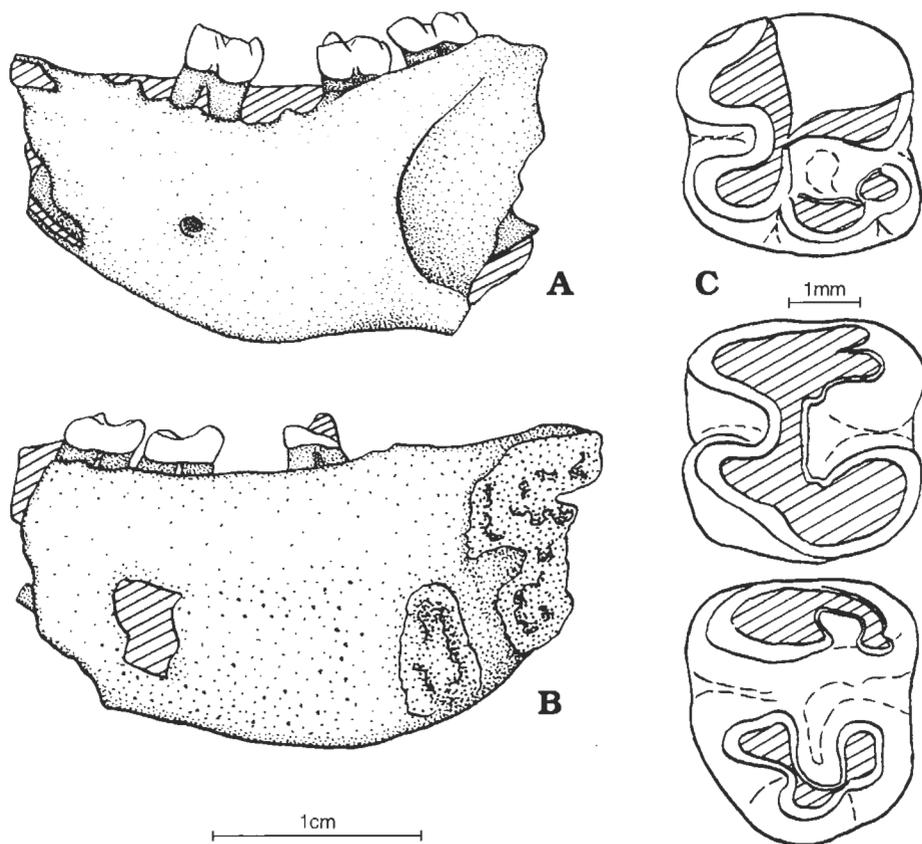
Fig. 3. *Anatolmylus rozhdestvenskii* gen. et sp. n., holotype. ZIN 79158, right dentary fragment; Early Eocene, Kyrgyzstan, Andarak 2. A–B. Labial and lingual view of dentary. C. Occlusal view of p4 and m2–3.

Anatolmylus rozhdestvenskii sp. n.

Figs 3–4.

Holotype: ZIN 79158, right mandible fragment with i2, p4, m2 and m3, and alveoli of i3, p3 and m1.

Type horizon and locality: Andarak 2, Southern Ferghana Valley, Kyrgyzstan; lower part of the Alay beds; Late Ypresian (Cuisan), Early Eocene.

Diagnosis. — As for the genus.

Description. — The type specimen, ZIN 79158 (Fig. 3) is a dentary fragment with a part of i1 and p4, m2 and m3 in place. The i1 extends up to the posterior root of m3. An edentulous dentary fragment with alveoles of i1–i2, p3–p4, m1–m2 (ZIN 79164) and two fragments with alveoles of i1 and p3 and remnants of i2 in place (ZIN 79163 and ZIN 79165) are also present in the collection. The i2 is short, horizontally procumbent and vertically compressed. The symphysis of the dentary is deep and robust,
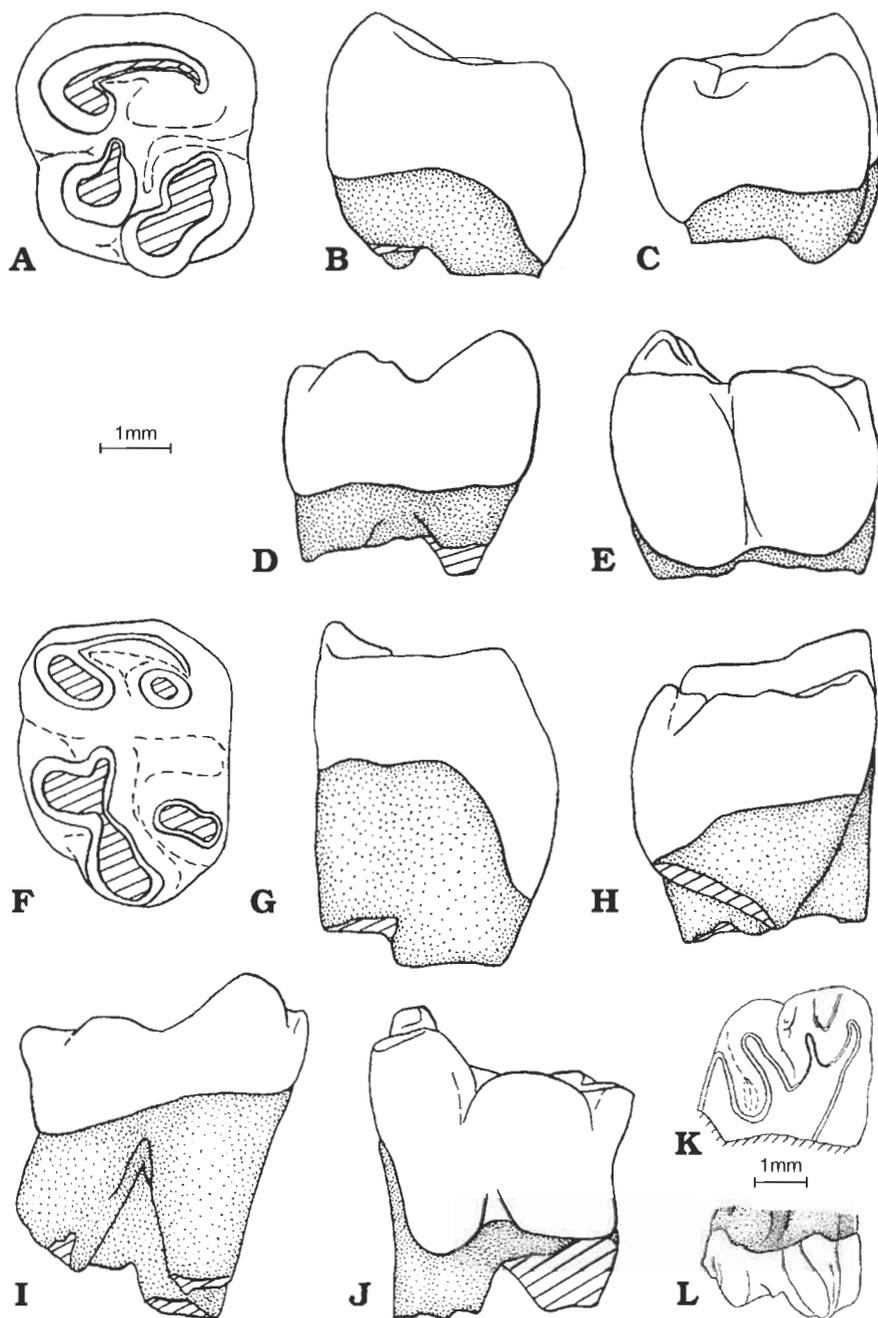
Fig. 4. *Anatolmylus rozhdestvenskii* gen. et sp. n. ⊐A–E. Early Eocene. Kyrgyzstan, Andarak 2. Right m1, ZIN 79159 in occlusal (A), anterior (B), posterior (C), lingual (D), and labial (E) views. ⊐F–J. Right m2, ZIN 79160, in occlusal (F), anterior (G), posterior (H), lingual (I), and labial (J) views. ⊐K–L. Labial half of the right M1, ZIN 79161, in occlusal (K) and labial (L) views.

with a smaller accessory symphysis posteriorly (Fig. 3B). The masseteric fossa is shallowly excavated and originates at the level of the posterior root of m2.

The lower cheek teeth are approximately subquadrate in outline in occlusal view. The p4 and molars of equal size.

The p3, judging from its alveolus, is distinctly smaller and with a shorter anterior root. In the holotype the cheek teeth are worn.

In m2 and m3 there are no traces of a paraconid, in m2 the hypoconulid is small and indistinct, in m3 it is larger, nearly equal in size to the entoconid and hypoconid. Metaconids are noticeably higher than paraconids. Trigonids are strongly compressed in antero-posterior direction and separated from talonids by their high posterior walls. The talonid cusps are low and their bases fill the talonid basins completely. Entoconids are higher than hypoconids. Hypoflexids are broad and transversely oriented, extending to the center of the tooth.

The right m1 (ZIN 79159) and m2 (ZIN 79160) are only weakly worn. These teeth (Fig. 4A–J) preserve a small and low mesoconid joined to the anterior-lingual corner of the hypoconid.

The upper molars have a large postcingulum which on M3 occupies nearly half of the crown. The left M1 (ZIN 79161, Fig. 4K, L) has large paracone and metacone and a minute mesostyle. There are no traces of conules. Lingually the crown is at least two times as high as labially. The right M3 is badly worn (ZIN 79162).

Measurements. —

		Length	Width
ZIN 79158	p4	–	3.4
	m2	3.7	3.5
	m3	4.3	3.3
ZIN 79159	m1	3.6	3.7
ZIN 79160	m2	3.8	3.3
ZIN 79161	M1	3.2	–
ZIN 79162	M3	3.3	4.5

Remarks. — Among mixodontians only *Zagmys insolitus* (Mixodontia *incertae sedis* in the original description (Dashzeveg *et al.* 1987) and a monotypic subfamily within Eurymylidae in Dashzeveg & Russell (1988)) from the Early Eocene of Mongolia shares a deep mandible and a short diastema with *Anatolmylus*. The new genus differs from *Zagmys* in its higher crowns of cheek teeth, in the absence of a distinct paraconid and by the presence of one large instead of two small mental foramina.

The dental formula of *Zagmys* appears to have been misinterpreted. As it is clear from comparison with the specimen described here (Fig. 3A–B), the only teeth preserved in the holotype of *Z. insolitus* (Dashzeveg *et al.* 1987: Figs 1–2) are the talonid of p3 and the crown of p4, but not p4 and
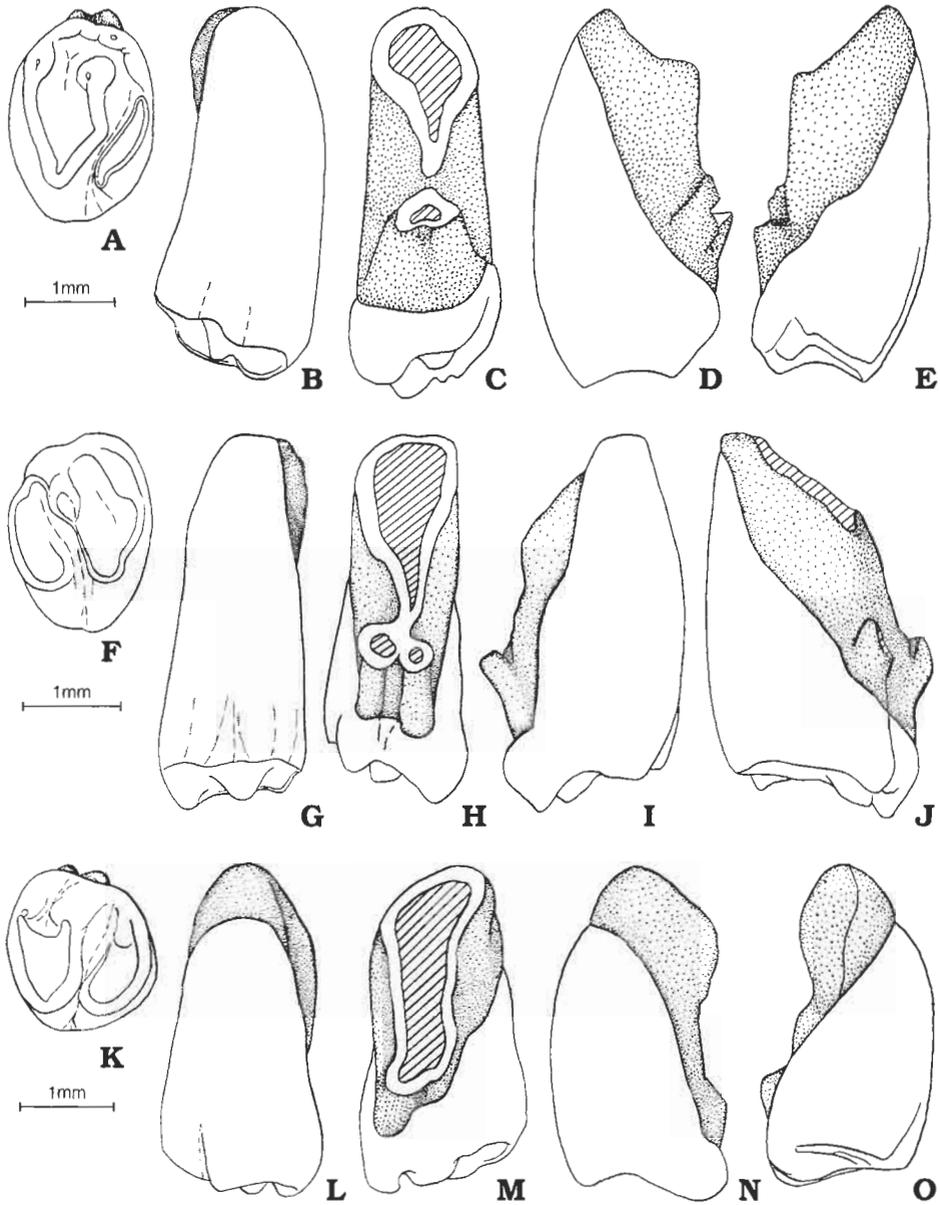
Fig. 5. *Aktashmys montealbus* gen. et sp. n. ❑A–E. Early Eocene, Kyrgyzstan, Andarak 2. Left M1. CCMGE 3/12676, holotype, in occlusal (A), lingual (B), labial (C), anterior (D), and posterior (E) views. ❑F–J. Right M2, ZIN 79156 in occlusal (F), lingual (G), labial (H), anterior (I), and posterior (J) views. ❑K–O. Left M3, ZIN 79157, in occlusal (K), lingual (L), labial (M), anterior (N), and posterior (O) views.

m1, as was determined in the original description. In this case, *Zagmys* shares with the mimotonids *Anatolmylus* gen. n. and *Gomphos* the molariform p4 and should be placed in the Mimotonidae.

Anatolmylus gen. n. and *Zagmys* appear to be closely related, but at the moment there are not enough data to clarify the validity of the distinct subfamily Zagmyinae Dashzeveg & Russell 1988 within the Mimotonidae.

Genus *Aktashmys* gen. n.

Type species: *Aktashmys montealbus* sp. n.

Etymology: 'Ak tash' (Kirgiz), white stone, the name of a local mountain in the area of the locality Andarak 2.

Diagnosis. — A relatively small mimotonid. Differs from *Mimotona*, *Gomphos*, *Zagmys*, and *Anatolmylus* gen. n. by the extremely developed unilateral hypsodonty of the upper molars: the crown height is at least four times as high lingually as labially. The crowns of the upper molars are oval in shape in occlusal view. Paracone and metacone are small, conules absent. The area of postcingulum is greatly expanded.

Aktashmys montealbus sp. n.

Figs 5–6.

Holotype: CCMGE 3/12676, left M1(?).

Type horizon and locality: Andarak 2, Southern Ferghana Valley, Kyrgyzstan; lower part of the Alay beds; Late Ypresian (Cuisan), Early Eocene.

Etymology: From 'Monte alba' (L.), white mountain, the translation of the mountain name.

Diagnosis. — As for the genus.

Description. — The type specimen, CCMGE 3/12676 (Fig. 5A–E) is a left upper molar, most probably M1. Its occlusal surface has a simple morphology and is divisible into two parts: (1) the trigon formed by protocone, small central cusps (paracone and metacone), and wide smooth trigon basin, and (2) the postcingulum area. The metacone is much higher than the paracone and situated nearly in the center of the occlusal surface. In the proposed M2 (ZIN 79156, Fig. 5F–J) and M3 (ZIN 79157, Fig. 5K–O) the postcingulum area occupies about half of the occlusal surface of the tooth. The labial roots of the upper molars are small but distinct, the lingual one is extremely large, forming the column of the tooth.

The part of right maxillary ZIN 79155 (Fig. 6C), with the base of the jugal arch preserved, apparently belongs to *A. montealbus*. It bears badly eroded M1 and M2 and alveolae of P3, P4 and M3. The remnants of M1 and M2 show unilateral hypsodonty. By their size and remaining morphology they are comparable to the upper teeth of *A. montealbus*. The base of the jugal arch is thick and slopes posteriorly with respect to the tooth row. It extends from the P4 anteriorly to the posterior half of M2 posteriorly. Such a structure of the muzzle, without any abrupt widening of the base of the snout (as in *Eurymylus* and *Heomys*: Sych 1971; Dashzeveg & Russell 1986) is more similar to the condition of *Mimotona* and *Rhombomylus*.

The maxillary of *Aktashmys* gen. n. differs from that of *Mimotona* by its more slender base of the jugal arch. In the maxillary fragment just described there is a sharp ridge on the ventral surface of the jugal arch opposite to the M1 and perpendicular to the tooth row, possibly for
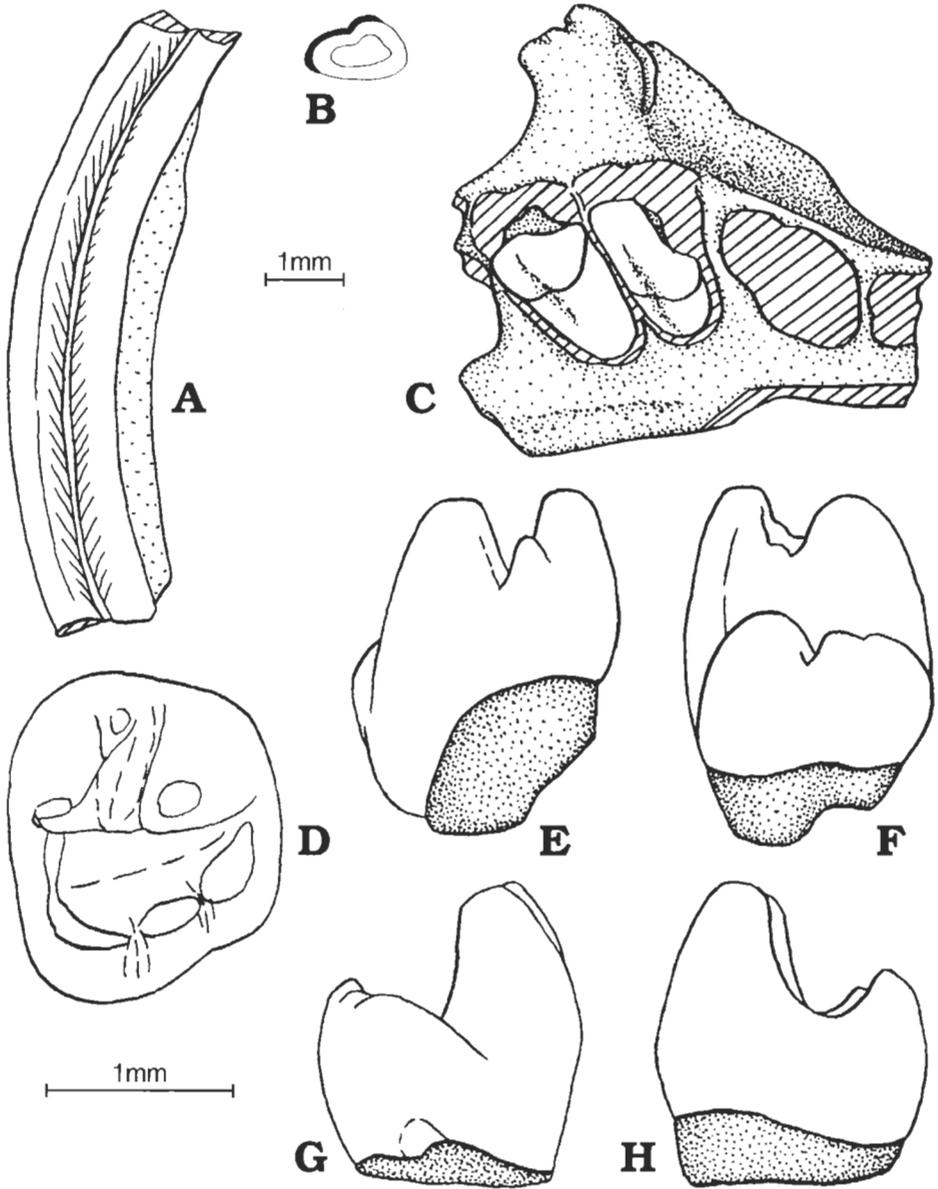
Fig. 6. *Aktashmys montealbus* gen. et sp. n. Early Eocene, Kyrgyzstan, Andarak 2. □A–B. Left I2, ZIN 79154, anterior view (A) and cross section (B). □C. Fragment of the right maxilla, ZIN 79155 with M1–2 and alveolae of P3–4 M3, occlusal view. □D–H. Right p4. CCMGE 2/12676, possibly belonging to this species in occlusal(D), anterior (E), posterior (F), labial (G), and lingual (H) views.

attachment of the musculus masseter lateralis (pars superficialis?). The infraorbital canal seems to be small.

The isolated right I2, ZIN 79154 (Fig. 6A–B), is provisionally referred here to *A. montealbus*. It correlates better in size (mesio-distal length 1.7) with the cheek teeth of this species than with *A. rozhdestvenskii*, as can be calculated from the figures of *Mimotona wana* (Li & Ting 1993: Figs 11.1 and 11.3). The shape of the cross section of this tooth is the same as in *M. wana*. It is covered by enamel only on the anterior surface, where there is a shallow notch without cement. This notch is closer to the mesial than to the distal margin of the tooth.

The right p4, CCMGE 2/12676 (Fig. 6D–H), is tentatively assigned to this species. This, principally four cusped, tooth is close in general morphology and size to p4 of *Mimotona lii*, *M. wana*, and *M. robusta* (Dashzeveg & Russell 1988: Figs 12, 14, and 15), but lacks any precingulid and has a small but distinct hypoconulid. The trigonid basin is a narrow valley which opens anteriorly. At the base of the metaconid there is a minute cusp (anteroconid?, greatly reduced paraconid?). The metaconid is slightly higher than the paraconid. The talonid basin is a narrow valley oriented transversely. The entoconid is the highest of the talonid cusps. There is a marked unilateral hypsodonty of the tooth crown: the labial height is twice the lingual one.

Measurements. —

		Length	Width
CCMGE 2/12676	p4	1.8	1.7
CCMGE 3/12676	M1	1.5	1.6
ZIN 79156	M2	1.6	1.9
ZIN 79157	M3	1.5	1.8

Remark. — According to the great degree of unilateral hypsodonty on the upper molars and their simplified morphology, *Aktashmys* gen. n. is the most derived mimotonid and mixodontian known.

Systematic position of new taxa

Both new genera are classified within the Mimotonidae because they have the following features, which are believed to be diagnostic for the family (Li & Ting 1985): (1) there are two incisors in the lower jaw (known for *Anatolmylus* only): greatly enlarged chisel-like and persistently growing i2 extending far behind m2 and short and horizontally procumbent i3; (2) incisor enamel is restricted to the anterior surface of the tooth (known for *Anatolmylus* only); (3) there is a large cusp in the centre of the upper molars (in *Aktashmys* only); (4) the molars exhibit unilateral hypsodonty (extremely developed in the upper molars of *Aktashmys* and to lesser extent developed in the molars of *Anatolmylus*). This feature may occur on the upper molars in some eurymylids (*Eomylus*, *Nikolomylus*), but is more

typical for mimotonids; (5) the paracone and metacone on the upper molars are isolated and situated labially (both genera).

Due to the incompleteness of the material of the newly described taxa, as well as of most of the taxa of mixodontians described previously, only preliminary considerations about the phylogenetical relationships of both new genera to other mimotonids and their systematic position within the family can be made. These considerations are summarized in the clado-gram presented on Fig. 1F. *Anatolmylus* gen. n. is closer to *Zagmys* in having a deep dentary and molariform p4. By the latter character both genera are similar to *Gomphos*, and differ from *Mimotona* which has a more simple p4. *Aktashmys* gen. n. shares with *Mimotona* the anteriorly notched I2, but is much more advanced than the latter genus in the great degree of unilateral hypsodonty of the upper cheek teeth. By this feature it is more advanced even than the contemporaneous lagomorphs from the Andarak 2 locality.

Acknowledgements

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Содержание

Семейство Mimotonidae является сестринской группой для Lagomorpha, которая характеризуется отсутствием важной синапоморфии зайцеобразных в структуре p3. Семейство состоит из шести родов (Mimotona, Gamphos, Zagmys, Mimolagus и два новых рода, описываемых здесь). Вместе с Eurymylidae мимотониды образуют эволюционную ступень (граду) древних Glires, что позволяет считать концепцию Mixodontia валидной. Два новых мимотонида, *Anatolmylus rozhdestvenskii* gen. n., sp. n. и *Aktashmys montealbus* gen. n., sp. n. описаны из отложений конца раннего эоцена (поздний ипр) местонахождения Андарак 2 в Киргизии.

Streszczenie

W tej pracy opisane są trzy nowe gatunki eoceńskich ssaków z rodziny Mimotonidae, należącej do grupy anatomicznie pośrednich między gryzoniami a zającokształtnymi Mixodontia. Zwierzęta te, choć bliskie zającokształtnym, nie miały typowych dla nich złożonych przedtrzonowców p3 ani też uproszczonego układu guzków na zębach policzkowych. Rozmiary zębów były coraz większe ku tyłowi żuchwy, odwrotnie niż u zającoksztłtnych, co sugeruje odmienność anatomii i funkcjonowania mięśni żuchwy.