Early Miocene Small Mammals from the North Aral Region (Kazakhstan) with Special Reference to Their Biostratigraphic Significance

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Received April 28, 2003

Paleontological Journal, Vol. 38, Suppl. 3, 2004, pp. S217–S323.

Abstract—The Aral Faunal Assemblage is rich in small mammals. Insectivores there include the hedgehogs *Galerix* sp., *Exallerix efialtes* Lopatin, *Amphechinus akespensis* Lopatin, *A. microdus* Lopatin, and *Amphechinus* sp.; the moles *Desmanella compacta* sp. nov., *Pseudoparatalpa lavrovi* (Bendukidze), *Myxomygale asiaprima* sp. nov., and *Hugueneya* sp.; and the soricids *Gobisorex akhmetievi* sp. nov., *Atasorex edax* gen. et sp. nov., and *Aralosorex kalini* Lopatin. Lagomorphs are represented by *Desmatolagus simplex* (Argyropulo), *D. periaralicus* Lopatin, *D. veletus* Lopatin (Desmatolagidae), and *Sinolagomys pachygnathus* Li et Qiu (Ochotonidae). Rodents are very diverse and include the aplodontids *Prosciurus daxnerae* Lopatin and *Ansomys crucifer* Lopatin; the beavers *Steneofiber kumbulakensis* (Lytschev), *S. schokensis* (Bendukidze), and *Asiacastor* sp.; the eomyids *Eomyodon bolligeri* Lopatin and *Pseudotheridomys yanshini* Lopatin; the zapodids *Plesiosminthus tereskentensis* Lopatin, *Parasminthus debruijni* Lopatin, and *Bohlinosminthus cubitalus* Lopatin; the cricetids *Eucricetodon occasionalis* Lopatin, *Eumyarion tremulus* Lopatin, *Eumyarion* sp., and *Aralocricetodon schokensis* Bendukidze; the primitive mole rat *Argyromys aralensis* (Argyropulo); the tachyoryctoidids *Tachyoryctoides glikmani* (Vorontzov), *Tachyoryctoides* sp., *Aralomys gigas* Argyropulo, and *Eumysodon spurius* Argyropulo; and the ctenodactylid *Yindirtemys birgeri* Bendukidze. Based on taxonomic composition, the assemblage is dated as the beginning of the Miocene (Early Aquitanian) and compared to the MN1 European Mammal Zone. It is proposed to consider the Aral biochron as the reference level NMU1, that is, the basal unit of the biochronological scale of the Neogene of inner Asia, which corresponds to the earliest phase of the Xiejian Asian Land Mammal Age (Earliest Xiejian or Aralian).

Key words: Small mammals, insectivores, lagomorphs, rodents, Early Miocene, biostratigraphy, biochronology, paleozoogeography, North Aral Region, inner Asia.

INTRODUCTION

Fossil remains of mammals are widely used in biostratigraphic correlation of Paleogene and Neogene continental deposits. They hold considerable promise because of the high rate of mammalian evolution and the wide geographical and stratigraphic ranges of the majority of mammal groups. The land mammal ages recognized in Europe, North and South America, Africa, and central Asia reflect successive alterations, which are provided by the stepwise nature of mammalian evolution and prochoreses, in regional faunas. Small mammals (especially rodents) are used for the establishment of minute biostratigraphic units, i.e., zones (in Europe) and local faunas (in Asia). The European mammal zones are comparable in comprehensiveness to the zones established on the basis of marine microorganisms, such as foraminifers, radiolarians, and nanoplankton. These zones have been recognized based on minute faunal changes. According to the classification of biostratigraphic units, they are concurrent range zones with boundaries that are established by the combined method, i.e., on the basis of the first appearance or disappearance of species of a certain evolutionary lineage; a characteristic faunal association; and, in some cases, the presence of index species and immigration events (see Daams and Freudenthal, 1981; Mein, 1999; Steininger, 1999). The mammal zones are commonly used as biochronological (rather than biostratigraphic) units. Thus, each zone is considered a time interval during which a certain mammal assemblage occurred. This corresponds to the conception of the *typical local fauna* (see Qiu and Qiu, 1995) and the Russian term *faunisticheskii kompleks* (faunal assemblage). The first complete zonation of the Neogene of Europe (MN1–MN17 zones) was proposed by Mein (1975, 1976, 1990). The presently accepted zonation was adopted in 1990 by an international congress in Reisensburg, Germany (Bruijn *et al.*, 1992), and work in this field is still in progress ("*Actes*…," 1997; Fejfar *et al.*, 1998; Agusti, 1999; Mein, 1999; Steininger, 1999). The mammal-based zonation of the Paleogene (MP1–MP30 zones) was established in 1987 at the International Symposium on Mammalian Biostratigraphy and Paleoecology of the European Paleogene (Mainz, Germany) (see Schmidt-Kittler, 1987); and the latest zonation was accepted in 1997 by the International Congress on Mammalian Biochronology of the Cenozoic of Europe and Adjacent Areas (Montpelier, France) ("*Actes*…," 1997). The Neogene mammal biochronological units correlate with a zonation proposed based on marine microorganisms (Steninger *et al.*, 1990, 1994; Steininger, 1999) and magnetostratigraphic units and is controlled by the geochronological methods (Schlunegger *et al.*, 1996; Steininger *et al.*, 1996; Kempf *et al.*, 1997; Legendre and Léveque, 1997; Mödden, 1997; Steininger, 1999; Lindsay, 2001).

Local faunas, which are determined as associations of simultaneously existing species (from the same stratigraphic level), are operational biochronological units that are used by paleotheriologists. Particular localities are arranged in biochronological order (and in a time scale) mainly based on evolutionary criteria (using the method of evolutionary lineages). This technique has often been criticized (Martinez, 1995) because it seems to rest upon a vicious circle in which the age of a locality is determined on the basis of the evolutionary stage of a taxon of a certain lineage, while the age of this taxon is determined on the basis of the age of association, that is, on the age of the locality. Recently, quantitative techniques with a more formalized nature have been proposed that enable one to determine the exact biochronological position of assemblages from individual localities in the general faunal sequence on the basis of the mammal composition (and the number of taxa from certain evolutionary lineages), i.e., *the evolutionary method for the biostratigraphic correlation of faunal assemblages* (Lytschev and Kochenov, 1988) and *the method of cladochronograms* (Martinez, 1995). Additionally, in a number of studies, zonation (recognition of the concurrent range zones, biozones, zones of assemblages, etc.) was performed on the basis of selected groups of small mammals, primarily rodents, e.g., eomyids, theridomyids, cricetids, etc. (see Agusti *et al.*, 1987, 1988; Sümengen *et al.*, 1990; Freudenthal, 1994; Ünay *et al.*, 2001).

The faunal assemblages of Paleogene and Neogene mammals from Asia are much more poorly understood than those from Europe, although considerable progress has been achieved in the study of localities in China, Mongolia, Kazakhstan, Turkey, and Pakistan over the past two decades (Mein, 2001). The first detailed biochronological study of Asian localities was undertaken in the 1980s. Li *et al.* (1984) proposed the first division of the Neogene of northern China on the basis of mammals; subsequently, it was supplemented to a great extent and developed in more detail (Qiu, 1990; Qiu and Qiu, 1995; Qiu *et al.*, 1999). Recently, the first attempts to elaborate a uniform mammalian biochronological scale for the Neogene of inner Asia based on the Chinese scale have been undertaken (Lindsay, 2001; Lopatin, 2002a). Specific land mammal ages for the Paleogene of central Asia were established in 1987 (Russell and Zhai, 1987). When this is done, the type local faunas (Qiu and Qiu, 1995) or Neogene mammal faunal units (Qiu, 1990; Steininger *et al.*, 1990; Qiu *et al.*, 1999), i.e., biochrons (Flynn, 2000), are hierarchically subordinated to land mammal ages and correlated with the European Zonal Scale. The correlations for the Oligocene and Early Miocene are of low precision because of considerable differences in the taxonomic composition of European and central Asian mammals and general problems of long-distance correlation (Dam, 2001; Ünay *et al.*, 2001).

From this point of view, the study of Early Miocene mammals from the North Aral Region is a topical area in current research, since, in the period in question, this region was in contact with the northeastern extremity of the Eastern Paratethys and displayed faunal relationships to both Europe and central Asia. The Aral (or *Paraceratherium*) Mammal Fauna, which includes abundant mammalian remains, is of special interest in this respect. It is dated to the Oligocene–Miocene boundary and seems to has no analogues among the currently known assemblages from central Asia. Small mammals from the Aral Fauna, which are considered in the present study, are chosen as the basic tool for the interregional correlation. In addition, comparative faunal analysis of other localities in Kazakhstan, Mongolia, and China was performed to supplement and specify the previously proposed mammal-based biochronological chart (Neogene Mammal Units, NMU) for the Early Miocene of inner Asia (Qiu and Qiu, 1995; Lopatin, 2002a).

From 1991 to 1993, I investigated the stratigraphy and taphonomy of a number of localities of Early Miocene mammals in western Kazakhstan: Akespe, Kumbulak, Altynshokysu, Sayaken, Kuzhasai, Bishtyubya, and Mynsualmas. Extensive material on mammals and other vertebrates was collected and examined in subsequent studies (Lopatin, 1994a, 1994b, 1994c, 1994d, 1995, 1996, 1997, 1998, 1999a, 1999b, 2000a, 2000b, 2002a, 2003).

The main material (about 700 specimens) consists of small mammals from the Aral Fauna. They were collected by the author in 1992 and 1993 during fieldwork of the Kazakhstan Party of the Paleontological Institute of the Russian Academy of Sciences (PIN) in localities of the North Aral Region, i.e., Altynshokysu (collection PIN, no. 4516) and Akespe (collection PIN, no. 210). The specimens were washed out of bone-bearing sediments and collected in the excavation and on the exposed surface of the strata of the Aral Formation. In addition, I examined small mammals that had been collected earlier from the Akespe and Zherlepes localities of the North Aral Region (collected by Yu.A. Orlov in 1938 and N.S. Shevyreva in 1968) and about 700 specimens from the Altynshokysu locality that were collected by foreign colleagues during a field excursion within the framework of the International Symposium on the Oligocene–Miocene Transition in the Northern Hemisphere (Kazakhstan, August 16–28, 1994) and placed at my disposal (H. de Bruijn, Institute of Earth Sciences, Utrecht University, Netherlands; G. Daxner-Höck, Natural History Museum of Vienna, Austria; T. Bolliger, Paleontological Institute of Zurich University, Switzerland; and D. Kälin, Basel, Switzerland).

A total of about 2.5 tons of rock worth of specimens were washed with the use of sieves with a 5–10 mm screen opening. Analysis of the specimens was performed in laboratory conditions. The material was studied with the aid of a binocular MBS-9 microscope equipped with a measuring device and a binocular MFO-90 microscope with a drawing apparatus.

In the chapter devoted to systematics, the morphological descriptions of fossil remains of members of various groups are based on a terminology and measurement technique accepted in the majority of modern studies of the Erinaceidae (Van Valen, 1966; Rich, 1981; Wang and Li, 1990; Frost *et al.*, 1991; Gould, 1995), Talpidae (Hutchison, 1974; Storch and Qiu, 1983; Hoek Ostende, 1989, 2001a), Soricidae (Hoek Ostende, 2001b; Lopatin, 2004), Lagomorpha (Tobien, 1974, 1978, 1986; McKenna, 1982; Erbajeva, 1988; Averianov, 1998), Aplodontidae (Rensberger, 1975; Rensberger and Li, 1986; Wang, 1987; Qiu and Sun, 1988; Lopatin, 1997), Castoridae (Lytschev and Shevyreva, 1994; Hugueney, 1999a; Korth, 2002), Eomyidae (Wang and Emry, 1991; Engesser, 1999), Zapodidae (Martin, 1994), Cricetidae (Freudenthal *et al.*, 1994), Tachyoryctoididae (Klein Hofmeijer and Bruijn, 1985), and Ctenodactylidae (Wang, 1991, 1994, 1997).

The following abbreviations for institutions are used in this study: (DK) private collection by D. Kälin, Basel, Switzerland; (GIN) Geological Institute of the Russian Academy of Sciences, Moscow; (IAUU) Institute of Earth Sciences, Utrecht University, the Netherlands; (IP) Institute of Paleobiology of the Academy of Sciences of Georgia, Tbilisi; (IVPP) Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; (IZ) Institute of Zoology of the Academy of Sciences of Kazakhstan, Almaty; (MGU) Moscow State University; (NMB) Natural History Museum of Basel, Switzerland; (NMW) Natural History Museum of Vienna, Austria; (PIN) Paleontological Institute of the Russian Academy of Sciences, Moscow; and (PIUZ) Paleontological Institute of Zurich University, Switzerland.

CHAPTER 1. HISTORY OF THE STRATIGRAPHIC AND PALEONTOLOGICAL STUDY OF THE REGION

The first studies of the North Aral Region were performed more than 150 years ago. In the 19th century, they were mainly restricted to reconnaissance surveys and examination of general naturalistic characteristics. The first geological and paleontological observations were made by mining engineers, zoologists (E.A. Eversmann, A.I. Lehman, N.A. Severtsov, M.I. Bogdanov, and V.D. Alenitsyn), botanists (F.I. Basiner and I.G. Borshchov), statisticians (G.Ya. Meyendorff), ethnographers (N.V. and V.Ya. Khanykovs), and military topographers (A.I. Butakov, A.I. Moksheev, L.I. Meyer, and N.A. Ivashintsev). The paleontological material brought to St. Petersburg and Moscow was examined by the outstanding experts in paleontology G.P. Helmersen, E.J. Eichwald, H.W. Abich, and G.A. Trautschold (Yanshin, 1953; Akhmetiev, 1994b).

From the early 20th century onward, studies of the area became more thorough. There was considerable interest in the sources of raw materials and other natural resources in this area. At that time, the North Aral Region was explored by the geologists S.N. Nikitin, V.V. Bogachev, M.M. Prigorovsky, N.G. Kassin, and A.N. Zamyatin. A.D. Arkhangelsky, M.V. Pavlowa, G.P. Mikhailovsky, I.V. Palibin, and A.N. Kryshtofovich participated in the study of paleontological material.

From 1925 to 1950, a geological survey of the region was performed. The development of various and complex approaches, elaboration of new methods, and extensive work on the part of local geological institutions were characteristic of this stage of research. Studies carried out by the geologists V.A. Vakhrameev, O.S. Vyalov, G.S. Klebanov, N.K. Ovechkin, B.A. Petrushevsky, L.B. Rukhin, V.A. Sergeev, and L.N. Formozov and the paleontologists A.K. Alekseev, A.N. Kryshtofovich, P.A. Mchedlishvili, A.A. Borissiak, A.I. Argyropulo, Yu.A. Orlov, A.Ya. Tugarinov, and L.I. Khozatsky were of special theoretical and practical significance. A.L. Yanshin carried out a detailed geological study of the North Aral Region, and his monograph devoted to the stratigraphy and geological development of this region (Yanshin, 1953) retains its significance in the present.

A geological survey on a 1 : 200 000 scale was performed in the 1950s and 1960s by geologists from the association “Aerogeologiya” (All-Union Aerogeological Trust). In the early 1960s, Ovechkin and his team studied the biostratigraphy of Paleogene deposits in the Turgai Depression and the North Aral Region. A section on the northern coast of Perovsky Bay was taken as the key section for most of these deposits (Ovechkin, 1962).

In the 1960s and 1970s, V.A. Bronevoi, O.N. Zhezhel’, S.G. Zhilin, R.G. Garetskii, L.G. Kiryukhin, R.L. Merklin, V.V. Lavrov, R.K. Makarov, L.V. Mironova, A.I. Korobkov, L.S. Glikman, E.D. Zaklinskaya, T.I. Bondareva, V.G. Pronin, G.S. Rayushkina, L.A. Panova, and many other researchers studied the stratigraphy of sediments in the North Aral Region and the Ustyurt Plateau and their correlation with strata in other areas (Lavrov, 1959; Bronevoi *et al.*, 1963, 1967; Bronevoi and Kiryukhin, 1966; etc.). Subsequently, Russian biostratigraphers (M.A. Akhmetiev, A.A. Voronina, L.A. Nevesskaja, S.V. Popov, and others) implemented a number of important studies devoted to detailed stratigraphic investigation of particular areas combined with a wide regional approach to the study of historical development of the Eastern Paratethys (Nevesskaja *et al.*, 1984, 1986; Khondkarian *et al.*, 1986; Popov *et al.*, 1993a, 1993b). An international symposium on the questions of the Paleogene–Neogene boundary in Asia (International Program of Geological Correlation, project no. 326) that was organized by V.Yu. Reshetov and M.A. Akhmetiev in Aktyubinsk in August, 1994 was of especially high theoretical significance. It was accompanied by excursions to certain localities in the North Aral Region, which gave an additional impulse to the intensification of biostratigraphic and paleontological studies in this field (Akhmetiev and Lopatin, 1994; Lopatin, 1996; Lucas *et al.*, 1998).

The study of fossil vertebrates from the North Aral Region commenced in the late 1930s after extensive excavations in the Akespe (Agyspe) locality performed by M.G. Prokhorov in 1932 and 1933 and by Yu.A. Orlov in 1936 and 1938 (Orlov, 1939; Borissiak and Beliajeva, 1948). Borissiak (1939, 1944, 1954), Beliajeva (1954), and Gromova (1959) studied large mammals (Rhinocerotoidea); Tugarinov (1940) examined birds; and Khozatsky (1945) studied turtles. In the

1970s–1990s, O.G. Bendukidze, V.M. Chkhikvadze, and V.V. Lavrov performed an extensive study of the vertebrate composition in the Aral Formation (Bendukidze, 1977, 1989, 1993, 1994, 1997, etc.; Lavrov *et al.*, 1985). In subsequent years, mammals from the Aral Faunal Assemblage were studied by Bayshashov (1994a, 1994b) and Tyutkova (1994), while fish were studied by Sytchevskaya (Sytchevskaya and Gurov, 1994, 1995).

Orlov (1939) was the first to indicate the presence of small mammals (an insectivore closely resembling *Palaeoscaptor acridens*; lagomorphs; and rodents, including cricetids and beavers) in the Aral Formation of the Akespe locality. In 1939 and 1940, A.I. Argyropulo published the first descriptions of new rodent taxa, including *Eumysodon spurius*, *E. orlovi*, *Aralomys gigas*, *Schaubeumys aralensis*, *S. woodi*, and *Protalactaga borissiaki*, and the lagomorph *Agispelagus simplex*. Subsequently, *Aralomys glikmani*, from the Zherlepes locality (Vorontzov, 1963), and *Propalaeocastor kumbulakensis*, from Kumbulak (Lytschev, 1970), were described, and Gureev (1960) reexamined *Agispelagus simplex*. In a series of studies, Bendukidze and coauthors provided lists of small mammals from various localities of the Aral Faunal Assemblage, i.e., Akespe (Bendukidze, 1989), Sayaken, and Kuzhasai (Lavrov *et al.*, 1985). In the monograph devoted to small mammals from the Miocene of southwestern Kazakhstan and Turgai, Bendukidze (1993) paid special attention to morphological descriptions of the taxa from the Aral Fauna of the Akespe, Altynshokysu, Akotau, Sayaken, Kumbulak, Kuzhasai, and Zhilansai localities. The researcher registered 34 species in the Aral Formation; seven (*Mygalea lavrovi*, *Eucricetodon sajakensis*, *Aralocricetodon schokensis*, *Yindirtemys sajakensis*, *Y. birgeri*, *Capatanka schokensis*, and *Capacikala sajakensis*) were newly described, four were assigned to the previously known species (*Amphechinus minimus*, *Gobisorex kingae*, *Tachyoryctoides spurius*, and *Aralomys gigas*), and 23 were described in open nomenclature (*Lantanotherium* sp., *Amphechinus* cf. *rectus*, *Asthenoscapter* sp., *Proscapanus* sp., *Gobisorex* aff. *kingae*, *Amphilagus* aff. *robustus*, *Desmatolagus* aff. *shargaltensis*, *D.* aff. *gobiensis*, *Sinolagomys* aff. *gracilis*, *S.* aff. *kansuensis*, *Palaeosciurus* sp., *Parasminthus* aff. *tangingoli*, *Eucricetodon* aff. *caducus*, *E.* aff. *youngi*, *Tachyoryctoides* aff. *obrutschewi*, *Aralomys* sp., *“Tataromys”* cf. *sigmodon*, *Steneofiber* aff. *kumbulakensis*, *Palaeocastor* sp., *Capatanka* aff. *schokensis*, *Capacikala* aff. *sajakensis*, *C.* cf. *sciuroides*, and *Asiacastor* aff. *orientalis*).

From 1994 to 2004, I examined small mammals collected in 1992 and 1993 in the Aral Formation of Altynshokysu; as a result, I revised a number of taxonomic groups and described new taxa (Lopatin, 1994a, 1995, 1996, 1997, 1998, 1999a, 1999b, 2000a, 2000b, 2003, 2004).

The data on Miocene mammals from Kazakhstan were first generalized in the 1960s and 1970s; mammal assemblages, which were composed of faunas from the localities assigned to approximately the same age, were established. In fact, some of these faunas are clearly diachronous. For example, the so-called paracerathere–mastodont–muntjac assemblage (Bazhanov and Erofeev, 1971) includes the Aral (Aquitanian), Kushuk (Burdigalian), and Tarkhan-Chokrak (Middle Miocene) faunas, which undoubtedly differ in age. Biryukov *et al.* (1968) recognized seven mammal assemblages in the Miocene and Pliocene of Kazakhstan, including the *Paraceratherium* (Akespe) and *Gomphotherium* (Kushuk) assemblages, which were assigned to the Early Miocene. Devyatkin (1981) used the uniqueness of the *Paraceratherium* Assemblage for the establishment of the Agyspe Regional Stage, which he recognized in the Lower Miocene of central Asia. Gabunia (1981, 1986) was the first to correlate the Miocene mammal localities in this region with the European and Asian mammalian biochronological chart. The study in this field was continued by Agadjanian (1986), Bendukidze (1993, 2000), Lucas *et al.* (1998), and Lopatin (1996, 1997, 1998, 1999a, 1999b, 2000a, 2002a).

CHAPTER 2. STRATIGRAPHY OF LOWER MIOCENE DEPOSITS IN WESTERN KAZAKHSTAN

The localities containing the Aral Mammal Fauna were discovered in the steep slopes near the northern coast of Perovsky Bay (Akespe and Kumbulak), the residual plateau Altynshokysu (Akotau and Altynshokysu), the northwestern part of the Aral Region (Sayaken and Zherlepes), and in the northeastern Ustyurt Plateau (Kuzhasai and Zhilansai). The younger Early Miocene mammals were found in the Ustyurt Plateau (Kintykche, Bishtyubya, and Mynsualmas localities) (Fig. 1). The localities investigated in the present study are located in the steep slopes of the northern coast of Perovsky Bay (Akespe and Kumbulak) and in the Altynshokysu Plateau (Altynshokysu locality). The outcrop of bone beds in this region is associated with physical weathering, primarily with the erosion caused by water flows, which are formed during rains.

Mammal remains from the North Aral Region and the Ustyurt Plateau come from the Lower Miocene beds of various age and lithological structure, which are subdivided into a number of formations and layers (Fig. 2).

The Upper Oligocene and Lower Miocene strata in western Kazakhstan are represented by the Baygubek (northern Ustyurt Plateau) and Aral (North Aral Region, Ustyurt Plateau) formations. It is generally believed that the Lower Miocene is represented by the Kintykche Beds of the Baygubek Formation, the Bishtyubya Formation (*Oncophora* Beds), and the lowermost beds of the Tarkhanian Regional Stage of the Ustyurt Plateau (Popov *et al.*, 1993b).

Fig. 1. Schematic geographical position of localities of Early Miocene mammals in western Kazakhstan. Designations: (triangles) localities of the Aral Faunal Assemblage, Aquitanian; and (circles) localities of the Kushuk Faunal Assemblage, Burdigalian.

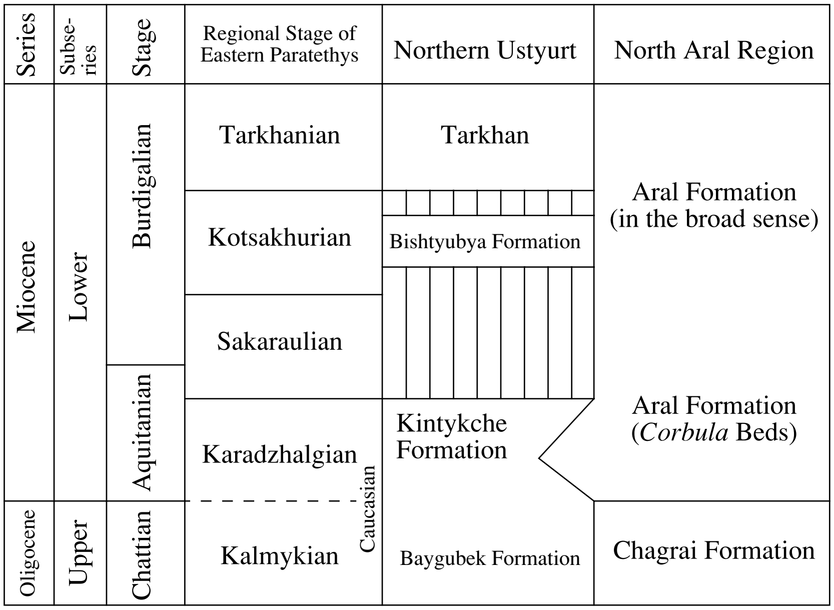


Fig. 2. Correlation of stratigraphic units in the Lower Miocene of the North Aral Region and the northern Ustyurt Plateau (after Popov *et al.*, 1993b).

According to the modern concept (Popov *et al.*, 1993b), the Baygubek Formation is dated as the Late Oligocene–Early Miocene. It was originally established by R.L. Merklin (Garetskii *et al.*, 1958) on the western coast of the Aral Sea north of the Baygubek-Murun Cape and consisted of a sandy "member with *Cardium levinae* (= *Cerastoderma prigorovskii*)," which contained a rich molluskan assemblage. Subsequently, Merklin (1960) extended this name to the underlying clayey strata (Lower Baygubek Subformation), which is currently considered to be the separate Karatomak Formation assigned to the Oligocene (Popov *et al.*, 1993b). In the stratotype region, clays of the Karatomak Formation are overlain by the strata (25–30 m thick) composed of thin interbedding siltstone clays and light sands; the roof and bottom layers contain interbeds (3–7 cm thick) of hard ferruginous sandstones. These strata are overlain with conformity by a member of greenish gray siltstone clays (6–7 m thick), which is followed by sands and siltstones (10–16 m thick) with *Cerastoderma prigorovskii, Nucula comta, Nuculana gracilis, Arctica rotundata, Glossus subtransversus, Lentidium kuzhasaicum, Corbula helmerseni*, and other bivalves (Popov *et al.*, 1993b). Northwards, sands of this member become coarser, while the molluskan assemblage decreases in diversity (*Cerastoderma prigorovskii, Corbula helmerseni*, and *Mytilus* sp.); southwards, sands are gradually replaced by clays and are covered by multicolored sandy–clayey sediments of the Aral Formation.

The Kintykche Beds were initially recognized by Merklin (Garetskii *et al.*, 1958) in the composition of the Baygubek Formation on the basis of a unique molluskan assemblage, including not only typical Baygubek forms (*Cerastoderma prigorovskii, Corbula helmerseni, Angulus nysti, Lentidium kuzhasaicum, Solen* sp., and *Cyrtodaria* sp.) but also several more thermophilic and more stenohaline taxa that were not registered in the Oligocene, i.e., *Callista uretzkii* and *Laevicardium* sp. In the stratotype region (Kintykche gully), the Kintykche Beds are composed of siltstones and sands (7 m thick), which overlie with unconformity (because of erosion) the strata of the Aral Formation (Popov *et al.*, 1993b). These beds are correlative with the upper part of the Baygubek Formation (Pleshcheev *et al.*, 1978). In the northwestern Aral Region, they occur from the Kuzhasai gully to the Baygubek-Murun Cape. The Kintykche Beds contain various vertebrates (Bendukidze, 1977; Gabunia, 1986) and are overlain by the transgressively bedding strata of the Bishtyubya Formation.

The Aral Formation is widespread in the North Aral Region and in the Ustyurt Plateau up to the stow of Mynsualmas. It is composed of multicolored sandy–clayey and carbonate strata up to 70 m thick, which are rich in interbeds and contain *Corbula helmerseni* (occasionally forming lumachelles); *Cerastoderma prigorovskii, Angulus* sp., *Mytilus* sp., and *Balanus* (Popov *et al.*, 1993b) occur as well. The Aral Formation (Akespe, Altynshokysu, Sayaken, etc.) yielded abundant vertebrate faunas and provided material for studies of mollusks (Yanshin, 1953; Popov *et al.*, 1993b), ostracodes (Yanshin, 1953), leaf imprints, spores and pollen (Panova, 1979), and gyrogonites of charophytes (Nikol'skaya, 1988; Zhamangaraeva, 1994). The Aral Formation overlies conformably or with erosion the Baygubek or Chagrai formations and is overlain by the Kintykche Beds, with erosion, by the Bishtyubya Formation, or the Quaternary strata.

The age of the Aral Formation (Late Oligocene or Early Miocene) remained uncertain for a long time. Nikitin was the first to recognize this formation as a separate stratigraphic unit ("beds with *Corbula helmerseni*") as early as 1907; he assigned it to "the First Mediterranean Stage" (Burdigalian). In 1909, Mikhailovsky proposed the name *Aralian Stage* for the *Corbula* Beds in the North Aral Region and their analogues in Ukraine (Yanshin, 1953). Zhizhchenko (1940) extended the term Aralian Stage to all brackish water sediments from the Miocene of the North Aral Region and proposed to assign them to the Aquitanian–Early Burdigalian. Vyalov (1945) dated the *Corbula* Beds as the Burdigalian, while Vakhrameev (1949) assigned the Aral Formation to the Aquitanian because it yielded a vertebrate fauna that was older than the Burdigalian. Yanshin (1953) believed that the Aral Formation should be referred to as the Early Miocene (Burdigalian) and, in complete sections, as the Early–Middle Miocene. However, he proposed that the Aral Formation includes not only the *Corbula* Beds but also certain younger beds of the so-called formation of salt-bearing clays in the Aral Region and Turgai. Some other researchers (Lavrov, 1959; Ovechkin, 1962) proposed that the Aral Formation additionally includes the Middle–Upper Miocene gypsiferous clays of the Turgai Lowland and central Kazakhstan depressions and beds that are presently designated as the Svetlaya Formation (Trans-Ural Region), the Kalkaman Formation (Western Siberia), and the Rubtsovo Formation (Altai Region) (*Stratigraphic Dictionary…*, 1982). Merklin (1962) was the first to divide the Aral Formation into the Upper Oligocene and Lower Miocene parts. Vyalov (1964) narrowed the Aral Formation to the initial volume, i.e., the beds with *Corbula helmerseni.* He showed that the Baygubek Provincial Stage also contained *C. helmerseni* and dated the Aral Formation as the Aquitanian, because, in his opinion, the overlying Kintykche Formation (presently regarded as the Kintykche Beds of the Baygubek Formation) should be dated as the Burdigalian. Prusova (1964) correlated the Aral Formation and the Upper Maikopian (Lower Miocene) based on her study of the foraminiferal assemblage from the Aral Formation of the northern Ustyurt Plateau. V.A. Bronevoi, S.G. Zhilin, L.G. Kiryukhin, and R.L. Merklin (Bronevoi *et al.*, 1967) studied the age of the Aral Formation and concluded the following: (1) the Aral Formation is confined to the beds containing *Corbula helmerseni*; (2) geographically, the Aral Formation is confined to the North Aral Region; and (3) the Aral Formation should be assigned to the same stratigraphic interval as the upper part of the Baygubek Provincial Stage (Upper Oligocene). It was shown that the Aral Formation is in fact a lagoon–continental facies of the Baygubek Formation and the Kintykche Beds (Khondkarian *et al.*, 1986; Popov *et al.*, 1993b). Currently, both the Baygubek (Upper Baygubek Provincial Substage) and Aral formations are assigned to the uppermost part of the Upper Oligocene and the Lower Miocene based on combined paleontological and geological data (Popov *et al.*, 1993a, 1993b).

Thus, the Aral Formation (in the broad sense) corresponds to a long period, including the terminal Chattian (terminal Late Oligocene), Aquitanian, and Burdigalian (Early Miocene). In the strict sense (*Corbula* Beds, strata with *Corbula helmerseni*), the Aral Formation corresponds to the Baygubek Formation of the Ustyurt Plateau (including the Kintykche Beds) and is dated as the terminal Chattian–Aquitanian (Popov *et al.*, 1993a). Thus, within the regional stratigraphic chart for the Neogene of the Eastern Paratethys, the Aral Formation corresponds to the uppermost beds of the Kalmykian Regional Stage and the Karadzhalgian Regional Stage (Popov *et al.*, 1993b) or, according to the newest chart developed by Nevesskaja *et al.* (2003) and accepted by the Bureau of the International Stratigraphic Commission in 2002, to the Caucasian Regional Stage.

CHAPTER 3. CHARACTERISTICS OF LOCALITIES

Akespe Locality

The locality is named after the nearest village of Akespe. In some studies, different spellings were used, i.e., Agyspee (Orlov, 1939; Bendukidze, 1979, 1989, 1993), Agyspe (Borissiak, 1943; Borissiak and Beliajeva, 1948; Yanshin, 1953; Gabunia, 1986; etc.), Agispe (Gureev, 1964), and Akespe (Tleuberdina and Rayushkina, 1993; Lopatin, 1996; etc.). Preference is given to the name Akespe, since it corresponds to the name of the geographical object.

The locality was discovered by A.K. Alekseev in 1931. Initially, excavations were performed by the Paleontological Institute of the Academy of Sciences of the USSR in 1932 and 1933 (M.G. Prokhorov) and in 1936 and 1938 (expeditions headed by Yu.A. Orlov). In the 1970s–1990s, expedition work was performed by O.G. Bendukidze (IP). From 1991 to 1993, expeditions were organized by the IZ and PIN (with the participation of the author).

Location. Kazakhstan, Kyzyl-Orda Region, Aral'skii District; northern coast of Perovsky Bay, 50 km from the Saksaul'skaya Railroad Station, 4 km east of the village of Akespe.

Stratigraphy. In the upper part of a steep slope facing the Aral Sea, clayey carbonate strata of the Aral Formation outcrop (Fig. 3):

Layer 1. Hard light gray marls 2 m thick. The lower part of the layer is grass-covered.

Layer 2. Bright green with bluish tint lumpy clays 1.2 m thick. The layer contains shell molds of small freshwater mollusks and the main bone-bearing bed.

The following mammals were registered in Layer 2: the insectivores *Amphechinus akespensis* and *Amphechinus* sp.; the lagomorphs *Desmatolagus simplex* and *Sinolagomys pachygnathus*; the rodents *Steneofiber kumbulakensis*, *Eumyarion tremulus*, *Argyromys aralensis*, and *Aralomys gigas*; and the artiodactyl *Amphitragulus* sp.

Layer 3. Dark brownish green clays containing lenses and injections of greenish gray marls with ferruginous spots. The layer is 0.7–0.8 m thick and contains a thin interbed of light gray marlacious clays (5 cm thick).

Layer 4. Light gray and yellowish gray platy limestones 3.3 m thick. The layer contains shells of *Corbula helmerseni* and isolated bones of large mammals.

Layers 3 and 4 yielded fragmentary bones and teeth of rhinocerotoids.

In 1938, researchers from the PIN discovered small ruminants in Layer 2 that were originally identified as *?Prodremotherium* sp., *?Lophiomeryx* sp., and *?Miomeryx* sp.; subsequently, Vislobokova (1997) assigned them to *Amphitragulus*. In addition, Layer 2 yielded the carnivore Felidae indet.; the rodents *Steneofiber* sp., *Aralomys gigas, Eumysodon spurius,* and *Argyromys aralensis* (= *?Protalactaga borissiaki*); the lagomorph *Desmatolagus simplex* (= *Agispelagus simplex*); the bird *Anas oligocaena* Tug.; and the turtle *Testudo aralensis* Khoz. (Orlov, 1939; Argyropulo, 1939a, 1939b, 1939c, 1940; Tugarinov, 1940; Khozatsky, 1945). In 1991, an expedition of the IZ collected *Aprotodon borissiaki* Bel. and *"Gigantamynodon akespensis"* Baysh. (Bayshashov, 1994a, 1994b).

In the 1930s, layers 3 and 4 yielded large mammals collected by expeditions of the PIN (Orlov, 1939; Borissiak, 1939, 1944; Beliajeva, 1954; Gromova, 1959): *Paraceratherium prohorovi* (Boriss.), *Aceratherium aralense* Boriss., *Aprotodon borissiaki* Bel., *Aprotodon* sp., and *Protaceratherium* sp.

Taphonomy. Orlov (1939) provided a comprehensive taphonomic description of the locality considered. He indicated that rhinocerotoid remains—skulls, lower jaws, vertebrae (including those in natural articulation), ribs, and limb bones—formed large accumulations in layers 3 and 4. Isolated bones occurred up to the strata located 2.5 m above the bottom of Layer 4. Orlov proposed that this locality was formed in nearshore marine conditions; apparently, large bones from layers 3 and 4 were partially buried in the shoreline zone, while small bones of rodents, ruminants, and others were transported by water flows and buried away from large bones at a greater depth on the silty floor. Kostenko (1972) assumed that fossil remains of mammals and other vertebrates occurred in the Aral Formation because of redeposition from the earlier Oligocene beds (explaining the Upper Oligocene appearance of the Aral Fauna). However, this assumption seems to have been groundless: it is disproved by the good state of preservation of the small bones and teeth and the presence of articulated skeletal elements.

Kumbulak Locality

The locality is named after Mt. Kumbulak. It was discovered by G.F. Lytschev (IZ) in the 1960s. It was also investigated by O.G. Bendukidze (IP) in the 1970s and 1980s and by expeditions of the IZ and PIN from 1991 to 1993 (with the participation of the author).

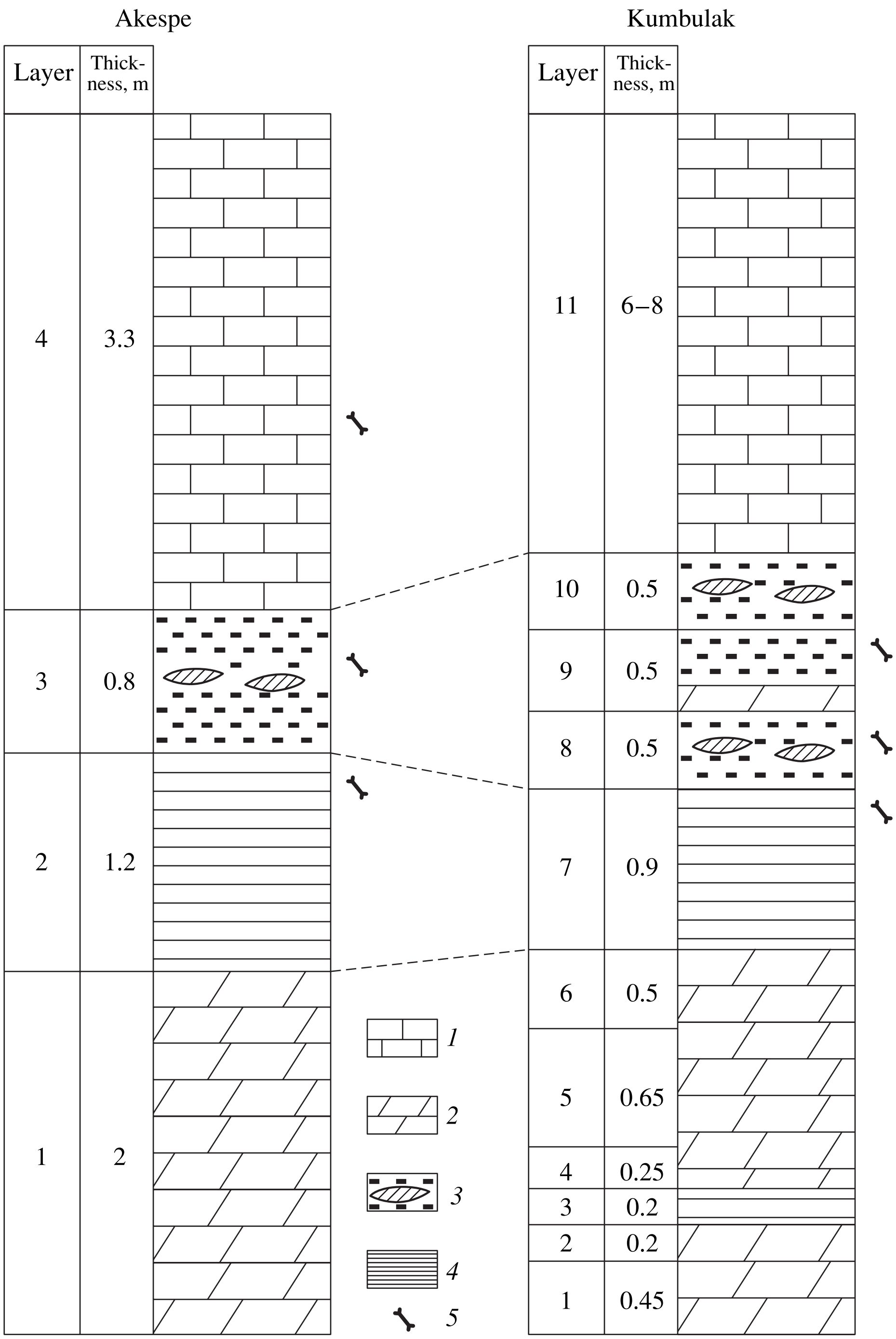


Fig. 3. The structure and correlation of sediments of the Aral Formation in the Akespe and Kumbulak localities. Designations: (*1*) *Corbula* limestones, (*2*) marl, (*3*) clay with marl lenses, (*4*) clay, and (*5*) bone beds.

Location. Kazakhstan, Kyzyl-Orda Region, Aral'skii District; northern coast of Perovsky Bay, about 50 km from the Saksaul'skaya Railroad Station, 2.5 km northeast of the village of Akespe.

Stratigraphy. The Aral Formation outcrops in a steep slope of Mt. Kumbulak and is divided into the following members and layers (from below upsection):

Member 1. Pelitomorphic marls 2.3 m thick.

Layer 1. Light gray lumpy marls 0.45 m thick.

Layer 2. Light gray, dense, and massive marls 0.2 m thick.

Layer 3. Light gray, dense, platy clays 0.2 m thick.

Layer 4. Light gray marl similar to that of Layer 2 with lenses of brownish green clays. The layer is 0.25 m thick.

Layer 5. Pinkish gray, lumpy, and strongly calcareous marls 0.65 m thick.

Layer 6. Light gray, massive, compact marls 0.5 m thick.

Member 2. Greenish lumpy marls and green clays with carbonate–phosphate nodules. The member is 2.4 m thick.

Layer 7. Bright dark green with bluish tone clays. The weathered sites are lumpy brecciated and grayish blue. The roof of the layer yielded mammal bones. The layer is 0.9 m thick.

The mammals from Layer 7 are the insectivore *Amphechinus* sp., the lagomorph *Sinolagomys* sp., the rodent Cricetidae indet., and the rhinocerotoids *Paraceratherium prohorovi* and *Aceratherium aralense.*

Layer 8. Dark greenish khakilike clays with widely spaced small marl clayey injections. The weathered sites are brownish green and lumpy brecciated. The layer is 0.5 m thick. The surface of contact with the underlying layer is uneven. The layer yielded abundant rounded fragments of large bones, complete small bones of mammals, and shells of *Corbula helmerseni.*

Layer 9. Grayish green carbonate clays with marl injections. The basal part contains a clearly outlined light gray marl interbed. The layer is 0.5 m thick and contains scarce fragments of mammal bones.

Layer 10. Interbedding brownish green clays and grayish green marl clays enclosing marl nodules. The layer is 0.5 m thick.

Member 3. Platy limestones and lumachelles containing *Corbula helmerseni.* The member is up to 8 m thick.

Layer 11. Yellowish gray platy limestones with *Corbula*. The layer is 6–8 m thick. Bones have not been found.

The Kumbulak locality is situated approximately 1.5 km from the Akespe locality (excavated by the PIN). Layer 6 in the section of the Kumbulak locality seems to correspond to Layer 1 in Akespe (the underlying marl layers in Akespe are covered by a talus and sod); judging from the lithological characteristics, layers 7, 8–10, and 11 in the section of Kumbulak correlate with layers 2, 3, and 4 in Akespe, respectively (Fig. 3).

Taphonomy. The bones collected in this locality are usually isolated, damaged, and rounded; however, articulated bones (e.g., a skull with the lower jaw of *Aceratherium* from Layer 7) occur as well. Apparently, bodies of large animals that died not far from the burial were buried in lagoon conditions together with fossils that underwent substantial transportation (possibly initially buried in sites located closer to the shore of the water body and then transported by temporary water flows) to the site of the taphocenosis.

Altynshokysu Locality

This locality is named after the Altynshokysu Plateau. Different spellings for this locality have been used, namely, Altyn-chokusu (Yanshin, 1953); Chokusu (Bendukidze, 1979); Altyn-Chokusu (Khondkarian *et al.*, 1986); Altan-Chokusu (Vislobokova *et al.*, 1996); Altyn-Shokysu, Altyn-Shoky-su, and Shokysu (Bendukidze, 1993); Altyn-Shokysy (Tleuberdina and Rayushkina, 1993); and Altynshokysu (Lopatin, 1994a, 1996; etc.). Preference is given to the name Altynshokysu, since it corresponds to the name of the geographical object.

The locality was discovered by O.G. Bendukidze (IP) in 1973, and he investigated it from the 1970s to the 1990s. From 1991 to 1993, it was studied by expeditions organized by the IZ and PIN (with the participation of the author).

Location. Kazakhstan, Aktyubinsk Region, Chelkarskii District; 4 km northeast of the Chokusu Railroad Station, about 58 km from the coastline of the northern coast of the Aral Sea; the southwestern slope of the eastern spur of the Altynshokysu Plateau, which was named the Sarybulak Plateau by Yanshin (1953) and Bendukidze (1993).

Stratigraphy. The Eocene–Lower Miocene strata (Chegan, Kutanbulak, Chilikty, Chagrai, and Aral formations) about 40 m of exposed thickness outcrop in a steep slope.

The Aral Formation overlies conformably the sand of the Chagrai Formation. Fine-grained, light gray, horizontally bedded, well-sorted, micaceous, largely kaolinized sands with numerous ferruginous and manganese nodules and pebbles up to 4 cm in size and mainly composed of quartz and mudstone.

The Aral Formation exposed in the upper part of the slope is 15–20 m thick. It is composed of clayey and carbonate-clayey rocks with an admixture of clastic matter (Fig. 4). The formation is subdivided into three members that are clearly distinguished by lithological characteristics (from below upsection):

Member 1. Light gray clayey siltstone 1 m thick.

Layer 1. Light bluish gray clayey siltstone, which is more sabulous in the upper part. This layer is 1 m thick and includes bone-bearing lenses and interbeds. The roof of the layer contains Bone Bed 1 (Lopatin, 1996). Bone fragments are usually confined to fine pebble and gravel sites.

Bone Bed 1 yielded the following vertebrates:

Fishes: *Odontaspis* sp., *Acipenser* sp., *Alosa* sp., *Esox* sp., *Rutilus tungurikensis, R.* cf. *frisii, ?Palaeoleuciscus* sp., *?Tribolodon* sp., *Varhostichthys* sp., *Proaspius* sp., *?Vladymiria* sp., *Palaeotinca* sp., Abramidini gen. indet., *Perca* sp., *Leobergia* sp., and Percidae gen. indet. (determined by E.K. Sytchevskaya, PIN).

Amphibians: the giant salamander Cryptobranchidae gen. indet. (determined by M.A. Shishkin, PIN).

Layer		Thickness, m	Lithological characteristics	Paleontological characteristics
10		0.5	sandy limestone	Bone Bed 6 with mammals
9		1	light gray sand	Bone Bed 5 with mammals
8		5.5	greenish gray clay	Bone Bed 4 with birds, mammals, and abundant opercula of the gastropod *Bithynia adornatus*
7		3	interbedding gray and greenish gray clays	fossils absent
6		2.5	light gray clay	Bone Bed 3 with teleost skeletons
5		1.5	dark green clay	fossils absent
4		0.5	yellowish gray clay	fossils absent
3		1.5	greenish gray clay	fossils absent
2		2	greenish gray clay with coquina lenses	Bone Bed 2 with teleosts and mammals
1		1	bluish gray siltstone	Bone Bed 1 with fish, amphibians, reptiles, and mammals

Fig. 4. Stratigraphic scheme for the Aral Formation in the Altynshokysu locality.

Reptiles: turtles and the crocodile *Diplocynodon* sp. (determined by M.B. Efimov, PIN).

Mammals: insectivores *Amphechinus microdus, Myxomygale asiaprima* sp. nov., and *Atasorex edax* gen. et sp. nov.; the lagomorph *Desmatolagus periaralicus*; the rodents *Steneofiber kumbulakensis, Eomyodon bolligeri, Plesiosminthus tereskentensis, Eucricetodon occasionalis, Eumyarion tremulus, Eumyarion* sp., and *Aralocricetodon schokensis*; the whale ?Delphinoidea indet.; and the artiodactyl *Amphitragulus* sp.

Member 2. Light gray and greenish gray clay with marl interbeds. The member is up to 18 m thick.

Layer 2. Bright gray, green, and rather dense clays form the gently sloping main part of the slope. The layer is 2 m thick and contains numerous shells of *Corbula helmerseni* Mikh., which often form lenses and interbeds (up to 15 cm thick) of white coquina composed of detritus, fragmentary and complete shells of *Corbula*. Bone Bed 2 is confined to these lenses and interbeds. The layer includes quartz pebbles up to 3 cm in size. Its roof contains pinkish gray marls (up to 10 cm thick).

Bone Bed 2 yielded the following fish and mammals:

Fish: Percidae indet. (determined by E.K. Sytchevskaya).

Mammals: the insectivores *Galerix* sp., *Amphechinus microdus, Amphechinus* sp., *Desmanella compacta* sp. nov., *Atasorex edax* gen. et sp. nov., and *Aralosorex kalini*; the lagomorphs *Desmatolagus periaralicus, D. simplex*, and *Sinolagomys pachygnathus*; and the rodents *Prosciurus daxnerae, Eomyodon bolligeri, Pseudotheridomys yanshini, Parasminthus debruijni, Bohlinosminthus cubitalus, Eucricetodon occasionalis, Eumyarion tremulus,* and *Aralocricetodon schokensis.*

Layer 3. Greenish gray (lighter than in Layer 2) clays 1.5 m thick.

Layer 4. Yellowish gray clays. The weathered sites are yellowish brown. The layer is 0.5 m thick.

Layer 5. Rather dense carbonate clays, dark gray in the fresh state and greenish gray in the weathered state, brecciated. The layer is 1.5 m thick. The roof contains an interbed of pinkish gray siltstone marls (7 cm thick).

Layer 6. Light gray clays (in the weathered site, yellowish gray) 2.5 m thick. Bone Bed 3 is located 1 m above the floor of the layer. It yielded skeletons of the fish Clupeidae indet. (determined by E.K. Sytchevskaya).

Layer 7. A series of interbedding gray (yellowish gray in the weathered sites) and greenish gray clays 3 m thick.

Layer 8. Greenish gray clays, which are plastic in the fresh state and chipped in the weathered state and contain abundant opercula of the freshwater gastropod *Bithynia adornatus* Tolst. The layer is 5.5 m thick. Scarce molds of the bivalve *Corbula helmerseni* and gastropods occur. The upper third of the layer contains Bone Bed 4.

Bone Bed 4 yielded turtles, birds, and mammals.

Birds: Anatidae indet., *Urmiornis brodcorbi* Karhu, and Charadrii indet. (determined by Karhu, 1997).

Mammals: the insectivores *Exallerix efialtes, Amphechinus microdus, Amphechinus* sp., *Pseudoparatalpa lavrovi, Hugueneya* sp., *Gobisorex akhmetievi* sp. nov., and *Atasorex edax* gen. et sp. nov.; the lagomorphs *Desmatolagus simplex, D. veletus*, and *Sinolagomys pachygnathus*; the rodents *Ansomys crucifer, Steneofiber kumbulakensis, S. schokensis, Asiacastor* sp., *Pseudotheridomys yanshini, Parasminthus debruijni, Eucricetodon occasionalis, Tachyoryctoides* sp., *Aralomys gigas*, and *Yindirtemys birgeri*; the carnivores ?Stenoplesictinae indet. and Mustelidae indet.; the perissodactyl Rhinocerotoidea indet.; and the artiodactyl *Amphitragulus* sp.

Member 3. Sabulous limestones, sandstones, and sand up to 1.5 m thick.

Layer 9. Light gray, fine-grained, aleuritic, and ferruginous sand 1 m thick. Scarce fragments of mammal bones occur (Bone Bed 5).

Layer 10. Sabulous, pinkish gray, and platy limestones up to 0.5 m thick. Scarce molds of *Corbula helmerseni* and strongly rounded fragments of mammal bones are present (Bone Bed 6). This layer covers and maintains the plateau.

Taphonomy. The bluish gray clayey siltstone from Layer 1 (Bone Bed 1) seems to facially correspond to marine lagoon deposits. This conclusion follows from the prevalence of the pelitic matter and presence of euryhaline mollusks (scarce shells of *Corbula helmerseni*) and inhabitants of inland areas (Gradzinski *et al.*, 1980). Bones of freshwater fish and mammals occur in lenses and interbeds in the upper third of the layer up to the boundary with the overlying green clays (Layer 2). They are mainly represented by bone fragments mixed with pebbles, gravel, and marl–clay balls. Bones of mammals and turtles and wood fragments often appear as strongly rounded pebbles. Fish bones are black, while bones of large mammals (fragments of ribs, vertebrae, and limb bones) are light brown, and teeth are black, dark brown, and reddish brown. Aquatic vertebrates are represented by both freshwater (the majority of fish and salamanders) and marine forms (*Alosa* sp., sharks, and whales). According to Mchedlidze (1964), extant marine mammals and fish co-occur mainly in the nearshore zone, where whale and pinniped dead bodies are brought by sea waves and currents. Mchedlidze remarked that isolated fish specimens were buried alone extremely rarely. At the present time, they are usually preserved in the case of mass mortality, for example, as a result of suffocation in bays rich in hydrogen sulfide.

The above suggests that abundant bone remains accumulated in relatively deep sites of a lagoon that was connected to the sea and were transported there along with pebbles and gravel from the nearshore areas of the water body. The freshwater fish (pike, bream, and perch) may have inhabited the lower reaches of the rivers running into lagoons and lowly saline sites of the water body; if this is the case, the mass mortality, which is attested to by large accumulations of fish remains, may have been caused by streams that brought fish to sites of higher salinity. These streams may also have transported terrestrial vertebrates.

Bone Bed 2 is confined to a layer that is composed of bright grayish green clay (Layer 2), which is most likely of lagoon origin. The fact that it was formed under brackish water conditions is corroborated by the presence of numerous lenses and interbeds of shells of the bivalve *Corbula helmerseni.* Marine animals have not been found in this site. Apparently, the burial was formed under almost the same conditions as in the previous case, but in a shallower site.

Bone Bed 3 (Layer 6, light gray clays) contains articulated skeletons and skeleton fragments of herring fishes (Clupeidae indet.). These bones are poorly preserved; the fish dead bodies appear to have been transported before burial. Therefore, the skeletons are partially disarticulated and deformed. Elder and Smith (1988) noticed that, as the water temperature is higher than 16°C, fish skeletons are damaged by bacteria and, consequently, are rarely preserved in conditions of warm shoals. It may be supposed that the fish remains discussed experienced a short period of transportation and were buried in a relatively deep area of a lowly saline lagoon.

Bone Bed 4 is confined to the upper part of the member of greenish gray clays (Layer 8) with abundant opercula of the freshwater gastropod *Bithynia adornatus* and scarce molds of the bivalve *Corbula helmerseni.* The small mammals collected in this layer are represented by fragmentary jaws with teeth, isolated teeth, vertebrae, limb bones, and fragments thereof. The teeth are yellow or light brown in color, while the bones are white, yellow, light gray, or pinkish gray. The abundance of specimens was not determined; however, excavation within a limited area (approximately 0.5 × 0.5 m) yielded up to two dozen small mammalian teeth and bones. Large mammal specimens are poorly preserved and consist of dental enamel fragments of rhinocero-

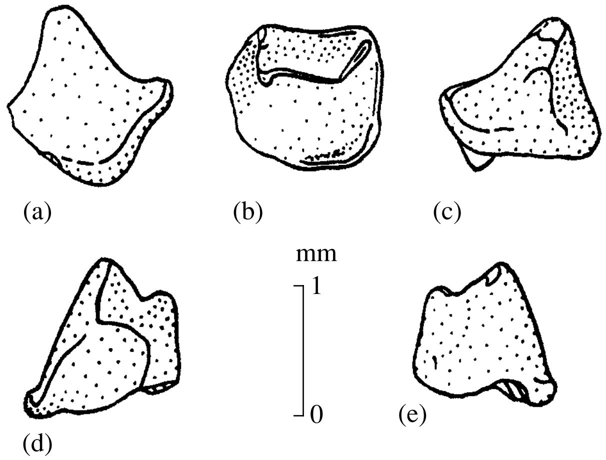


Fig. 5. *Galerix* sp., specimen PIN, no. 4516/612, fragmentary right P_4: (a) labial, (b) occlusal, (c) lingual, (d) frontal, and (e) rear views; Altynshokysu locality, Lower Miocene, Aral Formation, Bone Bed 2.

toids and indeterminable strongly rounded fragments of various large bones.

This suggests that bones were accumulated and buried under conditions of a lowly saline water body that was completely isolated from the sea. The greenish gray color caused by the presence of the hydroxide of bivalent iron $Fe(OH)_2$ is characteristic of pelitic lacustrine sediments (Gradzinski *et al.*, 1980). The highly carbonate clays are accounted for by the sedimentation of $CaCO_3$ because of photosynthesis and warming; this suggests that the lake was shallow and in a warm climate. The freshwater condition of the water body is evident from the abundance of opercula of *Bithynia* (Tolstikova, 1979) and relatively small number of *Corbula*. Bones were brought by permanent or temporary water currents; therefore, they were disarticulated, partially rounded, and buried in rapidly accumulated sediments.

The study of the taphonomic features of each bone bed displays the changes in the sedimentation basin in the course of its historical development. The Aral Formation was formed under conditions of gradually increasing continentality. As the sea basin retreated, the lagoon turned into a brackish water lake and, subsequently, gradually decreased in salinity. Sediments acquired more and more of a shallow water character, the siltstone (Member 1) was mainly replaced by clays (Member 2), the carbonate content increased, and marl and limestone interbeds developed (Member 3). As regards the formation of the burial, it most likely remained the same, so that bones were transported by water flows (temporary or permanent) and preserved in the nearshore zone of the water body.

According to the classification of sedimentation conditions that is accepted in the present study (Frolov, 1992), these sediments are assigned to the continental group, the lowland subgroup, the type of lacustrine–marine environments, and the subtype of lagoons and lakes of the seaside lowland. Thus, all the burials described are referred to the lacustrine–lagoon subtype of the taphonomic type of lakes–seas and seaside lowlands, which is recognized in the group of continental–marine types.

CHAPTER 4. SYSTEMATICS

Order Insectivora Bowdich, 1821

Family Erinaceidae Fischer von Waldheim, 1817

Subfamily Galericinae Pomel, 1848

Tribe Galericini Pomel, 1848

Genus *Galerix* Pomel, 1848

Galerix sp.

Plate 1, fig. 1

Description (Fig. 5). The trigonid of P_4 is stout, and its anterior edge is straight and expanded. The paraconid is low, long, wide, and shifted lingually.

Explanation of Plate 1

All specimens come from the Aral Formation.

Fig. 1. *Galerix* sp., specimen PIN, no. 4516/612, fragmentary right P_4, ×15; Altynshokysu locality, Bone Bed 2.

Fig. 2. *Exallerix efialtes* Lopatin, 1996, holotype PIN, no. 4516/1, right dentary fragment with P_4–M_2: (2a) labial view, ×3; (2b) occlusal view, ×3; and (2c) P_4–M_2, occlusal view, ×6; Altynshokysu, Bone Bed 4.

Figs. 3–5. *Amphechinus akespensis* Lopatin, 1999: (3) holotype PIN, no. 210/735, left dentary fragment with P_4–M_2; (3a) labial and (3b) occlusal views, ×5; (4) specimen PIN, no. 210/736, right dentary fragment with M_1, occlusal view, ×5; and (5) specimen PIN, no. 210/774, right M^1, ×5; Akespe locality.

Figs. 6–8. *Amphechinus microdus* Lopatin, 1999: (6) holotype PIN, no. 4516/7, left dentary fragment with the talonid of M_1 and complete M_2 and M_3: (6a) labial and (6b) occlusal views, ×10; Altynshokysu, Bone Bed 4; (7) specimen PIN, no. 4516/467, left M^1, ×7.5; Altynshokysu, Bone Bed 1; and (8) specimen IAUU, ALT no. 136, left P_4, ×15; Altynshokysu, Bone Bed 2.

Figs. 9 and 10. *Amphechinus* sp.: (9) specimen PIN, no. 210/737, right dentary fragment with M_3 and the alveoli of M_2, ×5; Akespe locality; and (10) specimen PIN, no. 4516/607, right dentary fragment with broken I_2, alveolus of I_3, and worn C_1–P_2, ×5; Altynshokysu, Bone Bed 4.

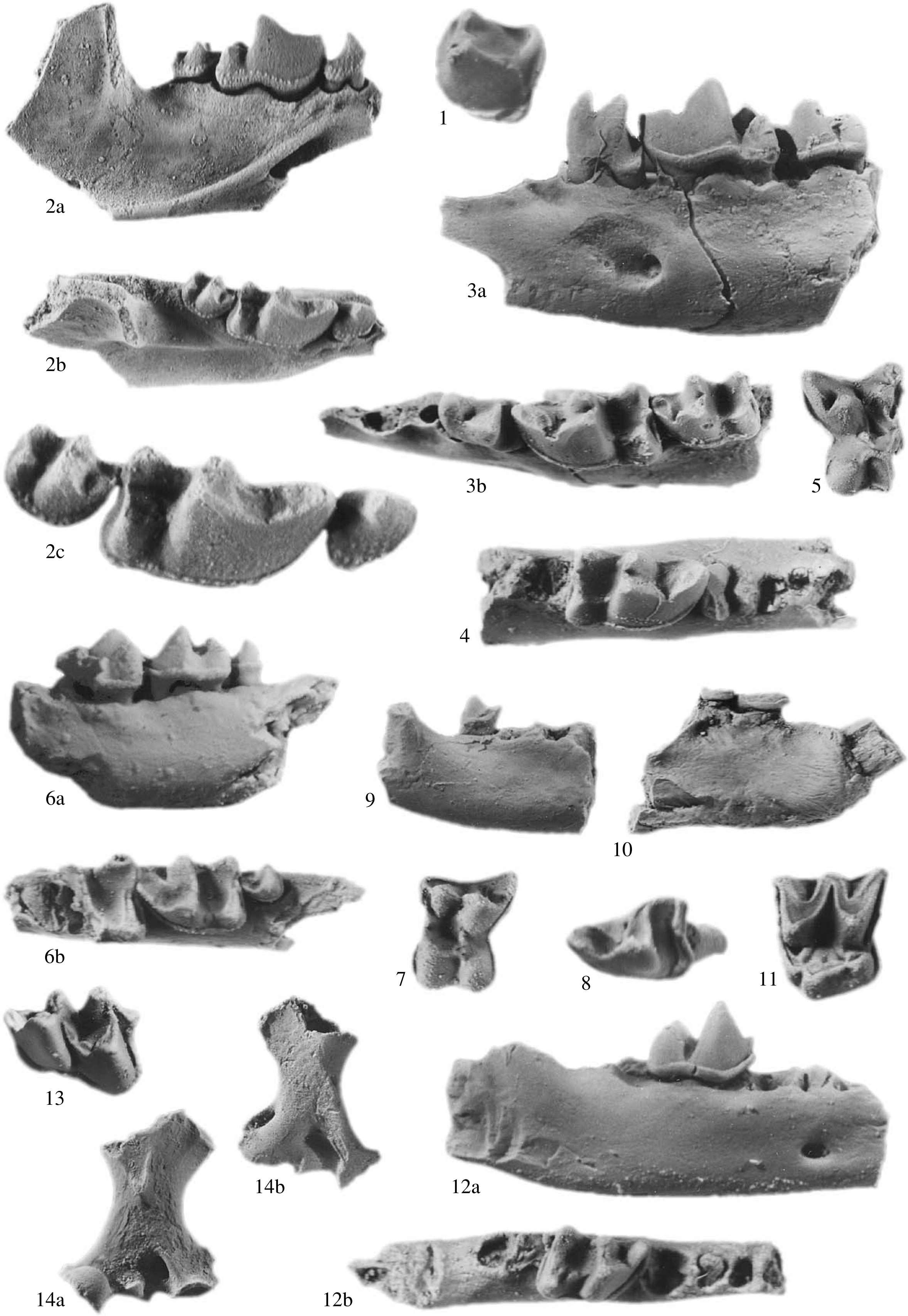
Fig. 11. *Desmanella compacta* sp. nov., holotype PIUZ, ALT no. 304, left M^2, ×15; Altynshokysu, Bone Bed 2.

Fig. 12. *Pseudoparatalpa lavrovi* (Bendukidze, 1993), specimen PIN, no. 4516/188, right dentary fragment with M_2 and the alveoli of P_4, M_1 and M_3: (12a) labial and (12b) occlusal views, ×7.5; Altynshokysu, Bone Bed 4.

Fig. 13. *Myxomygale asiaprima* sp. nov., holotype PIN, no. 4516/48, left M_1, ×15; Altynshokysu, Bone Bed 1.

Fig. 14. *Hugueneya* sp., specimen PIN, no. 4516/191, right humerus: (14a) frontal and (14b) rear view, ×3; Altynshokysu, Bone Bed 4.

Plate 1



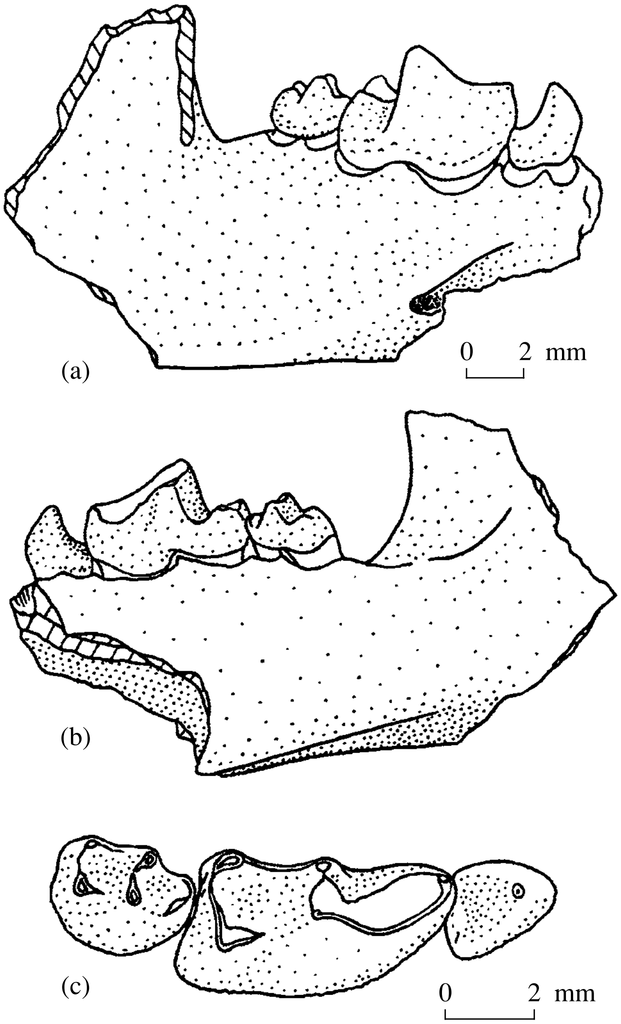


Fig. 6. *Exallerix efialtes* Lopatin, 1996, holotype PIN, no. 4516/1, right dentary fragment with P_4–M_2: (a) labial view, (b) lingual view, and (c) P_4–M_2, lingual view.

The protoconid is large and stout. The paracristid is well-pronounced. The metaconid is small but clearly pronounced and has a separate apex. The protocristid is transversely positioned. The lingual edge of the posterior wall base of the metaconid has a small prominence. The precingulid is well-developed, broad, and strongly projects anterolabially. The talonid is not preserved.

Measurements in mm. Trigonid length of P_4, 1.2; trigonid width, 1.05 (PIN, no. 4516/612).

Comparison and remarks. The stout trigonid and the low and long paraconid suggest that the P_4 fragment examined belongs to a member of the tribe Galericini. Within this tribe, a well-developed metaconid of P_4 is only known in Oligocene–Miocene *Galerix* and Miocene (MN5–MN13) *Schizogalerix* (Hoek Ostende, 2001e), while a long protocristid is characteristic of *Galerix* rather than *Schizogalerix*. Two M_1 that were referred by Bendukidze (1993, p. 7, pl. I, figs. 1, 2) to *Lantanotherium* sp. apparently belong to the same form, i.e., *Galerix* sp. At the same time, Lucas *et al.* (1998, p. 329) tentatively assigned these teeth to *Amphechinus*. However, it is impossible to agree with this identification, since they are extremely low-crowned, which is atypical for the Erinaceinae but is often observed in the Galericinae (see, e.g., Webb, 1961; Rabeder, 1973; Hoek Ostende, 2001c; etc.).

Material. Fragmentary P_4 (PIN, no. 4516/612) from Bone Bed 2 of the Aral Formation of the Altynshokysu locality.

Subfamily Brachyericinae Butler, 1948

Genus *Exallerix* McKenna et Holton, 1967

Exallerix efialtes Lopatin, 1996

Plate 1, figs. 2a–2c

Exallerix efialtes: Lopatin, 1996, p. 73, pl. I, fig. 6, text-fig. 3; Lopatin and Zazhigin, 2003, p. 65, text-figs. 1c, 1d, and 2c.

Holotype. PIN, no. 4516/1, right dentary fragment with P_4–M_2; Kazakhstan, North Aral Region, Altynshokysu locality; Lower Miocene, Aral Formation, Bone Bed 4.

Description (Fig. 6). The horizontal ramus of the lower jaw is very short and positioned at a right angle to the coronoid process. The masseteric fossa is very deep, and the masseteric crest is well-developed and broad, with its anterior edge located under P_4. The mental foramen is large and funnel-shaped and located under the anterior part of M_1. The alveolus of the anterior incisor is very long and extends to the posterior edge of M_1 (Fig. 6b).

The root of P_3 with its pulp cavity and complete and weakly worn P_4, M_1, and M_2 are preserved in the tooth row. P_4 is double-rooted. Its crown is strongly reduced—2.75 times shorter than that of M_1—and lacks the paraconid and metaconid. P_4 is slightly higher than the paraconid of M_1.

M_1 is large and has a shearing bladelike paralophid. The metaconid is reduced and substantially smaller and lower than the protoconid. Its apex is slightly displaced anteriorly relative to the apex of the protoconid and separated from it by a very small valley. The talonid is short and relatively high and has a well-developed hypoconid and entoconid.

M_2 is reduced—almost half as long as M_1. The trigonid is slightly longer than the talonid. The paraconid is flattened. The protoconid is the most massive cusp of the tooth. The metaconid is somewhat smaller than the protoconid; however, they are almost equal in height. The hypoconid and entoconid are relatively small and low.

P_4 and both molars have a labial cingulum with a clear relief composed of small round tubercles arranged in one longitudinal row.

Measurements in mm. Holotype: length of P_4–M_2, 10.5; distance from M_2 to the anterior edge of the coronoid process, 1.75; depth of the horizontal ramus on the labial side: under M_1, 6.1; and under M_2, 7.5; P_4: length, 2.0; width, 2.0; and protoconid height,

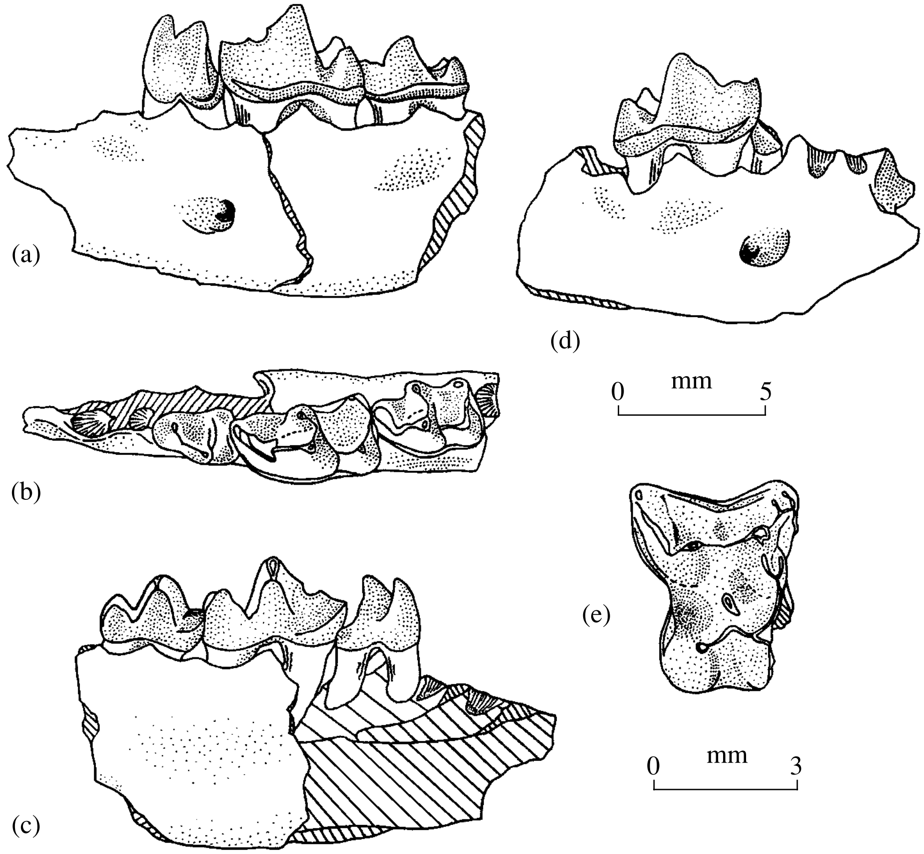


Fig. 7. *Amphechinus akespensis* Lopatin, 1999: (a–c) holotype PIN, no. 210/735, left dentary fragment with P_4–M_2: (a) labial, (b) occlusal, and (c) lingual views; (d) specimen PIN, no. 210/736, right dentary fragment with M_1; and (e) specimen PIN, no. 210/774, right M^1.

2.5; M_1: total length, 5.7; trigonid length, 4.0; lingual length of the talonid, 1.5; labial length of the talonid, 1.7; trigonid width, 2.8; talonid width, 1.7; and protoconid height, 3.75; and M_2: total length, 3.0; trigonid length, 2.0; trigonid width, 2.25; talonid width, 1.8; and protoconid height, 2.25.

Comparison. *Exallerix efialtes* differs from the type species *E. hsandagolensis* McKenna et Holton, 1967 from the Lower Oligocene of Mongolia in its smaller P_4 and larger M_1 (in *E. hsandagolensis*, P_4 is only half as long as M_1), narrow trigonid, shearing paralophid and more strongly reduced metaconid and talonid of M_1, and more massive masseteric crest of the lower jaw. It differs from *E. manahan* Lopatin et Zazhigin, 2003 from the Lower Oligocene of Mongolia and *E. gaolanshanensis* (Qiu et Gu, 1988) from the Upper Oligocene of northern China in its smaller dimensions, well-developed P_3, narrower trigonid and more strongly reduced talonid of M_1, smaller M_2, presence of well-pronounced enamel relief on the labial surface of the lower cheek teeth, and almost vertical angular process of the lower jaw.

Remarks. *E. gaolanshanensis* was originally assigned to a special genus, *Metexallerix* Qiu et Gu, 1988 (Qiu and Gu, 1988). Later, *M. junggarensis* Bi, 1999 from the Lower Miocene of China was also included in this genus (Bi, 1999). To date, the first species is transferred to the genus *Exallerix*, while the second is considered the type species of the Early Miocene genus *Synexallerix* Lopatin et Zazhigin, 2003, which also includes *S. otus* Lopatin et Zazhigin, 2003 from eastern Kazakhstan and *Synexallerix* sp. from MN4a of Germany (Lopatin and Zazhigin, 2003).

Material. Holotype.

Subfamily Erinaceinae Fischer von Waldheim, 1817

Tribe Amphechinini Gureev, 1979

Genus *Amphechinus* Aymard, 1850

Amphechinus akespensis Lopatin, 1999

Plate 1, figs. 3–5

Amphechinus akespensis: Lopatin, 1999a, p. 68, text-fig. 2.

Holotype. PIN, no. 210/735, left dentary fragment with P_4–M_2; Kazakhstan, North Aral Region, Akespe locality; Lower Miocene, Aral Formation.

Description (Fig. 7). A large member of the genus; the P_4–M_2 row is 10.5 mm long. M^1 is trapezoid, and the labial and posterior walls of the crown are concave. The metastyle strongly projects posterolabially. The cingula are developed on the anterior, labial, and posterior sides. The ectocingulum is narrow and extends from the parastyle to the metastyle. The postcingulum is relatively wide, becoming especially broad posterior to the lingual lobe. The apices of the main cusps are pointed. The metacone is higher and somewhat more massive than the paracone. The lingual wall of the paracone is flattened. The apices of the posterior cusps are located substantially more lingually than the apices of the anterior cusps. The parastyle is small. The paracrista is short and low and has a small posterolabial arm in the middle. The anterior wing of the centrocrista is distinctly developed. The postmetacrista is long, high, massive, and abruptly curved at the posterior base of the metacone. The paraconule is relatively small. The preparaconule crest is connected to the anterior side of the paracone, while the postparaconule crest is fused with the lingual wall of this cusp. The preprotocrista terminates short of reaching the paraconule. The postprotocrista is connected to a short and narrow crest that extends from the base of the hypocone. Slightly labial to the point of their fusion, there is an isolated small metaconule, which extends in a teardrop shape. A deep oval valley is located between the metaconule and the paracone.

The horizontal ramus of the lower jaw is high and relatively thin. The large mental foramen is located in line with the posterior root of P_4. Judging from the alveoli, the canine was substantially larger than P_2. The cingulids of P_4 are weakly developed on the labial and posterior sides of the crown and absent from the anterior and lingual sides. The paraconid is slightly higher than the protoconid. The apex of the protoconid slightly curves posteriorly. The metaconid is small, fused at the base with the posterolingual part of the protoconid, and looks like a relatively large protrusion with a vertical posterior wall and an absent apex. The talonid is short and at least as wide as the trigonid.

M_1 is large, and its ectocingulid and postcingulid are well-developed. The paralophid is strongly shifted anteriorly. The metaconid is approximately half as long as and noticeably lower than the protoconid and is somewhat displaced anteriorly with reference to its apex. The metastylid is weak and shaped into a small prominence. The entoconid is higher than the hypoconid and slightly shifted anteriorly relative to this cusp. The protocristid and postcristid curve posteriorly, while the entocristid and cristid oblique are positioned almost in parallel to the longitudinal tooth axis.

M_2 is almost 1.4 times as short as M_1. It is similar to M_1 in structure and differs in the less pronounced size difference between the protoconid and metaconid and between the entoconid and hypoconid. The trigonid and talonid of M_2 are also closer in length than those of M_1. One alveolus of M_3 is preserved.

Measurements in mm. Holotype (length × width): P_4, 2.8 × 1.8; M_1, 4.8 × 2.3; and M_2, 3.5 × 2.0; depth of the horizontal ramus under M_1, 6.5. M^1 (PIN, no. 210/774), 3.5 × 4.4; and M_1 (PIN, no. 210/736), 4.7 × 2.3.

Comparison. *A. akespensis* differs from the European *A. arvernensis* (Blainville, 1839), *A. edwardsi* (Filhol, 1879), and *A. ginsburgi* Baudelot, 1972; the North American *A. horncloudi* (Macdonald, 1970); and the Asian *A. kansuensis* (Bohlin, 1942), *A. minimus* (Bohlin, 1942), *A. microdus* Lopatin, 1999, and *A. bohlini* Bi, 2000 in its higher paraconid compared to the protoconid of P_4. It differs from the European *A. intermedius* (Gaillard, 1899) and *A. robustus* (Lavocat, 1951) in its substantially smaller dimensions. *A. akespensis* is substantially larger than *A. kansuensis*, *A. minimus, A. microdus*, and *A. bohlini* (see Lopatin, 2002b). It differs from the largest Asian species of the genus *Amphechinus, A. gigas* Lopatin, 2002 from the Oligocene of Mongolia, in its smaller dimensions, better developed metaconid of P_4, and certain structural details of the lower molars, i.e., a distinct postcingulid on M_1 and M_2 and the presence of the metastylid on M_1. It differs from *A. kreuzae* Munthe et West, 1980 from the Miocene of Pakistan in the broader M^1 (see Munthe and West, 1980, text-fig. 3B). *A. akespensis* is especially similar in dental structure and size to *A. rectus* (Matthew et Granger, 1924) from the Oligocene of central Asia and differs from this species in its larger P_4 with a reduced metaconid, somewhat longer but less massive (relatively narrower) molars, and relatively thinner horizontal lower jaw ramus.

Material. In addition to the holotype, a lower jaw fragment with M_1 (PIN, no. 210/736) and isolated M^1 (PIN, no. 210/774) from the type locality.

***Amphechinus microdus* Lopatin, 1999**

Plate 1, figs. 6–8

Amphechinus minimus: Bendukidze, 1993, p. 10, pl. II, figs. 1–4.

Amphechinus microdus: Lopatin, 1999a, p. 70, text-fig. 3.

Holotype. PIN, no. 4516/7, left dentary fragment with the talonid of M_1 and complete M_2 and M_3; Kazakhstan, North Aral Region, Altynshokysu locality; Lower Miocene, Aral Formation, Bone Bed 4.

Description (Fig. 8). A small member of the genus. The M_1–M_3 row is approximately 4 mm long. The metastyle of M^1 projects considerably. The cingula are narrow and stretch along the entire anterior, posterior, and labial sides. Each main cusp has a pointed apex. The metacone is higher and more massive than the paracone and is substantially displaced lingually relative to this cusp. The hypocone is substantially lower than the protocone. The parastyle is relatively small, and the paracrista is short. The postmetacrista is long. The paraconule is ridgelike, located at the anterior margin of the occlusal surface, and connected to the preprotocrista. The relatively long postprotocrista is connected to the base of the metacone. A small eminence that corresponds to the metaconule is located approximately in the middle of this crest. The hypocone

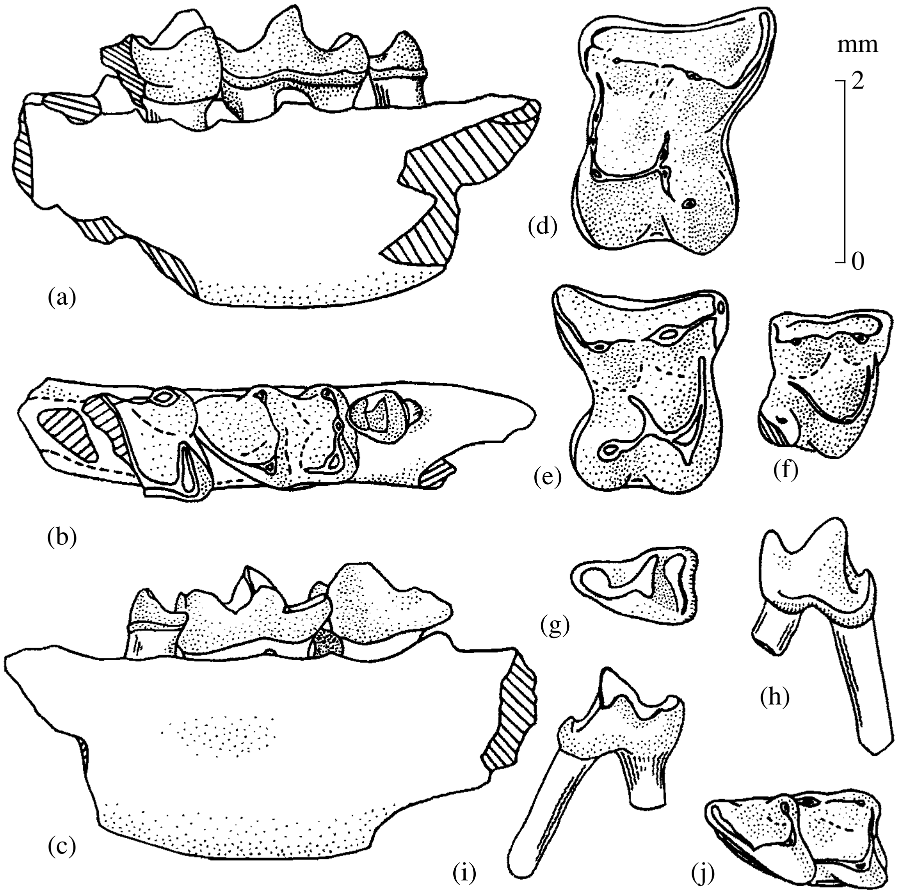


Fig. 8. *Amphechinus microdus* Lopatin, 1999 from the Aral Formation of the Altynshokysu locality: (a–c) holotype PIN, no. 4516/7, left dentary fragment with M_1–M_3: (a) labial, (b) occlusal, and (c) lingual views; Bone Bed 4; (d) specimen PIN, no. 4516/189, left M^1; Bone Bed 1; (e) specimen PIN, no. 4516/467, right M^1; Bone Bed 4; (f) specimen PIN, no. 4516/475, right M^2; Bone Bed 1; (g–i) specimen IAUU, ALT no. 136, left P_4: (g) occlusal, (h) labial, and (i) lingual views; Bone Bed 2; and (j) specimen PIN, no. 4516/66, left M_1; Bone Bed 1.

is connected to the base of this eminence by a short crest. As the tooth becomes worn, the paraconule and metaconule disappear, while the preprotocrista and the postprotocrista expand and become flattened.

M^2 is substantially smaller than M^1. The parastyle substantially projects anterolabially. The structure of the occlusal surface is similar to that of M^1; however, it differs in its less developed metastyle, reduced paraconule, absence of metaconule, isolated position of the hypocone, and short postprotocrista, which terminates short of the metacone.

M^3 is extremely small, at most one-third as long and half as narrow as M^2. The crown is oval in occlusal view. The small parastyle is anteriorly connected to the well-developed precingulum; lingually, it is connected to a small paracone, which is linked by the medial crest to a massive protocone. The postcingulum is distinct posterior to the paracone only. The smaller labial root and larger lingual root are fused at the base.

The horizontal ramus of the lower jaw is relatively deep. I_3 is small, oval in occlusal view, and has a low main cusp and a well-developed posterior cuspule. The shape of C_1 is typical of the Erinaceinae: it is flaglike and has a small posterior cuspule.

P_4 is relatively small. The protoconid is substantially higher than the paraconid and metaconid. The metaconid fuses with the protoconid from the base to the apex. The paralophid and protocristid are long. The talonid is short. The ectocingulid is well-pronounced and the postcingulid is well-developed (Figs. 8g–8i).

M_1 is approximately 1.2 times as long as M_2. The ectocingulid and postcingulid are well-developed. The postcingulid reaches the level of the middle of the postcristid. The trigonid is substantially longer than the talonid, and the paraconid strongly projects anteriorly. In an unworn tooth, the paralophid has a clear notch. The metaconid is displaced anteriorly relative to the protoconid. The protocristid curves posteriorly. The metastylid is small. The protoconid is higher than the metaconid, and the entoconid is substantially higher than the hypoconid. The entocristid is low. The cristid oblique is connected to the labial side of the base of the proto-

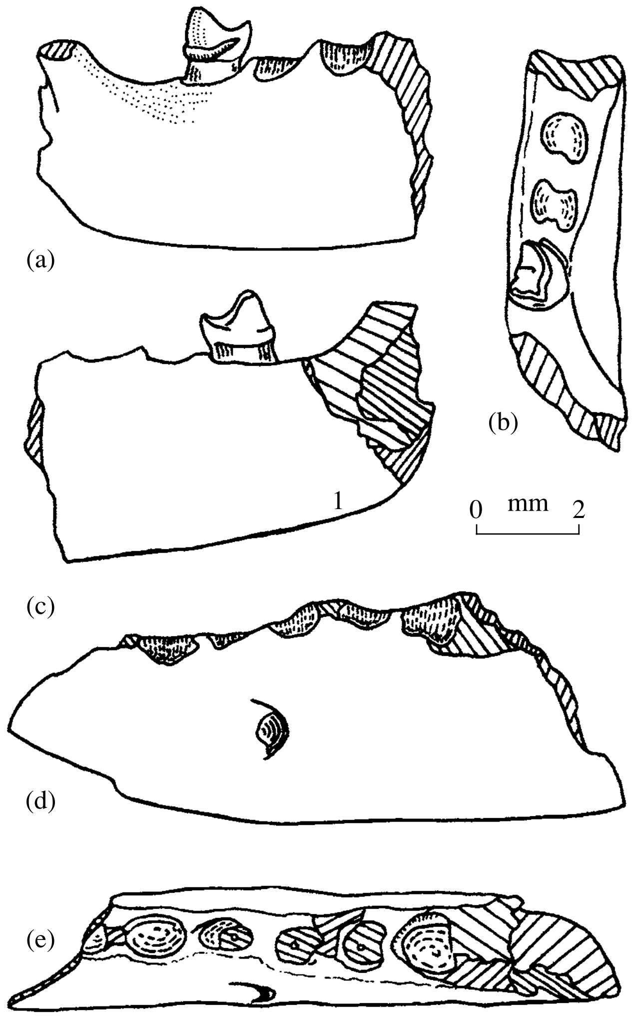


Fig. 9. *Amphechinus* sp.: (a–c) specimen PIN, no. 210/737, right dentary fragment with M_3: (a) labial, (b) occlusal, and (c) lingual views; (d, e) specimen PIN, no. 210/265, left dentary fragment with alveoli of I_2–M_1: (d) labial and (e) occlusal views; Akespe locality, Aral Formation.

conid. The postcristid is almost straight. M_2 is similar to M_1, but differs in its shorter trigonid.

M_3 is strongly reduced (40% of the M_2 length), single-rooted, and displaced to the lingual side of the tooth row. Its crown is rounded, triangular, and lacks a talonid. The paraconid extends anteriorly. The protoconid and metaconid are fused. The crown base is labially and posteriorly bordered by a distinct cingulid.

Measurements in mm. Holotype (length × width): M_2, 1.75 × 1.15; M_3, 0.7 × 0.55; talonid width of M_1, 1.3; depth of the horizontal ramus under M_1, 2.25. Isolated teeth (length × width): M^1 (PIN, no. 4516/189), 2.05 × 2.35; M^1 (PIN, no. 4516/467), 2.15 × 2.8; M^2 (PIN, no. 4516/475), 1.4 × 1.75; M^3 (PIUZ, ALT no. 300), 0.4 × 0.85; P_4 (IAUU, ALT no. 136), 1.4 × 0.95; M_1 (PIN, no. 4516/66), 2.1 × 1.15; M_1 (PIN, no. 4516/474), 2.1 × 1.3; M_2 (PIN, no. 4516/114), 1.8 × 1.15; and M_3 (PIN, no. 4516/609), 0.9 × 0.7.

Comparison. The species described differs from *A. minimus* in the relatively high horizontal ramus of the lower jaw and much more reduced M_3 (in *A. minimus*, M_3 is 50–55% as long as M_2). It differs from other species in the extremely small dimensions of the lower jaw and teeth.

Remarks. Rich and Rasmussen (1973, p. 32) proposed that small Oligocene Amphechinini from central Asia, i.e., *Amphechinus minimus* from the Upper Oligocene of China (Bohlin, 1942) and *A.* cf. *minimus* from the Lower Oligocene of Mongolia (Sulimski, 1970), belong to the North American Miocene genus *Parvericius* Koerner, 1940 and the species *P. montanus* Koerner, 1940; however, in my opinion, this is an unjustified assumption, since M_1 of Asian taxa has a longer trigonid.

Occurrence. North Aral Region; Lower Miocene, Aral Formation.

Material. In addition to the holotype, the PIN collection includes isolated M^1 (no. 4516/189) from Bone Bed 4 and isolated teeth from Bone Bed 1 of the Altynshokysu locality: M^1 (no. 4516/467), M^2 (no. 4516/475), I_3 (no. 4516/608), two M_1 (nos. 4516/66 and 474), M_2 (no. 4516/116), and M_3 (no. 4516/609). Three M^1, M^2, M^3, three I_3, C_1, three M_1, and M_3 are housed at the PIUZ; a fragment of P^4 and C_1 belong to DK; and fragments of M^1, M^2, and two P_4 are housed at the IAUU. These specimens come from Bone Bed 2 of Altynshokysu.

Amphechinus sp.

Plate 1, figs. 9 and 10

Description (Fig. 9). A medium-sized member of the genus. M^1 is trapezoid, and its labial side is substantially longer than its lingual side. The cingula are well-developed on the anterior, posterior, and labial sides of the crown. The entocingulum is well-pronounced between the protocone and the hypocone. The main cusps are stout, and the metacone and hypocone are more lingually positioned than the paracone and protocone, respectively. The parastyle is small, and the metastyle projects slightly posterolabially. The conules are well-developed. The crests of the postmetacrista, preprotocrista, and postprotocrista are more massive than the crests of the paracrista and centrocrista. The hypocone is connected by a small crest to the postprotocrista.

M^2 is substantially smaller than M^1 and differs from it in its asymmetrical shape (the parastyle projects strongly anterolabially) and complete absence of the entocingulum.

The horizontal ramus of the lower jaw is relatively low. The large mental foramen is on a level with the anterior root of P_4. I_2 is large, procumbent, and transversely compressed. The alveolus of I_3 is small and separated from I_2 by a small space. C_1 is relatively large and extended. Anteriorly, the crown of C_1 overlaps the alveolus of I_3. P_2 is small, substantially shorter than C_1, and round in occlusal view; its anterior edge is sharp, while the posterior side has a small cuspule.

P_4–M_2 are not preserves. The occlusal surface of M_3 is subtriangular in outline. The tooth is single-rooted and has a well-developed basal cingulid on the labial and posterior sides of the crown. The talonid is absent. The paraconid region is extensive. The protoconid and metaconid are positioned close to one another, and the protocristid slightly curves posteriorly. The protoconid is somewhat more massive and higher than the metaconid.

Measurements in mm. Upper teeth (length × width): M^1, 3.1 × 3.6; M^2, 2.0 × 2.4; lower teeth: I_2 (diameters at the base), 2.1 × 1.2; C_1 (length × width), 1.8 × 1.0, P_2, 1.25 × 0.9 (PIN, no. 4516/607), M_3, 1.35 × 0.95 (PIN, no. 210/737); length of the alveolus of C_1, 1.4; P_2, 0.65; length of P_4 along the alveoli, 2.0 (PIN, no. 210/265); length of M_2 along the alveoli, 2.8 (PIN, no. 210/737); and the depth of the horizontal ramus of the lower jaw: under P_4, 4.2 (PIN, no. 210/265); under M_2, 3.6; and under M_3, 3.25 (PIN, no. 210/737).

Comparison and remarks. The single-rooted M_3 lacking a talonid and the dental formula of the species described (three single-rooted teeth between I_2 and P_4) suggest that it belongs to the genus *Amphechinus*. Bendukidze (1993) described some better preserved specimens of this species (isolated upper molars and a lower jaw fragment with P_4–M_3) as *A.* cf. *rectus*. However, it is impossible to accept this determination, because, in the Oligocene *A. rectus*, the lower jaw and teeth are substantially larger (Trofimov, 1960; Huang, 1984) and M_3 is double-rooted. Orlov (1939) and Borissiak and Beliajeva (1948) registered *?Palaeoscaptor acridens* Matthew et Granger, 1924 in the Akespe locality; however, Trofimov (1960) noted that the specimens were subsequently lost. I have found a specimen of *Amphechinus* sp. in the material collected in Akespe in 1938. According to its label, it was preliminary identified as *?Palaeoscaptor acridens*. It is not improbable that the *Amphechinus* sp. discussed is conspecific to the *?Palaeoscaptor acridens* mentioned in those early studies. This species is substantially smaller than *A. gigas*, *A. rectus*, *A. akespensis*, *A. ginsburgi*, *A. intermedius*, and *A. robustus* and much larger than *A. minimus* and *A. microdus*. However, it is impossible to establish a new species, because the specimens are poorly preserved and lack the characters needed for comparison with species of approximately the same size, such as *A. kansuensis* and *A. bohlini*.

Material. A fragmentary dentary with M_3 and the alveoli of M_2 (PIN, no. 210/737) and a fragmentary dentary with alveoli of I_2–M_1 (PIN, no. 210/265) from Akespe; isolated M^1 and M^2 from Bone Bed 2 (collection DK); and fragmentary dentary with a broken I_2, alveolus of I_3, and worn C_1 and P_2 (PIN, no. 4516/607) from Bone Bed 4 of Altynshokysu.

Family Talpidae Fischer von Waldheim, 1817

Subfamily Uropsilinae Dobson, 1883

Genus *Desmanella* Engesser, 1972

Desmanella compacta Lopatin, sp. nov.

Plate 1, fig. 11

Astenoscapter (sic!) sp.: Bendukidze, 1993, p. 19, pl. V, figs. 3 and 4.

Desmanella sp.: Lopatin, 1999a, p. 66.

Etymology. From the Latin *compactus* (dense, strong, compact).

Holotype. PIUZ, ALT no. 304, left M^2; Kazakhstan, North Aral Region, Altynshokysu locality; Lower Miocene, Aral Formation, Bone Bed 2.

Description (Fig. 10). A small member of the genus. M^2 is trapezoid, the width slightly exceeds the length, the labial side is longer than the lingual side. The styles are small and only slightly project externally; the labial side slightly curves between them. The posterior side is weakly concave. The crests connecting the labial elements of the occlusal surface (i.e., cusps and styles) form a W-shaped pattern. Narrow precingulum and postcingulum are present. The precingulum is connected to the paraconule, which is connected to a massive protocone by a short preprotocrista. The wide postprotocrista connects the protocone to the well-developed metaconule. Lingually, the paraconule, protocone, and metaconule are separated from each other by small folds.

In M_2, the apices of labial cusps are strongly inclined lingually. The cingulids on the labial and posterior sides of the crown are well-developed, and the postcingulid ascends to a small entostylid. The hypo-

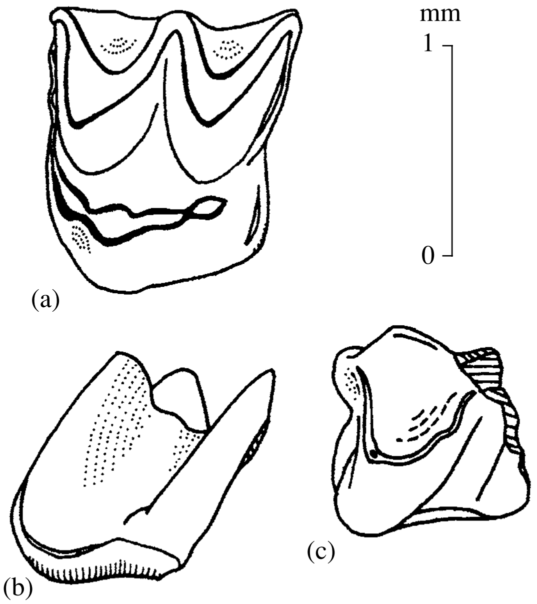


Fig. 10. *Desmanella compacta* sp. nov.: (a) holotype PIUZ, ALT no. 304, left M^2; (b, c) specimen IAUU, ALT no. 137, fragmentary right M_2: (b) labial view and (c) occlusal view.

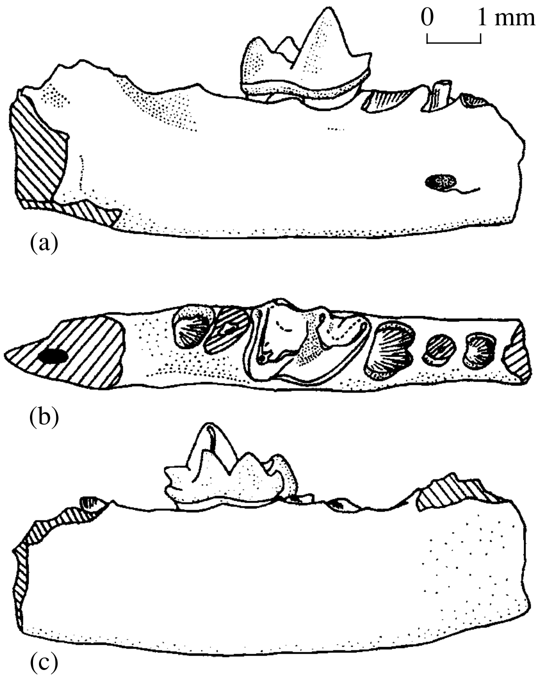


Fig. 11. *Pseudoparatalpa lavrovi* (Bendukidze, 1993), specimen PIN, no. 4516/188, right dentary fragment with M_2: (a) labial view, (b) occlusal view, and (c) lingual view; Altynshokysu locality, Aral Formation, Bone Bed 4.

flexid is very deep. The entoconid is relatively low and has a weak crenulation on the labial side. The entocristid is short, and the talonid notch is deep. The well-pronounced cristid oblique has an eminence in the middle part and extends to the metaconid base. The arms of the postcristid come into contact on the entostylid.

Measurements in mm. Holotype: M^2 (length × width), 1.22 × 1.40; width of M_2 (IAUU, ALT no. 137), 0.85.

Comparison and remarks. The specimens described undoubtedly belong to the genus *Desmanella*. This is evident from the structural features of the lingual elements of the occlusal surface of M^2 (see Hoek Ostende, 1989) and the structure of the talonid of M_2.

D. compacta sp. nov. is one of the smallest species of the genus, which is considerably smaller than the Miocene *D. stehlini* Engesser, 1972, *D. crusafonti* Rümke, 1974, *D. dubia* Rümke, 1976, *D. sickenbergi* Engesser, 1980, *D. cingulata* Engesser, 1980, *D. amasyae* Engesser, 1980, *D. storchi* Qiu, 1996, and *D. rietscheli* Storch et Dahlman, 2000 and the Pliocene *D. gardiolensis* Crochet, 1986. The new species is comparable in size to *D. fejfari* Gibert, 1975 (Spain) and *D. engesseri* Ziegler, 1985 (MN3b–MN4a, Germany) and certain earlier forms from Germany, which were discovered in Ulm-Westtangente, MN2a (Ziegler, 1990); Eggingen-Mittelhart 2, MP30/MN1 (Hoek Ostende, 1989); and Herrlingen 8 and 9, MP28 and MP29, respectively (Ziegler, 1998), and determined as different *Desmanella* n. sp. However, the new species differs from these forms in its outline and proportions of M^2 (the tooth is less expanded transversely and less concave on the labial, lingual, and posterior sides).

The genus *Desmanella* was widespread in Europe and western Asia from the Late Oligocene (MP28–MP30) to the Late Miocene (*D. gardiolensis* survived in the Balearic Islands up to the middle of the Pliocene, MN16) (Engesser, 1980; Jong, 1988; Hoek Ostende, 1989; Ziegler, 1990, 1998; Storch and Dahlman, 2000). One species (*D. storchi*) has been described from the Middle Miocene of China (Qiu, 1996). In the Zaisan Depression (eastern Kazakhstan), *Desmanella* sp. and cf. *Desmanella* were registered in the Early Oligocene Buran Fauna and the Early Miocene Akzhar Fauna (ca. MN4), respectively (Gabunia and Gabunia, 1987; Shevyreva, 1995; Gabunia and Chkhikvadze, 1997).

Judging from the measurements and the structure of M_2, the specimens described by Bendukidze (1993) as *Asthenoscapter* sp. from Altynshokysu are conspecific to *Desmanella compacta* sp. nov.

Occurrence. North Aral Region; Lower Miocene, Aral Formation.

Material. In addition to the holotype, one fragmentary M_2 (IAUU, ALT no. 137) from the type locality.

Subfamily Talpinae Fischer von Waldheim, 1817

Tribe Urotrichini Dobson, 1883

Genus *Pseudoparatalpa* Lopatin, 1999

Pseudoparatalpa lavrovi (Bendukidze, 1993)

Plate 1, figs. 12a and 12b

Migalea (sic!) *lavrovi*: Bendukidze, 1993, p. 11, pl. II, fig. 5, pl. III, figs. 1 and 2.

Pseudoparatalpa lavrovi: Lopatin, 1999a, p. 72, text-fig. 5.

Holotype. IP, no. 9/7, left dentary fragment; Kazakhstan, northwest area of the Aral Region, Sayaken locality; Lower Miocene, Aral Formation.

Description (Fig. 11). The horizontal ramus of the lower jaw is relatively low. The mental foramen is level with the anterior root of M_1 and displaced to the lower edge of the horizontal jaw ramus. The alveoli of double-rooted P_4, M_1, and M_3 and complete M_2 are preserved. M_1 is substantially smaller than M_2, while M_3 is smaller than M_1. M_2 has a well-developed ectocingulid that extends to the level of the anterior part of the hypoconid. The postcingulid reaches the entostylid. The paraconid is low. The paracristid has a deep notch. The trigonid basin is open lingually. The protoconid is substantially higher and more massive than the metaconid. The protocristid is short. The talonid is substantially wider than the trigonid. The metacristid is absent, while the entocristid is well-developed. The talonid notch is small and positioned close to the base of the metaconid. The hypoflexid is relatively small. The cristid oblique extends to the lingual part of the posterior base of the protoconid. The entoconid is substantially higher than the hypoconid. The entostylid is relatively small.

Measurements in mm. Teeth: M_2 (length × width), 2.4 × 1.6; length along the alveoli: M_1, 2.0; M_3, 1.6. Depth of the lower jaw under M_1, 2.5; under M_2, 2.8; and under M_3, 3.05.

Comparison. The species described differs from *P. shevyrevae* Lopatin, 1999 from the Oligocene of Kazakhstan in the better developed cingulid of the lower molars and in the lower horizontal ramus of the mandible.

Remarks. Ziegler (2003) has suggested without sufficient substantiation to regard the genus *Pseudoparatalpa* as a synonym for *Paratalpa* Lavocat, 1951. However, characters in the original diagnosis (Lopatin, 1999, p. 71) that distinguish *Pseudoparatalpa* from *Paratalpa* include the presence of a labial cusp on the talonid of P_4, very low cusps of the trigonid of M_1, and a more posterior position of the posterior mental foramen. These characters are clear evidence that *Paratalpa* and *Pseudoparatalpa* display different evolutionary trends, and the latter should be ranked as a separate genus.

Occurrence. North Aral Region; Lower Miocene, Aral Formation.

Material. A fragmentary dentary with M_2 and the alveoli of P_4, M_1, and M_3 (PIN, no. 4516/188) from Bone Bed 4 of the Aral Formation of the Altynshokysu locality.

Tribe Scaptonychini Van Valen, 1967

Genus *Myxomygale* Filhol, 1890

Myxomygale asiaprima Lopatin, sp. nov.

Plate 1, fig. 13

Myxomygale sp.: Lopatin, 1999a, p. 66; 2002c, p. 91.

Etymology. From the Latin *asiaticus* (Asian) and *primus* (first).

Holotype. PIN, no. 4516/48, left M_1; Kazakhstan, North Aral Region, Altynshokysu locality; Lower Miocene, Aral Formation, Bone Bed 1.

Description (Fig. 12). The preserved fragments of M^1 display a stout lingual root, a strongly projecting parastyle, anterolingually oriented paracone and metacone, and well-developed lingual cuspules of the paraconule, protocone, and metaconule. The lingual lobe is relatively long. The precingulum is present. The metaconule is weakly differentiated. The lingual cuspules are connected to each other by a common bead-like wear surface with expansions at the cusps and constrictions at the crests. The paraconule and protocone are positioned close together (the preprotocrista is reduced), the protocone and metaconule are connected by a wide postprotocrista, and a narrow postcingulum deviates from the metaconule and extends posterolabially.

M_1 is relatively low; its trigonid is narrow, while the talonid is broad. The paraconid is very low. The paracristid slightly curves. The trigonid basin extends strongly longitudinally. The protoconid is somewhat larger than the metaconid. These cusps are positioned close together, have rounded triangular wear facets, and are connected by a very short protocristid. The talonid is substantially wider than the trigonid. The hypoconid is strongly displaced posteriorly, relative to the entoconid, and its posterolabial side is angular. The stout and slightly labially curved cristid oblique reaches the trigonid at the point of fusion between the protoconid and the metaconid at a level with the middle of the protocristid. Its anterior end ascends along the posterior wall of the trigonid and closely approaches the protocristid. The entoconid is relatively small and extends

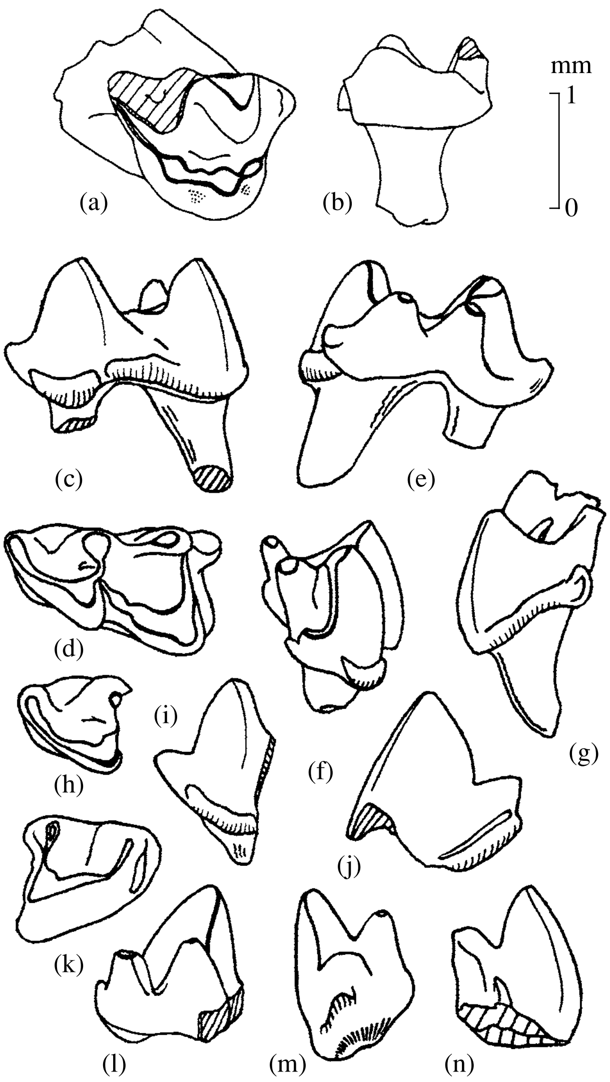


Fig. 12. *Myxomygale asiaprima* sp. nov.: (a) specimen IAUU, ALT no. 138, fragmentary right maxilla with M^1; (b) specimen NMW, no. 1994/00271/0001/2, fragmentary left M^1, lingual view; Bone Bed 2; (c–g) holotype PIN, no. 4516/48, left M_1: (c) labial, (d) occlusal, (e) lingual, (f) frontal, and (g) rear views; (h, i) specimen PIN, no. 4516/50, fragmentary left M_1: (h) occlusal and (i) labial views; (j–n) specimen PIN, no. 4516/476, fragmentary right M_2: (j) labial, (k) occlusal, (l) lingual, (m) frontal, and (n) rear views; Bone Bed 1.

longitudinally. The long entocristid deviates from the entoconid and extends anteriorly to adjoin a small metacristid. The talonid notch is weak. The postcristid is long and poorly developed in its lingual part. The talonid basin is rather large and closed. The entostylid is massive and 1.5 times shorter than the entoconid. The precingulid is broad and short, developed only at the level of the anterior part of the protoconid, and terminates short of the level of the paraconid apex. The ectocingulid is weak and extends from the posterolabial base of the protoconid to the level of the hypoconid apex. The postcingulid is stout and reaches the entostylid.

In M_2, the precingulid ascends to the anterior edge of the paraconid base, the paracristid curves lingually, the protoconid is substantially higher than the metaconid and is displaced posteriorly, and the protocristid is relatively long. The anterior end of the cristid oblique ascends along the posterior wall of the metaconid approximately to the midheight of the cusp. In a slightly worn tooth, the notch of the paracristid is well-developed.

Measurements in mm. Length × trigonid width—talonid width of M_1 (PIN, no. 4516/48), 1.95 × 0.85—1.15; trigonid width of M_2 (no. 4516/476), 1.1.

Comparison. The new species differs from *M. antiqua* Filhol, 1890 in the structural details of M_1: the narrow trigonid, low paraconid, weakly curved paracristid, high cristid oblique, and weakly developed precingulid and ectocingulid. From *M. vauclusensis* Crochet, 1995, it differs in its poorly developed precingulid and ectocingulid of M_1. It differs from *M. engesseri* Doukas, 1983, *M. hutchisoni* (Ziegler, 1985), *M. minor* Ziegler, 1990, and *M. gracilis* Ziegler, 2003 in having larger dimensions. In addition, it differs from *M. minor* in the long lingual lobe of M^1, the low paraconid of M_1, and the more lingual position of the cristid oblique of M_2; and from *M. gracilis* Ziegler, 2003, it differs in the presence of the parastyle and the better developed conule. It differs from *M. engesseri* in its better developed metaconule and the presence of the precingulum in M^1.

Remarks. The new species displays such typical characteristics of the genus *Myxomygale* (see Hugueney, 1972) as a curved paracristid with a clear notch, a high cristid oblique, broad talonid, closed talonid basin, presence of the metacristid, massive entostylid, and incomplete ectocingulid. The weakly developed ectocingulid is characteristic of Miocene species of this genus (Doukas, 1986; Ziegler, 1990).

Occurrence. North Aral Region; Lower Miocene, Aral Formation.

Material. In addition to the holotype, fragmentary M_1 (PIN, no. 4516/50) and M_2 (PIN, no. 4516/476) from Bone Bed 1 and a fragmentary maxilla with M^1 (IAUU, ALT no. 138) and fragmentary M^1 (NMW, no. 1994/00271/0001/2) from Bone Bed 2 of the Altynshokysu locality.

Tribe Scalopini Dobson, 1883

Genus *Hugueneya* Hoek Ostende, 1989

Hugueneya sp.

Plate 1, figs. 14a and 14b

Description (Fig. 13). The humerus is short and broad, as is characteristic of the Talpidae, which lead a subterranean mode of life. In specimen PIN, no. 4516/191, the body and the distal epiphysis of the bone are preserved; the epicondyles are broken off (Figs. 13a–13d). The pectoral ridge is short, and its medial portion is strongly developed, while the lateral portion is poorly pronounced. The pectoral tubercle is well-developed and high. The distal end of the pectoral ridge is approximately on a level with the narrowest region of the humerus. The head of the lateral condyle is semispherical, and its articular surface is flattened. The articular surface of the medial condyle faces distally. The circular crest of the trochlea is well-pronounced, wide, and displaced laterally. The supratrochlear fossa is large, deep, and round in shape. Posteriorly, closer to the lateral side, there is a large foramen for an artery. The entepicondylar foramen is large and oval in shape. The posterior surface of the trochlea has a weakly developed relief. The olecranon fossa is extensive and strongly displaced laterally. It contains a well-pronounced foramen.

Specimen PIN, no. 4516/192 is a smaller humerus (Figs. 13e, 13f). The medial edge of the proximal region, pectoral tubercle, trochlea (the circular crest is developed to a much lesser extent than in PIN, no. 4516/191), supratrochlear foramen, and medial condyle are preserved. The medial edge of the teres tubercle curves distally.

Specimen PIN, no. 4516/522 differs from PIN, no. 4516/191 in the less developed pectoral ridge, the larger olecranon fossa, and the small foramen for the artery. The medial part of the teres tubercle is preserved (Figs. 13g–13i).

Measurements in mm. Minimum diaphysial width, 3.7 (PIN, no. 4516/191) and 3.6 (PIN, no. 4516/522); width of the distal region without epicondyles, 8.0 (PIN, no. 4516/191) and 7.8 (PIN, no. 4516/522); distance between the pectoral tubercle and the distal edge of the trochlea, 5.8 (PIN, no. 4516/191), 5.8 (PIN, no. 4516/522), and 4.6 (PIN, no. 4516/192); and distance from the distal edge of the medial end of the teres tubercle to the distal edge of the medial condyle, 7.0 (PIN, no. 4516/522) and 5.5 (PIN, no. 4516/192).

Comparison. The form described differs from *H. primitiva* (Hutchison, 1974) in the larger maximum measurements of the humerus, deeper supratrochlear fossa, extensive olecranon fossa, and better developed pectoral tubercle.

Remarks. The humeri described are similar in structure to that of *Hugueneya* (Upper Oligocene–Lower Miocene of Germany) and *Proscapanus* (Mid-

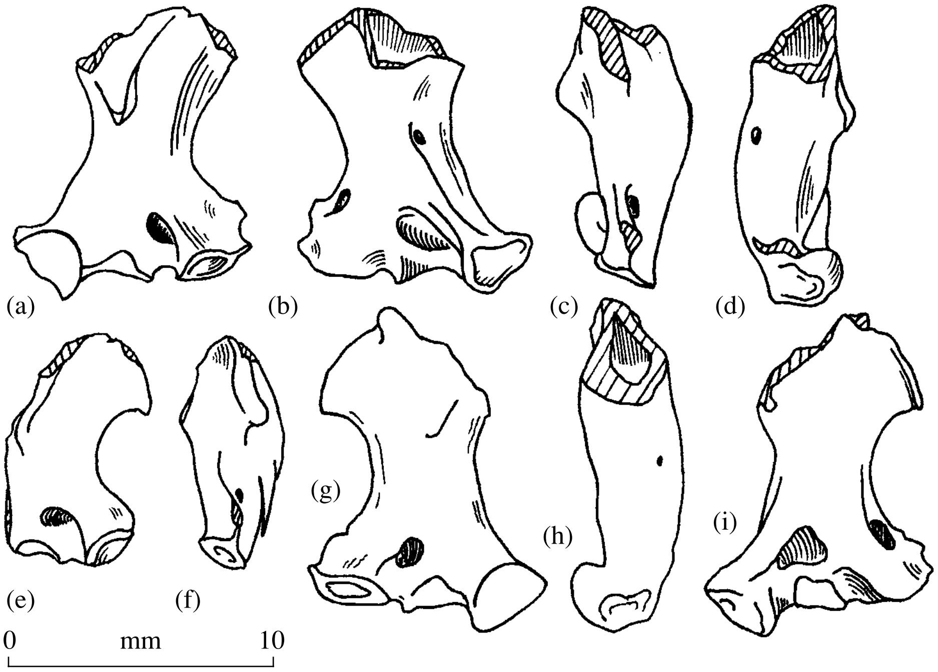


Fig. 13. *Hugueneya* sp.: (a–d) specimen PIN, no. 4516/191, fragmentary right humerus: (a) frontal, (b) rear, (c) medial, and (d) lateral side views; (e, f) PIN, no. 4516/192, fragmentary right humerus: (e) frontal and (f) medial views; (g–i) specimen PIN, no. 4516/522, fragmentary left humerus: (g) frontal, (h) lateral side, and (i) rear views; Altynshokysu locality; Lower Miocene, Aral Formation, Bone Bed 4.

dle–Upper Miocene of Europe). The lateral position of the trochlea and the large distance between the edge of the teres tubercle and the entepicondyle are primitive characters, suggesting assigning this form to the genus *Hugueneya*, which includes *H. primitiva* from the Lower Miocene of Germany (Haslach, MN2) and *Hugueneya* aff. *primitiva* (MN2) and *?Hugueneya* cf. *primitiva* (MP30, MP30/MN1) described by Ziegler (1990). In addition to teeth and lower jaws, a large number of isolated humeri assigned to this form have been registered (Hutchison, 1974; Hoek Ostende, 1989; Ziegler, 1990).

Bendukidze (1993, p. 20, pl. VI, figs. 1, 2) described lower jaw fragments of Scalopini from the Aral Formation of the Altynshokysu locality and identified these specimens as *Proscapanus* sp. This researcher indicated that the species in question is morphologically similar to *P. primitivus* Hutchison, 1974 from the Lower Miocene of western Europe, but larger in size (Bendukidze, 1993, p. 116). According to his description, in the molars of "*Proscapanus* sp.," the cingulids are better pronounced, the postcingulid is developed, and the ectocingulid is broken in line with the hypoconid. Based on its dental structure, *P. primitivus* is considered to be the type species of the genus *Hugueneya* (Hoek Ostende, 1989; Ziegler, 1990). Apparently, the specimens identified by Bendukidze (1993) as *Proscapanus* sp. and the *Hugueneya* sp. described above belong to the same species. *Hugueneya* sp. from the Aral Formation is probably a new species; however, formally establishing this species is impossible because teeth are absent and the humeri are incomplete (the proximal epiphyses are not preserved). The ranges of available measurements overlap those of *H. primitiva* (Hutchison, 1974; Ziegler, 1990), and the differences revealed in the structure of individual elements (pectoral ridge, olecranon fossa, etc.) are characterized by a wide range of individual variation; this precludes establishing *Hugueneya* sp. from the Aral Formation as a new species.

Material. Three incomplete humeri (PIN, nos. 4516/191, 192, 522) from Bone Bed 4 of the Aral Formation of the Altynshokysu locality.

Family Soricidae Fischer von Waldheim, 1817

Subfamily Heterosoricinae Viret et Zapfe, 1951

Genus *Gobisorex* Sulimski, 1970

Gobisorex akhmetievi Lopatin, sp. nov.

Plate 2, figs. 1a–1c

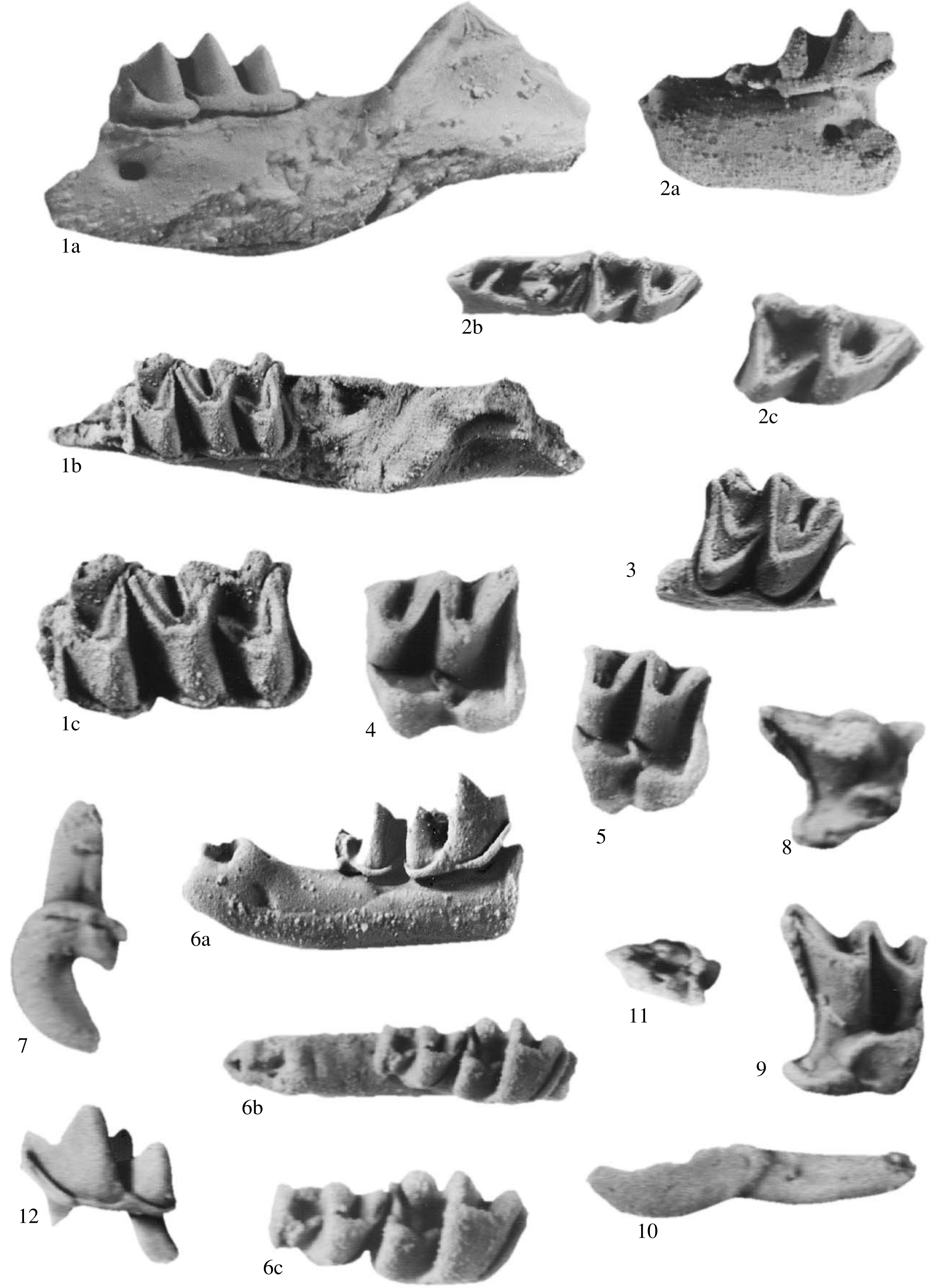
Gobiosorex (sic!) *kingae*: Bendukidze, 1993, p. 22, pl. VII, figs. 2–4.

Gobisorex sp.: Lopatin, 1999a, p. 66.

Etymology. In honor of the Russian paleobotanist M.A. Akhmetiev.

Holotype. PIN, no. 4516/6, left dentary fragment with a broken M_1, complete M_2, and the alveoli of M_3; Kazakhstan, North Aral Region, Altynshokysu locality; Lower Miocene, Aral Formation, Bone Bed 4.

Plate 2



Description (Fig. 14). The horizontal ramus of the lower jaw is high and massive. The mental foramen is located under the center of M_1. The masseteric fossa is relatively deep. The mandibular foramen is on a level with the tooth row.

The molar crowns are relatively low. The preserved fragment of M_1 has a well-pronounced ectocingulid, a broad talonid with a massive hypoconid, and a relatively small conical entoconid. The entocristid is stout and high. The postcristid reaches the posterolabial part of the entoconid and closely adjoins it.

M_2 is subrectangular in outline. The trigonid is equal in width to, and slightly longer than, the talonid. The angle between the paracristid and the protocristid is approximately 50°. The metaconid is worn to a substantially greater extent than the other cusps. The protocristid is broad. The entocristid is well-developed and high. The talonid is similar in structure to that of M_1. The cristid oblique is connected to the base of the protocristid at the point of fusion between the protocristid and the protoconid. The postcristid reaches the posterolabial part of the entoconid, which slightly curves lingually, and closely adjoins it. The entostylid is well-pronounced. The stout ectocingulid is broken under the protoconid; anteriorly, it reaches the base of the paraconid; and posteriorly, it extends to the entostylid. The entocingulid is poorly pronounced. Judging from the alveoli, M_3 was somewhat shorter than M_2 and had a relatively narrow talonid.

Measurements in mm. Holotype: M_2 (length × width), 2.0 × 1.45; depth of the horizontal ramus of the lower jaw under M_1, 2.2; under M_2, 2.3; and under M_3, 2.3.

Comparison and remarks. Bendukidze (1993) determined remains of this form (a lower jaw fragment and isolated upper molars) from Altynshokysu as *Gobisorex kingae* and marked the presence of five alveoli between the first incisor and M_1, which is characteristic of the genus *Gobisorex*. However, this species clearly differs from *G. kingae* from the Lower Oligocene of Mongolia (Tatal-Gol), which was described by Sulimski (1970), in the larger teeth, the high horizontal ramus of the lower jaw (in *G. kingae*, M_2 is 1.7 mm long and the depth of the lower jaw under M_1 is 1.7 mm: Sulimski, 1970, table 6), and the presence of the entocingulid on M_2. The absolutely and relatively higher horizontal ramus of the lower jaw of the Early Miocene *G. akhmetievi* sp. nov. (compared to that of the Early Oligocene *G. kingae*) displays the general evolutionary trend characteristic of the Heterosoricinae, which developed in parallel in different genera (see Engesser, 1975; Hoek Ostende, 1995).

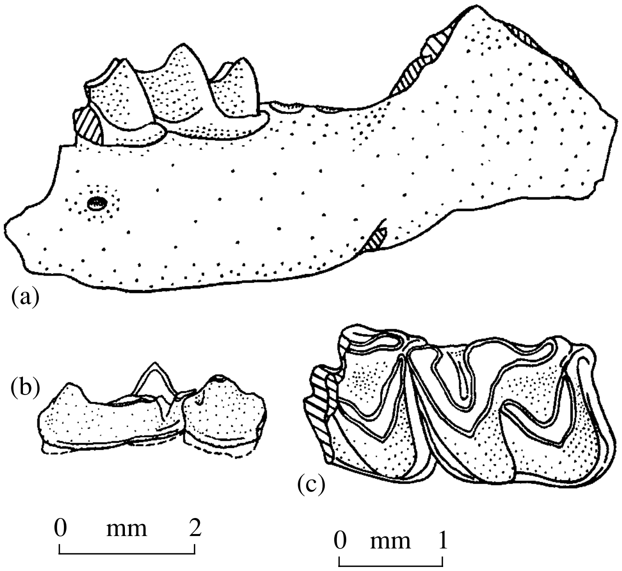


Fig. 14. *Gobisorex akhmetievi* sp. nov., holotype PIN, no. 4516/6, left dentary fragment with M_1 and M_2: (a) labial view; (b) teeth, lingual view; and (c) teeth, occlusal view.

Occurrence. North Aral Region; Lower Miocene, Aral Formation.

Material. Holotype.

Genus *Atasorex* Lopatin, gen. nov.

Etymology. From the Kazakh *ata* (father) and the generic name *Sorex*.

Type species. *A. edax* sp. nov.

Diagnosis. Primitive and small-sized member of Heterosoricinae. Horizontal ramus of mandible low. Mental foramen located under center of M_1. Labial side of M^2 weakly inclined posterolingually. Entocristid of M_1 and M_2 short and low, postcristid connected to pos-

Explanation of Plate 2

All specimens come from the Aral Formation of the Altynshokysu locality.

Fig. 1. *Gobisorex akhmetievi* sp. nov., holotype PIN, no. 4516/6, left dentary fragment with broken M_1, complete M_2, and the alveoli of M_3: (1a) labial and (1b) occlusal views, ×10; teeth, ×15; Bone Bed 4.

Figs. 2–5. *Atasorex edax* sp. nov.: (2) holotype PIN, no. 4516/190, right dentary fragment with M_1: (2a) labial and (2b) occlusal views, ×10; (2c) M_1, occlusal view, ×15; Bone Bed 4; (3) specimen PIN, no. 4516/610, right dentary fragment with M_2, ×15; Bone Bed 1; (4) specimen PIUZ, ALT no. 305, left M^1, ×15; Bone Bed 2; and (5) specimen PIN, no. 4516/367, left M^2, ×15; Bone Bed 1.

Figs. 6–12. *Aralosorex kalini* Lopatin, 2004: (6) holotype PIN, no. 4516/600, right dentary fragment with M_2 and M_3: (6a) labial and (6b) occlusal views, ×15; (6c) M_2 and M_3, occlusal view, ×20; (7) specimen PIN, no. 4516/596, left I^1; (8) specimen PIN, no. 4516/597, right P^4; (9) specimen PIN, no. 4516/598, right M^1; (10) specimen PIN, no. 4516/601, left I_1; (11) specimen PIN, no. 4516/604, left P_4; and (12) specimen PIN, no. 4516/605, left M_2, ×20; Bone Bed 2.

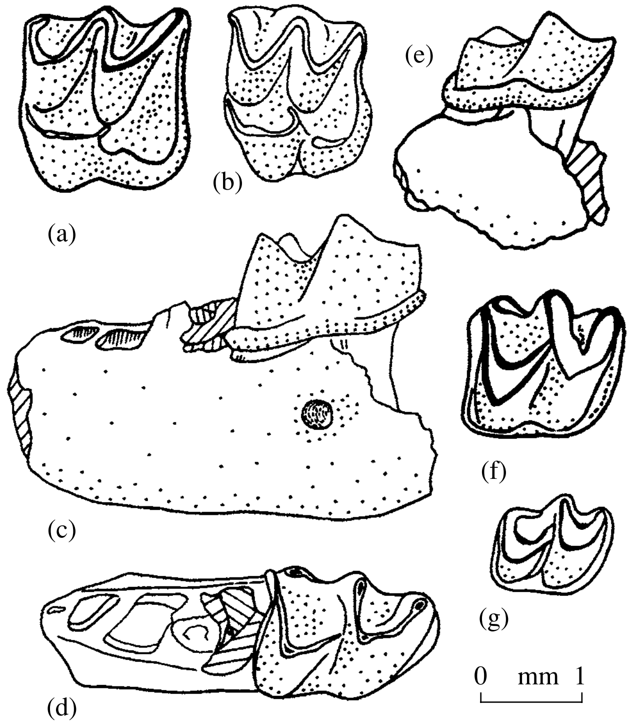


Fig. 15. *Atasorex edax* sp. nov. from the Aral Formation of the Altynshokysu locality: (a) specimen PIUZ, ALT no. 305, left M^1; Bone Bed 2; (b) specimen PIN, no. 4516/367, left M^2; Bone Bed 1; (c, d) holotype PIN, no. 4516/190, right dentary fragment with M_1: (c) labial and (d) occlusal views, Bone Bed 4; (e, f) specimen PIN, no. 4516/610, right M_2: (e) labial and (f) occlusal views; and (g) specimen PIN, no. 4516/407, right M_3; Bone Bed 1.

terior side of entoconid, entostylid weak. Trigonid of M_2 short, paracristid strongly inclined lingually, angle between paracristid and protocristid less than 40°. Ectocingulid of M_1 broken in line with protoconid. Ectocingulid of M_2 complete.

Species composition. Type species.

Comparison. The new genus differs from all known genera of the Heterosoricinae, except for *Domnina* Cope, 1873, *Gobisorex* Sulimski, 1970, and *Quercysorex* Engesser, 1975, in the low horizontal ramus of the mandible, the position of the mental foramen under M_1, and the shape of M^2. It differs from *Domnina* and *Quercysorex* in the presence of contact between the postcristid and the entoconid and in the relatively weak entocristid of M_1 and M_2. From *Gobisorex,* it differs in the weak entocristid of M_1 and M_2, poorly developed entostylid, shape of the trigonid of M_2, and continuous ectocingulid of M_2.

Atasorex edax Lopatin, sp. nov.

Plate 2, figs. 2–5

Gobiosorex (sic!) aff. *kingae*: Bendukidze, 1993, p. 23, pl. VII, fig. 5, pl. VIII, fig. 1.

Heterosoricidae gen. et sp. indet.: Lopatin, 1999a, p. 66.

Etymology. From the Latin *edax* (gluttonous, voracious).

Holotype. PIN, no. 4516/190, right dentary fragment with M_1; Kazakhstan, North Aral Region, Altynshokysu locality; Lower Miocene, Aral Formation, Bone Bed 4.

Description (Fig. 15). M^1 is subsquare in outline. The metastyle is in a slightly more labial position than the parastyle and mesostyle. The paracone and metacone are longitudinally compressed. The paracrista, centrocrista, and metacrista are well-pronounced. The preprotocrista is straight. In the postprotocrista, the posterior end abruptly curves labially and reaches the base of the lingual side of the metacone. The hypocone extends longitudinally, is located slightly more posterolingually than the protocone, and is connected by a small crest to the middle of the postprotocrista. A stout postcingulum is present.

M^2 is rectangular, and its labial edge is slightly oblique, so that the anterior side is a little longer than the posterior side. The parastyle and mesostyle occupy a slightly more labial position than the metastyle. The paracone and metacone are equal in size and compressed longitudinally. The preparacrista, centrocrista, and postmetacrista are well-developed. The protocone is substantially lower than the labial cusps but higher than the hypocone; its apex is in a more labial position than the apex of the hypocone, whereas the lingual part projects internally to a greater extent. The preprotocrista gently curves, and its anterior end is located anterior to the lingual region of the paracone. The posterior end of the postprotocrista abruptly curves labially and closely approaches the base of the lingual side of the metacone. The hypocone is isolated from other cusps and connected to the stout postcingulum. The ectocingulum and precingulum are extremely reduced; the ectocingulum is shaped into a very narrow border that extends along the base of the labial crown side, while the rudimentary precingulum is shaped like a small protrusion on the anterior wall of the tooth (located on a level with the apex of the paracone).

The horizontal ramus of the lower jaw is relatively massive and gradually decreases in depth from M_1 to M_3. The mental foramen is located under the middle of M_1; just anterior to this foramen, there is a small depression.

M_1 is large and has a long trigonid. The ectocingulid and postcingulid are well-pronounced and narrow. The ectocingulid is broken at the level of the posterior part of the protoconid. The entocingulid is absent. The paraconid is slightly lower than the metaconid. The paracristid is high and narrow. The protoconid is massive and high, while the metaconid is slightly lower than the protoconid. The metaconid occupies a posterolingual position relative to the protoconid. The protocristid gently curves posteriorly. The angle between the paracristid and the protocristid is approximately 50°. The talonid is substantially wider than the trigonid. The hypoconid and entoconid are approximately equal in height. The cristid oblique is connected to the posterolingual part of the protoconid. The entocristid is short and low but distinct. The talonid notch is deep. The entostylid is weak. The postcristid curves around the posterolabial corner of the entoconid and adjoins the base of its posterior wall.

M_2 is equal in width to M_1 but substantially shorter. It is similar in structure to M_1 and differs in the continuous ectocingulid and the strongly anterolingually inclined paracristid, which is positioned at about 35° to the protocristid.

M_3 is very small, and the talonid is substantially lower and somewhat shorter and narrower than the trigonid. The entoconid is small and low. The paracristid, protocristid, postcristid, and entocristid are well-developed. The cristid oblique is connected to the middle of the protocristid. The continuous cingulid borders the labial and posterior sides of the tooth (it originates under the paraconid and terminates under the middle of the postcristid).

Measurements in mm. Length × width: M^1, 1.65×1.75 (PIUZ, ALT no. 305); M^2, 1.4×1.75 (PIN, no. 4516/367); M_1, 1.9×1.25 (holotype); M_2, 1.6×1.25 (PIN, no. 4516/610); and M_3, 1.2×0.8 (PIN, no. 4516/407); depth of the horizontal ramus under M_1, 1.7; under M_2, 1.65; and under M_3, 1.55 (holotype).

Comparison. The sole species of the genus.

Occurrence. North Aral Region; Lower Miocene, Aral Formation.

Material. Isolated M^2 (PIN, no. 4516/367), two M_2 (PIN, no. 4516/610, 611), and M_3 (no. 4516/407) from Bone Bed 1 and isolated M^1 (PIUZ, ALT no. 305) from Bone Bed 2 of the Altynshokysu locality.

Subfamily Crocidosoricinae Reumer, 1987

Tribe Oligosoricini Gureev, 1971

Genus *Aralosorex* Lopatin, 2004

Aralosorex kalini Lopatin, 2004

Plate 2, figs. 6–12

Crocidosoricinae gen. indet.: Lopatin, 1999a, p. 66.

Aralosorex kalini: Lopatin, 2004, p. 95, text-figs. 1–3.

Holotype. PIN, no. 4516/600, right dentary fragment with M_2 and M_3; Kazakhstan, North Aral Region, Altynshokysu locality; Lower Miocene, Aral Formation, Bone Bed 2.

Description (Figs. 16, 17). A small-sized shrew. I^1 is slightly elongated. The anterior edge of the crown is convex, and the apex strongly curves posteriorly; therefore, the apex is positioned at an acute angle to the talon. The posterior cuspule is small and slightly forked. A clear labial cingulum is present.

The material examined includes one isolated upper intermediate antemolar, designated as A^x. It is very small, circular in occlusal view, and has a low and conical central cuspule and a stout and wide cingulum on the lateral sides of the crown base. The longitudinal crest is well-pronounced. The entocingulum is connected to the base of the posterior side of the central cusp.

In P^4, the styles strongly project, the anterior side is slightly concave, and the posterior side is strongly concave. The angle between the labial and lingual sides is approximately 50°. The paracone is slightly displaced anteriorly from the crown center. The parastyle is small and shaped like an elongated anterior process. The protocone is low, small, and connected to the parastyle by a clear crest of the preprotocrista. The metastyle is large, strongly projects posteriorly, and is connected to the paracone by a wide crest of the posterocrista. The hypoconal flange is flattened and strongly juts out posteriorly. Its lingual side is bordered by a narrow crest that originates from the protocone base. The hypoconal flange lacks a cusp. The postcingulum is stout at the metastyle and paracone level and becomes substantially narrower at the level of the hypoconal flange.

In M^1, the metastyle and the posterior part of the hypocone strongly project. The posterior side is strongly concave. The parastyle and mesostyle are clearly differentiated, and the mesostyle does not bifurcate. The metacone is substantially larger than the paracone and is somewhat displaced lingually relative to this cusp. The crests of the paracrista, centrocrista, and metacrista are well-developed. The protocone is located substantially more labially than the hypocone. The preprotocrista and postprotocrista have well-developed crests. The preprotocrista terminates at the base of the anterolingual projection of the paracone, while the postprotocrista turns toward the hypocone at a large distance from the lingual wall of the metacone. The hypocone is very small and isolated from the protocone by a narrow and deep valley, which is occasionally bounded posterolingually by a very weak entocingulum. A long crest deviates from the posterior region of the hypocone, forms the posterolingual projection of the crown, and, labially, becomes a wide postcingulum.

M^2 is similar in structure to M^1; however, it is smaller, more symmetrical (the metastyle and the hypocone are elongated to a lesser extent), and its hypocone is relatively weakly developed. M^3 is not available.

The horizontal mandibular ramus is low. Its lower edge is straight. The mental foramen is located under P_4. The pocket of the external temporal fossa extends to the level of the molar bases. The mandibular foramen is somewhat above the alveolar edge.

I_1 is relatively narrow and slightly curved. Its apex is weakly elevated. Its denticles are weakly developed, the posterior denticle is better developed than the anterior denticle. The crown base has a labial cingulid. The lingual edge of the crown is sharpened. The root weakly curves ventrally with reference to the longitudinal axis of the crown.

The number of the lower intermediate antemolars is not known with certainty. The available material includes only one isolated lower antemolar; this is presumably A_1 (Figs. 16g–16g^2). This tooth is approximately equal in length to P_4; however, it is much lower. The crown of A_1 is elongated cordate and has a deep

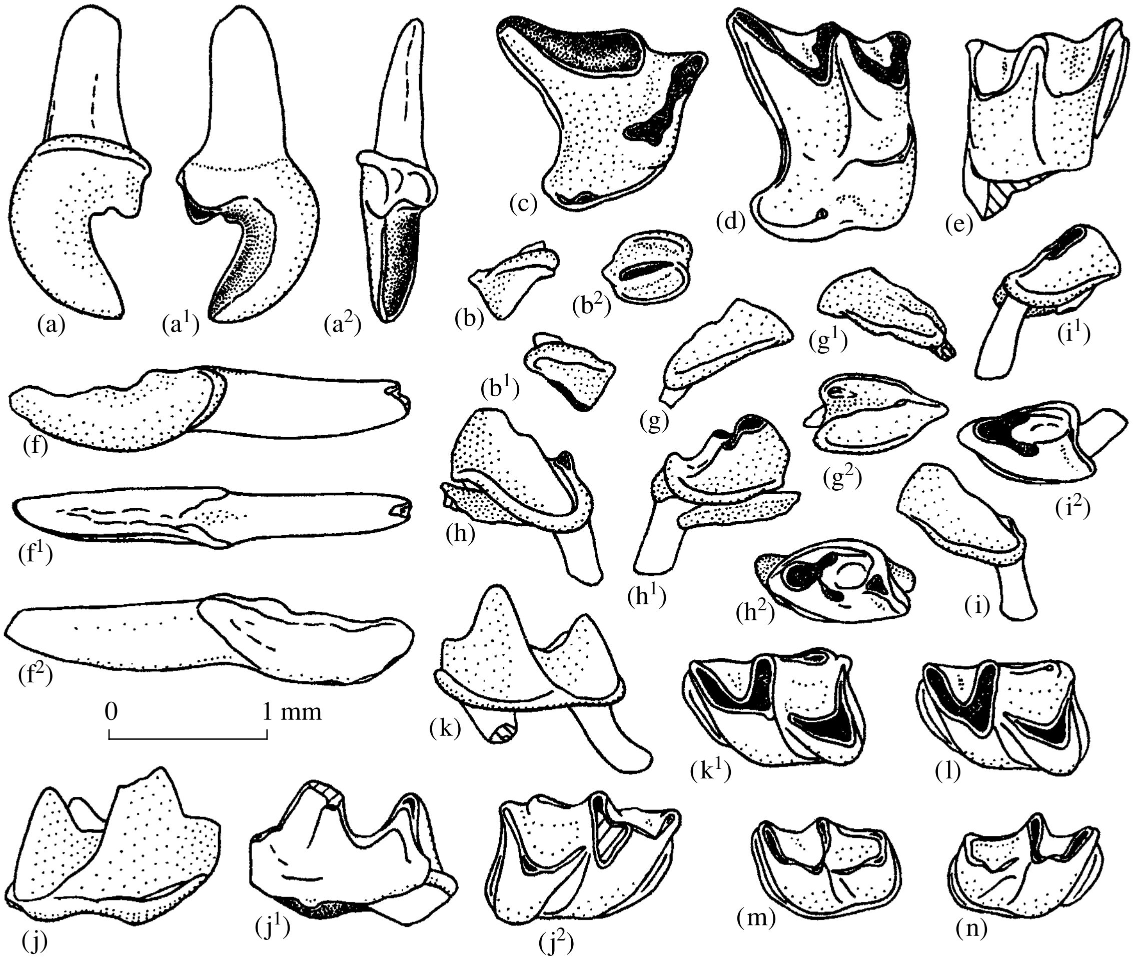


Fig. 16. *Aralosorex kalini* Lopatin, 2004: (a–a^2) specimen PIN, no. 4516/596, left I^1: (a) labial, (a^1) lingual, and (a^2) rear views; (b–b^2) specimen PIN, no. 4516/603, left A^x: (b) labial, (b^1) lingual, and (b^2) occlusal views; (c) specimen PIN, no. 4516/597, right P^4; (d) specimen PIN, no. 4516/598, right M^1; (e) specimen PIN, no. 4516/599, left M^2; (f–f^2) specimen PIN, no. 4516/601, left I$_1$: (f) labial, (f^1) occlusal, and (f^2) lingual views; (g–g^2) specimen PIN, no. 4516/602, right A$_1$: (g) labial, (g^1) lingual, and (g^2) occlusal views; (h–h^2) specimen PIN, no. 4516/604, left P$_4$: (h) labial, (h^1) lingual, and (h^2) occlusal views; (i–i^2) specimen PIN, no. 4516/606, left P$_4$: (i) labial, (i^1) lingual, and (i^2) occlusal views; (j–j^2) specimen PIUZ, ALT no. 264, right M$_1$: (j) labial, (j^1) lingual, and (j^2) occlusal views; (k, k^1) specimen PIN, no. 4516/605, left M$_2$: (k) labial and (k^1) occlusal views; (l) specimen PIUZ, ALT no. 265, left M$_2$; (m) specimen PIUZ, ALT no. 266, left M$_3$; and (n) specimen PIUZ, ALT no. 267, right M$_3$.

posterior fold. The central cusp is low and strongly transversely compressed. It gives rise to a longitudinal crest that has a small posterior cuspule (Fig. 16g). The stout lateral cingulids are well-developed. The ectocingulid is connected to the longitudinal crest in the posterolabial corner of the crown. A small supplementary cuspule occupies an isolated position on the posterolingual projection (Figs. 16g^1, 16g^2). One P$_4$ is preserved in articulation with a small bone fragment, which tightly adjoins the tooth base in the region of the anterior root (Figs. 16h, 16h^1). This suggests that the posterior single-rooted antemolar, which was located anterior to P$_4$, was not reduced to a diminutive tooth positioned under the anterior region of the crown base of P$_4$; on the contrary, it was relatively large and well-differentiated.

The crown of P$_4$ is relatively high and rounded triangular in occlusal view and its anterior end is pointed. The posterior edge of the crown has a shallow depression. The lateral sides are slightly convex, the labial side is longer than the lingual side and projects posteriorly to a substantially greater extent. The cingulid is well-developed on the lateral and posterior sides of the crown base. The protoconid is located in the anterior region of the crown. Two arms of the posterocristid extend posteriorly from the protoconid and form a Y-shaped border of the posterolingual basin. Each arm is connected to a small supplementary cuspule. The lingual arm terminates at the protoconid base, while the labial arm adjoins the central area of the postcingulid. Thus, the posterolingual basin is labially closed and posterolingually open.

M_1 is somewhat larger than M_2. The precingulid and the postcingulid are well-developed and wide. The ectocingulid is narrow and well-pronounced throughout its extent (Figs. 16j, 16k) or broken on a level with the anterior part of the hypoflexid (Fig. 17a). The entocingulid is only developed along the trigonid basin. The well-pronounced posterolabial crest of the protoconid is connected to the ectocingulid on a level with the hypoflexid or the anterior region of the hypoconid. The hypoflexid is very deep and extends to the level of the ectocingulid. The trigonid is slightly longer than the talonid, while the talonid is somewhat wider than the trigonid. The paraconid is relatively low. The paracristid is anterolingually curved and has a clear notch. The trigonid basin is relatively deep. The protoconid and the metaconid are positioned close to one another, the metaconid is substantially smaller than the protoconid. The talonid basin is deep and closed. The hypoconid is substantially larger than the entoconid. The cristid oblique rests against the posterior wall of the protoconid. The clearly pronounced entocristid is higher than the cristid oblique. The postcristid is free. The entostylid is small. M_2 is similar in structure to M_1 and differs in the smaller length, the shorter trigonid, and more widely spaced protoconid and metaconid.

M_3 is characterized by small dimensions and a narrow talonid. The talonid is slightly shorter than the trigonid. The hypoconid and entoconid are strongly reduced. The talonid basin is bordered posteriorly, labially, and lingually by low crests, i.e., the complete postcristid, cristid oblique, and entocristid, respectively (Figs. 16m, 16n, 17b). The cristid oblique terminates at the base of the posterior wall of the trigonid on a level with the notch of the protocristid. The entostylid is absent. The crown base is bordered anteriorly, labially, and posteriorly by cingulids; lingually, it is also bordered on a level with the trigonid basin.

Measurements in mm. Holotype: M_2 (length × width), 1.15 × 0.75; M_3 (length × trigonid width—talonid width), 0.95 × 0.6—0.45; lingual depth of the horizontal mandibular ramus under M_2, 1.05; under M_3, 1.05.

Incisors (height × length, n = sample size, Δ = mean value): I^1 ($n = 7$), 1.0–1.1 × 0.75–0.9 (Δ = 1.05 × 0.84); I_1 (specimen PIN, no. 4516/601), 1.35 × 0.6.

Antemolars (length × width): A^x (specimen PIN, no. 4516/603), 0.55 × 0.45; A_1 (specimen PIN, no. 4516/602), 0.9 × 0.6.

Cheek teeth (length × width): P^4 (specimen PIN, no. 4516/597), 1.3 × 1.15; M^1 ($n = 4$), 1.15–1.2 × 1.4–1.5 (Δ = 1.175 × 1.45); M^2 (specimen PIN, no. 4516/599), 1.1 × ?; P_4 ($n = 2$), 0.9–0.95 × 0.5; M_1 ($n = 6$), 1.15–1.23 × 0.7–0.8 (Δ = 1.19 × 0.72); M_2 ($n = 5$), 1.05–1.15 × 0.65–0.75 (Δ = 1.12 × 0.7); M_3 ($n = 5$), 0.95–1.0 × 0.55–0.6 (Δ = 0.97 × 0.58).

Comparison. The sole species of the genus.

Remarks. Although Oligosoricini Gureev, 1971 is the senior name, the term Crocidosoricinae Reumer, 1987 is not replaced by Oligosoricinae, according to Article 35.5 of the International Code of Zoological Nomenclature (see Lopatin, 2004).

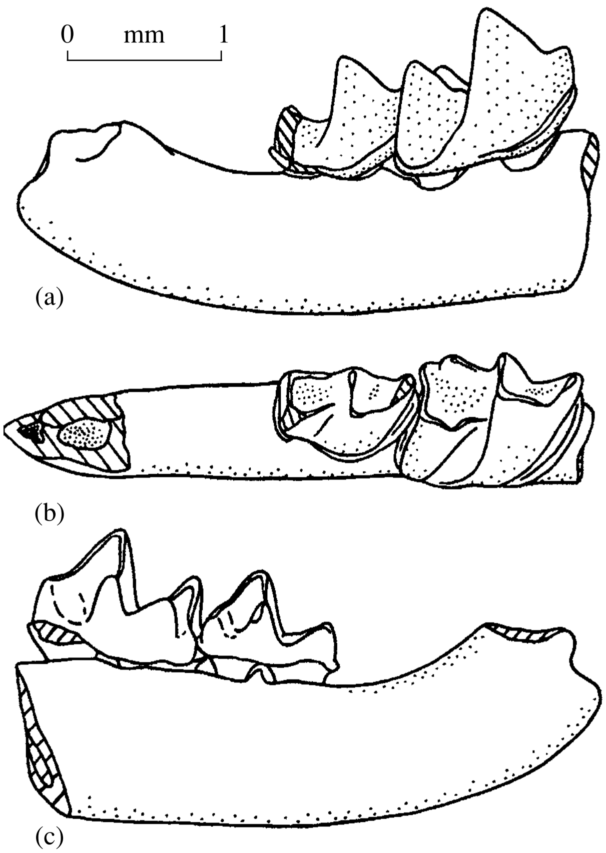


Fig. 17. *Aralosorex kalini* Lopatin, 2004, holotype PIN, no. 4516/600, right dentary fragment with M_2 and M_3: (a) labial, (b) occlusal, and (c) lingual views.

Material. In addition to the holotype, six lower jaw fragments and 45 isolated teeth and tooth fragments from Bone Bed 2 of the Altynshokysu locality: isolated I^1, A^x, P^4, M^1, M^2, I_1, A_1, two P_4, and M_2 stored at the PIN; three dentary fragments (two with M_2 and one with M_3), I^1, three P^4, five M^1, two M^2, M_1, M_2, and two M_3 stored at the PIUZ; two lower jaw fragments without teeth, two I^1, two M_1, two M_2, and M_3 stored at the IAUU; a dentary fragment without teeth, four I^1, M^1, three M_1, and M_2 stored at the NMW; and M^1, two M^2, and three M_2 stored at the DK.

Order Lagomorpha Brandt, 1855

Family Desmatolagidae Burke, 1941

Genus *Desmatolagus* Matthew et Granger, 1923

Desmatolagus simplex (Argyropulo, 1940)

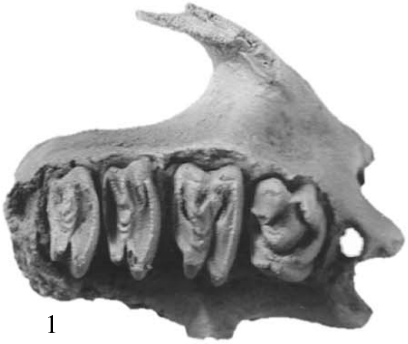
Plate 3, figs. 1–6

Agispelagus simplex: Argyropulo, 1940, p. 76; Gureev, 1960, p. 25, text-fig. 10A; 1964, p. 106, text-fig. 42.

Desmatolagus aff. *shargaltensis*: Bendukidze, 1993, p. 28, pl. X, figs. 5 and 6; pl. XI, fig. 1.

Desmatolagus simplex: Lopatin, 1998, p. 77, pl. V, figs. 1–3, text-fig. 1.

Plate 3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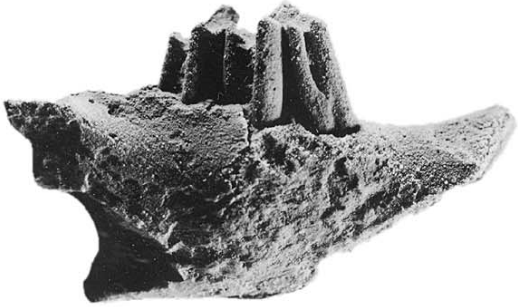
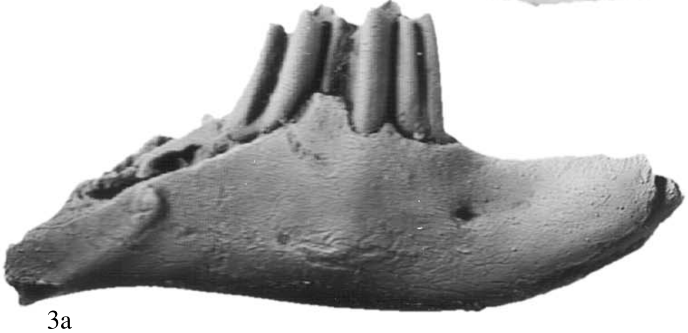

4a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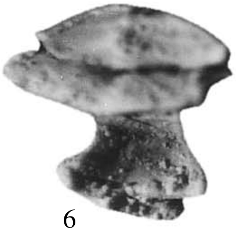
4b


3b


5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Lectotype (Gureev, 1960). PIN, no. 210/609, fragmentary right maxilla with P^3–M^2; Kazakhstan, North Aral Region, Akespe locality; Lower Miocene, Aral Formation.

Description (Fig. 18). The upper jaw has a relatively thin zygomatic process. A small foramen premolare is located lingual to the space between P^3 and P^4.

The upper incisors have a deep longitudinal groove on the anterior surface; therefore, a small incisure is formed in the cutting edge and divides it into two blades that are roundish in section. The cement is absent.

Judging from the alveolus, P^2 was strongly reduced. P^3 is short but relatively wide; it has a small metastyle bordered by a clear labial cingulum. A small fold lacking cement is located between the cingulum and the metastyle. The crescentic fold is relatively narrow, deep, filled with cement, and wedges out at the mid-height of the crown. The external fold is shallow, narrow, and approximately half as long as the crescentic fold. The fold that isolates the anterocone from the protocone descends almost to the crown base. The internal groove is only slightly developed, the protocone and hypocone are faintly isolated. P^3 of young individuals displays that the anterocone is initially located dorsal to the occlusal surface; therefore, the anteroloph is formed when the tooth is substantially worn. The anteroloph is short and straight and extends parallel to the tooth row axis. The anterior cingulum is weakly developed.

The labial root of P^4–M^2 is fused with the lingual root for one-third or half of its length. P^4 is the largest tooth in the row and is rounded rectangular in outline. The anterior wall of the tooth is thickened. The hypostria is shallow. The protocone projects inward to a greater extent than the hypocone. The crescentic valley is V-shaped. The external fold is small and extends parallel to the crescentic valley. All the folds are filled with cement.

M^1 is shorter than P^4, its occlusal surface is lenticular. The hypostria is deep and juts out into the crown for about one-third of the occlusal surface width; as the tooth is worn, it forms a closed teardrop-shaped lake and, subsequently, disappears. The protocone is larger than the hypocone and projects lingually to a much greater extent. The paracone projects labially to a greater extent than the metacone. The middle region of the crescentic fold extends close to the labial region of the hypostria.

M^2 is similar to M^1 in structure, but smaller and more rounded in outline. The hypostria is relatively wide and deep; at early stages of wear, it closely approaches the center of the occlusal surface. M^3 is considerably reduced (to judge from the alveoli).

The horizontal ramus of the lower jaw is relatively thin and low. The mental foramen is located anterior to P_3. The lower incisor is ovoid and triangular in cross section, its anterior edge is round, and the posterior edge of its alveolus lies under the talonid of M_1.

In cross section, P_3 appears to be a triangle with a wide base. Its anteroexternal fold is deep and wide, lacks cement, and extends to the crown base.

The anterior conid of DP_3 is relatively small, and its anterior surface is smooth and lacks grooves. The posterior and medial conids are approximately equal in width.

P_4–M_2 are similar in structure. The trigonids of these teeth strongly expand transversely, and their lingual edges are sharpened and raised. The talonid is round, while its labial edge narrows. The anterolingual wall abruptly rises upward and closely approaches the posterior border of the occlusal surface of the trigonid. The lower cheek teeth of young individuals have a strongly reduced hypoconulid, which is shaped like a very small, narrow, and only slightly differentiated protrusion of the talonid (Pl. 3, fig. 6; Figs. 18m–18o). As these teeth are worn, the hypoconulid rapidly disappears. M_3 is single-rooted and very small.

The roots of P_4–M_2 tend to become fused (Figs. 18s–18x). They are parallel to each other, and the posterior root is somewhat labially displaced. The anterior root of P_4 and M_1 is flattened, reduced (in P_4, it is approximately half as large as the posterior root, and in M_1, it is three or four times smaller), and connected with the posterior root along the entire extent; however, it has a separate canal. The roots of M_2 are completely fused and form a dentin tubule, which opens at the base; the lateral walls of this tube bear distinct grooves corresponding to the lines of fusion of the roots.

Explanation of Plate 3

All specimens come from the Aral Formation.

Figs. 1–6. *Desmatolagus simplex* (Argyropulo, 1940): (1) lectotype PIN, no. 210/609, fragmentary right maxilla with P^3–M^2, ×5; Akespe locality; (2) specimen PIN, no. 4516/30, fragmentary left maxilla with P^3–P^4, ×5; Altynshokysu locality, Bone Bed 4; (3) specimen PIN, no. 210/610, right dentary fragment with P_3–M_1: (3a) labial and (3b) occlusal views, ×5; Akespe; (4) specimen PIN, no. 4516/3, right dentary fragment with P_3–M_1, ×5: (4a) labial and (4b) occlusal views; (5) specimen PIN, no. 4516/16, left dentary fragment with P_4–M_3, ×5; and (6) specimen PIN, no. 4516/165, left P_4, ×15; Altynshokysu, Bone Bed 4.

Figs. 7–13. *Desmatolagus periaralicus* Lopatin, 1998: (7) holotype PIN, no. 4516/99, right P^3; (8) specimen PIN, no. 4516/105, left P^4; (9) specimen PIN, no. 4516/98, left M^1; (10) specimen PIN, no. 4516/104, left M^2; (11) specimen PIN, no. 4516/115, left DP_3; (12) specimen PIN, no. 4516/81, left P_3; and (13) specimen PIN, no. 4516/102, right P_4, ×9; Altynshokysu, Bone Bed 4.

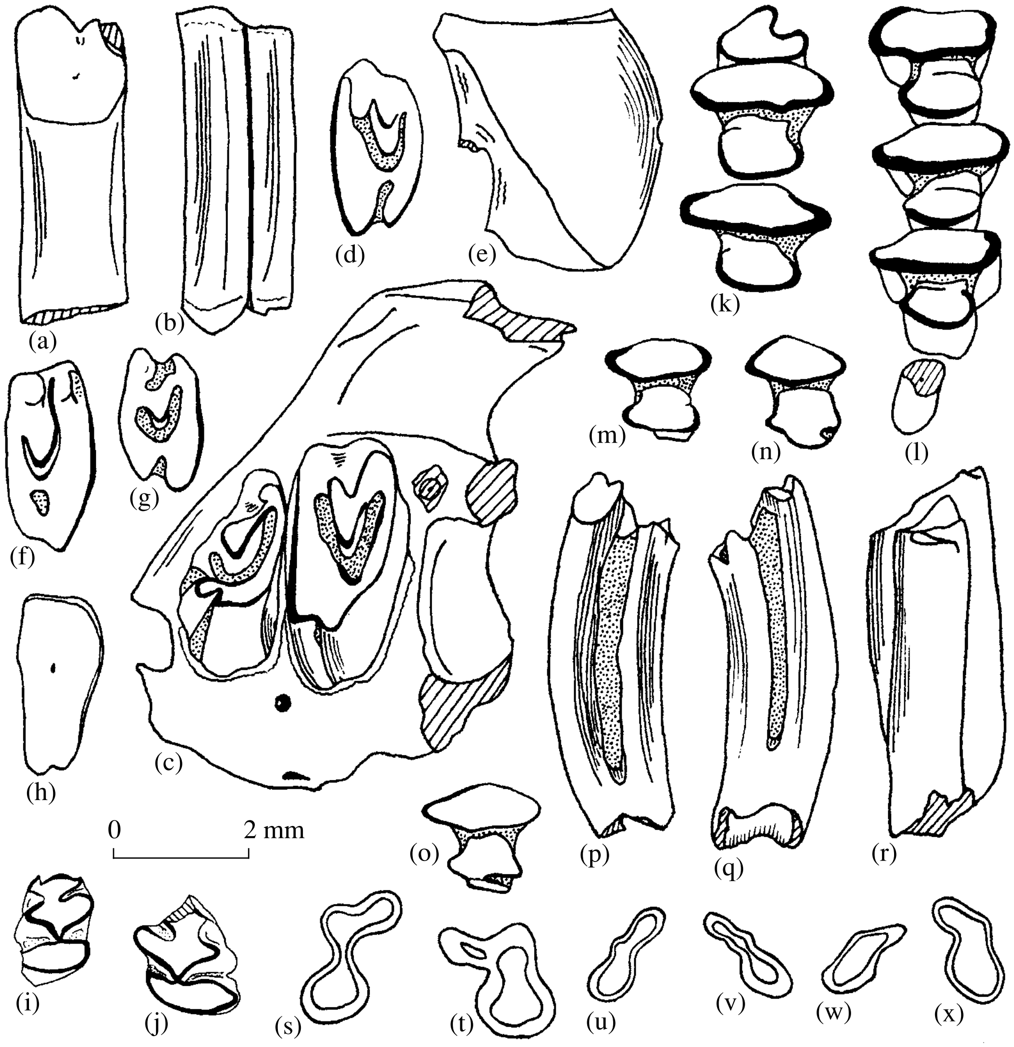


Fig. 18. *Desmatolagus simplex* (Argyropulo, 1940) from the Aral Formation of the Altynshokysu locality: (a, b) specimen PIN, no. 4516/45, right anterior upper incisor: (a) occlusal and (b) frontal views; (c) specimen PIN, no. 4516/30, fragmentary left maxilla with P^3 and P^4; (d, e) specimen PIN, no. 4516/152, left M^1: (d) occlusal and (e) frontal views; (f) specimen PIN, no. 4516/153, right M^1; (g) specimen PIN, no. 4516/158, right M^2; (h) specimen PIN, no. 4516/185, right lower incisor; Bone Bed 4; (i) specimen NMW, no. 1994/00271/0001/3, left DP_3; (j) specimen PIN, no. 4516/613, right DP_3; Bone Bed 2; (k) specimen PIN, no. 4516/3, right P_3–M_1; (l) specimen PIN, no. 4516/16, left P_4–M_3; (m) specimen PIN, no. 4516/163, left P_4; (n) specimen PIN, no. 4516/164, left P_4; (o–r) specimen PIN, no. 4516/165, left P_4: (o) occlusal, (p) labial, (q) lingual, and (r) rear views; (s) specimen PIN, no. 4516/167, right P_4, root side; (t) specimen PIN, no. 4516/168, left P_4, root side; (u) specimen PIN, no. 4516/178, right M_1, root side; (v) specimen PIN, no. 4516/177, left M_1, root side; (w) specimen PIN, no. 4516/183, right M_2, root side; and (x) specimen PIN, no. 4516/184, left M_2, root side; Bone Bed 4.

Measurements in mm. Lectotype: length of P^3–M^2, 7.5; length of P^3–M^2 along the alveoli, 9.6; tooth dimensions (length × width): P^3, 1.65 × 2.7; P^4, 2.0 × 3.15; M^1, 1.5 × 3.05; and M^2, 1.3 × 2.9.

Specimen PIN, no. 210/610 from Akespe: length of P_3–M_1 (along the crown bases), 5.9; tooth dimensions: P_3 (occlusal surface), 0.9 × 1.15; P_4 (length × trigonid width—talonid width), 1.8 × 2.0—1.75; M_1, 1.7 × 2.0—1.75; and depth of the horizontal ramus of the lower jaw at P_3, 4.3.

Specimens from Bone Bed 4 of the Altynshokysu locality (collection housed at the PIN): length of P^3–P^4 (no. 4516/30), 3.0; length of P_3–M_1 (no. 4516/3), 4.25; P_4–M_3 (no. 4516/16), 5.75; depth of the horizontal ramus of the lower jaw at P_3, 4.5; at M_3, 5.5 (no. 4516/3) and 5.7 (no. 4516/16).

Measurements of isolated teeth:

Tooth	Length			Width				
	n	limits	mean	*n*	limits		mean	
P^3	12	0.8–1.4	1.15	6	2.0–2.9		2.28	
P^4	7	1.6–1.75	1.65	6	2.8–4.0		3.2	
M^1	6	1.3–1.6	1.46	6	2.6–3.5		3.0	
M^2	3	1.2–1.5	1.3	4	2.1–2.5		2.3	
P_3	2	0.8–0.9	0.85	2	1.25–1.35		1.3	
					trigonid	talonid	trigonid	talonid
P_4	10	1.5–1.85	1.75	12	1.5–2.21	1.1–1.3	1.84	1.17
M_1	8	1.5–1.75	1.58	5	2.0–2.1	1.1–1.25	2.03	1.17
M_2	4	1.4–1.75	1.56	4	1.8–2.0	1.0–1.3	1.89	1.13
M_3	1	0.5	–	1	0.55		–	

Measurements of the hypoconulid of P_4 (length × width), 0.1 × 0.6 (PIN, no. 4516/163); 0.15 × 0.6 (PIN, no. 4516/165); and 0.3 × 0.6 (PIN, no. 4516/164).

Comparison. *D. simplex* is substantially smaller than *D. robustus* Matthew et Granger, 1923, *D. veletus* Lopatin, 1998, *D. ardynense* Burke, 1941, *D. gobiensis* Matthew et Granger, 1923, and *D. periaralicus* Lopatin, 1998; in addition, it differs from these species in its short P^3, the deep hypostria of P^4–M^2, and the reduced hypoconulids of P_4–M_2. As compared with *D. shargaltensis* Bohlin, 1937 and *D. chinensis* Erbajeva et Sen, 1998, it is somewhat larger and its hypoconulids are more reduced. In addition, *D. simplex* is distinguished from these species by reduced roots of P^4–M^2 and P_4–M_1.

Remarks. Argyropulo (1940) placed this species in the genus *Agispelagus*, which he considered to be close to *Desmatolagus*. However, this researcher noticed the presence of deep hypostriae (internal reentrant folds). In *Desmatolagus*, these folds are developed to a much lesser extent. Subsequently, based on this genus, Gureev established a new subfamily, Agispelaginae Gureev, 1953, and assigned it to the Leporidae. This point of view was substantiated by the absence of supplementary conids (hypoconulids) on P_4–M_2, the narrow and pointed trigonids, and the deep internal reentrant folds of the upper cheek teeth in these forms (Gureev, 1964). In addition, the researcher described *Agispelagus simplex* and *A. youngi* Gureev, 1960 from the Oligocene of Mongolia. Sych (1975) showed that, at the early ontogenetic stages, *Desmatolagus gobiensis* and *D. robustus* have a well-developed hypostria on P^4–M^2, while in heavily worn teeth, the third supplementary conid (hypoconulids) of P_4–M_2 disappears. He correctly regarded *A. youngi* as a junior synonym for *D. robustus*. Reexamination of specimens of "*A. simplex*" from the Oligocene of Mongolia that were studied by Gureev (1960) has shown that, in actual fact, this form belongs to *D. gobiensis* (the lower teeth are heavily worn). "*Agispelagus*" *simplex* from the Aral Formation displays a number of advanced characters typical of the latest Desmatolagidae: deep hypostria, presence of cement in the folds and valleys of cheek teeth, rudimentary hypoconulids, and reduced roots. It would not be reasonable to assign this form to a separate genus, since similar characters occur in other late representatives of the genus *Desmatolagus*. However, this form should be ranked as a separate species, because its differences from all known members of *Desmatolagus* are rather significant. Thus, *Agispelagus* is a junior synonym for *Desmatolagus*, and the name Agispelaginae Gureev, 1953 should be abolished (Lopatin, 1998).

The Middle Miocene "*Desmatolagus*" *kazachstanicus* Bendukidze, 1993 and the Late Miocene "*D.*" *turmeensis* Bendukidze, 1993 from Kazakhstan (Bendukidze, 1993) display certain characters that compel us to exclude them from the genus *Desmatolagus* and transfer them to the Amphilaginae. This concerns the structure of P^3 and P_3 and the fused roots of P_4–M_2. *?D. moergenensis* Qiu, 1996 from the terminal Middle Miocene of China and the closely similar form *?D. schizopetrus* Dawson, 1965 from North America most likely belong to a separate genus (see Qiu, 1996).

Occurrence. North Aral Region; Lower Miocene, Aral Formation.

Material. In addition to the lectotype, the collection housed at the PIN includes the following specimens: jaw fragments (with P^3–M^2; with M^2; with incisor, P_3, and P_4; two with P_3 and P_4; two with P_3–M_1; with M_1 and M_2; and with M_1) and isolated teeth (two fragmentary upper incisors, P^3, P^4, two fragmentary lower incisors, two P_3, two P_4, four M_1, and three M_2) from the type locality. A fragmentary maxilla with P^3 and P^4 (PIN, no. 4516/30), two fragments with P^4 (nos. 4516/43, 44), two lower jaw fragments with P_3–M_1 (no. 4516/3) and with P_4–M_3 (no. 4516/16), and 76 isolated teeth: 14 fragmentary upper incisors (nos. 4516/45, 288–300), 13 P^3 (PIN, nos. 4516/14, 131–142), six P^4 (PIN, nos. 4516/25, 143–147), nine M^1 (PIN, nos. 4516/148–156), seven M^2 (PIN, nos. 4516/5, 157–162), two fragmentary lower incisors (PIN, nos. 4516/185 and 186), P_3 (PIN, no. 4516/9), ten P_4 (PIN, nos. 4516/125, 163–171), eight M_1 (nos. 4516/126, 172–178), and six M_2 (nos. 4516/179–184) from Bone Bed 4 of the Altynshokysu locality. In addition, a fragmentary maxilla with P^3–M^1, three P^3, two P^4, two M^1, M^2, P_4, M_1, and M_2 from Bone Bed 4 of Altynshokysu (stored at the PIUZ); and isolated teeth from Bone Bed 2 of Altynshokysu: P^3, P^4, four M^1, M^2, two DP_3, P_4, and M_1 (stored at the NMW); a fragmentary upper incisor, P^4, three M^1, M^2, and DP_3 (stored at the DK); and M^2 (stored at the PIUZ).

Desmatolagus periaralicus **Lopatin, 1998**

Plate 3, figs. 7–13

Desmatolagus aff. *gobiensis*: Bendukidze, 1993, p. 30, pl. XI, figs. 2–5.

Desmatolagus periaralicus: Lopatin, 1998, p. 80, pl. V, figs. 4–7, text-fig. 2.

Holotype. PIN, no. 4516/99, right P^3; Kazakhstan, North Aral Region, Altynshokysu locality; Lower Miocene, Aral Formation, Bone Bed 1.

Description (Fig. 19). The zygomatic process of the upper jaw is relatively stout. Lingual to the space between P^3 and P^4, there is a large foramen premolare.

The upper incisors are stout and have a deep longitudinal groove on the anterior surface. The cutting edge has a clear notch, which divides it into two slightly sharpened blades. The lingual blade is somewhat narrower than the labial one. Cement is absent.

P^3 is large and has three shallow reentrant folds on the anterior surface and a well-developed groove on the lingual side of the crown. The metastyle is relatively small but clearly differentiated. The anteroloph is long and pointed and gradually transforms into a long anterior cingulum. The crescentic fold terminates on a level with the anterior cingulum. The external fold looks like a small depression on the anterior side of the tooth. The fold that separates the anteroloph from the protocone descends to the level of the base of the anterior labial root.

P^4 is very large, rounded rectangular in outline, and has a shallow hypostria. The crescentic and external folds are V-shaped and displaced to the posterior border of the tooth.

M^1 is smaller than P^4, and its paracone clearly projects. The hypostria is deep and appears on the occlusal surface as a long enamel loop that extends inward for about one-third of the crown width.

M^2 is shorter and narrower than M^1, and its hypostria is deeper (up to half width of the occlusal surface). The external valley is shaped into a small rounded triangular lake in the posterolabial corner of the occlusal surface.

In a considerably worn tooth, the hypostria forms a lenticular lake on the occlusal surface of M^1 and M^2. All the valleys and folds of P^4–M^2 are filled with cement. The labial roots of these teeth are clearly isolated from the lingual root and located at approximately the same level. P^2 and M^3 are absent from the material; however, judging by the alveoli, they were relatively small.

The lower incisors are triangular oval in cross section with a rounded anterior edge. P_3 is stout and has a deep anteroexternal fold lacking cement. P_3 has a supplementary conid at the base of the anterior side of the crown. This conid looks like a narrow border that is developed to a greater or lesser extent (Pl. 3, fig. 12; Fig. 19k). The roots of P_3 are partially fused, so that the posterior surface of the anterior root and the anterior surface of the posterior root are fused, but the canals remain isolated (Fig. 19o).

DP_3 consists of three well-developed low conids connected by narrow bridges and labially and lingually delineated by deep folds that are all filled with cement. Anteriorly, the anterior conid has two shallow grooves.

DP_4 is low-crowned and has a hypoconulid. The hypoconulid is very short, located somewhat lower than the occlusal surface of the talonid, and lingually and labially bordered by shallow folds filled with cement (the lingual fold is closed).

P_4–M_2 are stout; the trigonids are somewhat longitudinally compressed, while the talonids are round and their labial sides slightly narrow. The anterolingual wall of the talonids is anterosuperiorly raised; however, it is a little lower than the occlusal surface of the trigonid. The roots of P_4 and M_1 are well-developed and separate. The posterior root is more massive and lies at an angle to the anterior root. The roots of M_2 are partially fused. M_3 is absent from the material.

Measurements in mm. Length of P^3–M^3 (along the alveoli), 9.2; length of P^4–M^2 (along the alveoli), 4.3 and 4.5; supplementary conid of P_3 (length × width), 0.5 × 1.5 (PIN, no. 4516/81) and 0.3 × 1.0 (PIN, no. 4516/80); and hypoconulid of DP_4 (length × width), 0.4 × 0.9 (PIN, no. 4516/345).

Measurements of isolated teeth: upper teeth (length × width): P^3: 1.5 × ? (PIN, no. 4516/63), 1.5 × 3.0 (PIN, no. 4516/97), 1.7 × 3.0 (holotype), and 1.75 × 3.1 (PIN, no. 4516/123); P^4: 2.0 × 5.0 (PIN, no. 4516/113) and 2.25 × 3.5 (PIN, no. 4516/105); M^1: 1.5 × 3.5 (PIN, no. 4516/112), 1.6 × 3.3 (PIN, no. 4516/98), 1.6 × 4.5 (PIN, no. 4516/84), and 1.65 × 3.45 (PIN, no. 4516/106); and M^2: 1.75 × 3.0 (PIN, no. 4516/104); lower cheek teeth: P_3 (length × width): 1.3 × 1.8 (PIN, no. 4516/80) and 1.5 × 1.8 (PIN, no. 4516/81); total length (talonid length) × trigonid width—talonid width: DP_3 (PIN, no. 4516/115), 2.25 (0.75) × 1.5—1.6; P_4 (PIN, no. 4516/102), 2.5 (1.3) × 2.5—1.8; M_1 (PIN, no. 4516/101), 2.15 (1.2) × 2.5—1.6; and M_2 (PIN, no. 4516/83), 2.3 (1.1) × 2.5—1.6.

Comparison. *Desmatolagus periaralicus* differs from *D. gobiensis* and *D. shargaltensis* in its larger size and reduced hypoconulids. P^3 of *D. periaralicus* is

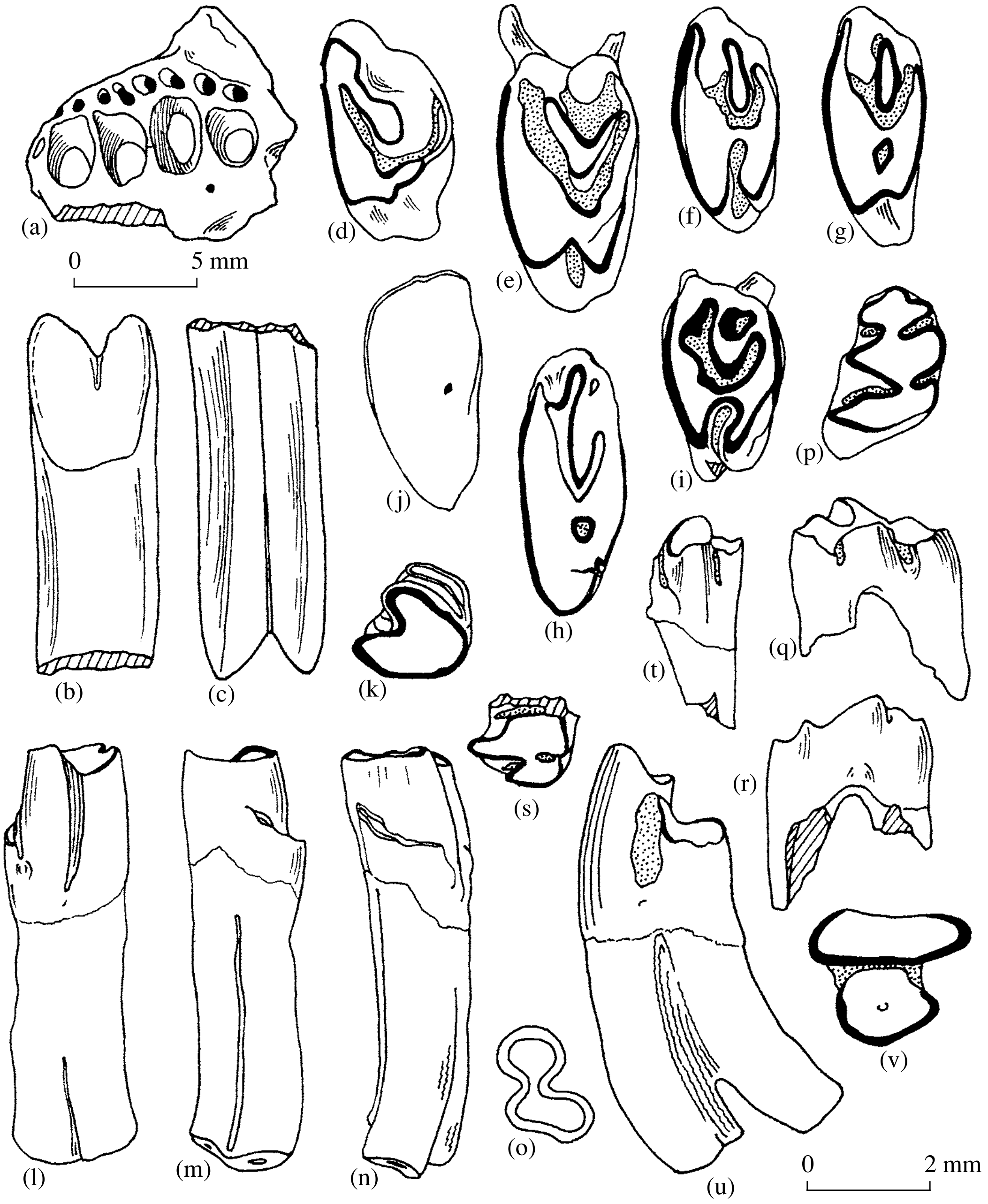


Fig. 19. *Desmatolagus periaralicus* Lopatin, 1998: (a) specimen PIN, no. 4516/100, fragmentary right maxilla; (b, c) specimen PIN, no. 4516/110, right anterior upper incisor: (b) occlusal and (c) frontal views; (d) holotype PIN, no. 4516/99, right P^3; (e) specimen PIN, no. 4516/105, left P^4; (f) specimen PIN, no. 4516/98, left M^1; (g) specimen PIN, no. 4516/112, left M^1; (h) specimen PIN, no. 4516/84, left M^1; (i) specimen PIN, no. 4516/104, left M^2; (j) specimen PIN, no. 4516/109, left lower incisor; (k–o) specimen PIN, no. 4516/81, left P_3: (k) occlusal, (l) labial, (m) lingual, and (n) frontal views and (o) root side; (p–r) specimen PIN, no. 4516/115, left DP_3: (p) occlusal, (q) labial, and (r) lingual views; (s, t) specimen PIN, no. 4516/345, fragmentary left DP_4: (s) occlusal and (t) labial views; (u, v) specimen PIN, no. 4516/102, right P_4: (u) labial and (v) occlusal views; Altynshokysu locality, Aral Formation, Bone Bed 1.

more massive and longer than P^3 of *D. gobiensis*; however, they are approximately equal in width, and the metastyle of the former is smaller, while the central area is larger. In addition, *D. periaralicus* differs from *D. gobiensis* in its well-developed anterior cingulum and long anteroloph of P^3 and relatively deep hypostriae of P^4–M^2. It differs from *D. robustus*, *D. veletus*, and *D. ardynense* in the smaller dimensions and rudimentary hypoconulids of P_4–M_2; and it differs from *D. simplex* in its larger size and the structure of P^3, P_3, and P_4–M_2.

Plate 4


1


2


3


4


5

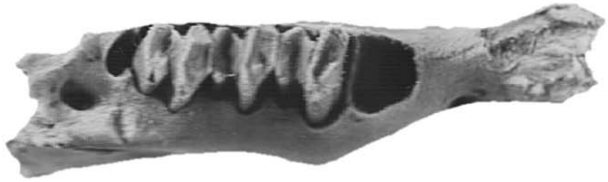

10


6a


7


8


9


6b


11


12


13a


13b

Remarks. The structure of the deciduous teeth of *Desmatolagus* was described by Tobien (1986). The researcher noticed that DP_3 of *Desmatolagus* has a relatively small anterior lobe comparable in size to the second and third lobes. In his opinion, the supplementary anterior denticle (or cingulum) of P_3 corresponds to this structure. From this point of view, the large supplementary conid of P_3 and the well-developed anterior lobe of DP_3 of *D. periaralicus* are of particular interest.

Occurrence. North Aral Region; Lower Miocene, Aral Formation.

Material. In addition to the holotype, the collection of the PIN contains the following specimens from Bone Bed 1 of the Altynshokysu locality: three fragmentary maxillae with alveoli of teeth (nos. 4516/100, 129, and 130) and 36 isolated teeth and their fragments, including eight upper incisors (nos. 4516/64, 69, 110, 111, 117–120), four P^3 (nos. 4516/63, 97, 123, and 463), three P^4 (nos. 4516/105, 113, and 114), four M^1 (nos. 4516/84, 98, 106, and 112), M^2 (no. 4516/104), three lower incisors (nos. 4516/107–109), two P_3 (nos. 4516/80 and 81), two DP_3 (nos. 4516/115 and 478), two P_4 (nos. 4516/102 and 103), DP_4 (no. 4516/345), and six $M_{1–2}$ (nos. 4516/82, 83, 101, 346, 464, and 486); DP_3 stored at the DK; and fragments of the upper cheek stored at the DK and NMW from Bone Bed 2 of the Altynshokysu locality.

Desmatolagus veletus Lopatin, 1998

Plate 4, figs. 1–5

Amphilagus aff. *robustus*: Bendukidze, 1993, p. 26, pl. IX, figs. 1–8, pl. X, figs. 1–4.

Desmatolagus veletus: Lopatin, 1998, p. 84, pl. V, figs. 8–10, text-fig. 3.

Holotype. PIN, no. 4516/208, left P_3; Kazakhstan, North Aral Region, Altynshokysu locality; Lower Miocene, Aral Formation, Bone Bed 4.

Description (Fig. 20). The upper incisors are massive and have a superficial longitudinal groove (without cement) on the anterior surface and a superficial incisure in the cutting edge. The cutting edge of the incisor blades is rounded.

P^4 is very large and rounded rectangular in outline. The lingual side of the crown has a shallow hypostria represented on the occlusal surface by a shallow triangular fold. The crescentic valley is V-shaped and displaced to the posterior margin of the tooth. The labial fold is parallel to the crescentic valley. As the tooth is worn, the occlusal surface widens and the hypostria closes. M^1 is wide and lenticular, and its paracone strongly projects labially. The hypostria is deep; as the tooth is worn, it closes and forms a small lake. The labial roots of P^4 and M^1 are well-developed. P^2, P^3, M^2, and M^3 are absent from the material.

The lower incisor is rounded triangular in cross section, and its anterior edge is flattened. A slightly worn P_3 has an extensive but relatively shallow anteroexternal fold with a crimped pattern in the inner area, which is characteristic of early ontogenetic stages, as well as a shallow posterolingual fold and a fine groove on the anterior side of the crown. The anteroexternal fold is very broad; at this stage of wear, it occupies approximately one-third of the width of the occlusal surface, closely approaches the crown base, and is abundantly filled with cement. Apparently, the posterointernal fold rapidly disappeared because of wear, since, on the posterolingual side of the crown, it is only represented by a short groove. P_3 has two distinctly isolated roots, the posterior one being somewhat wider than the anterior.

P_4–M_2 have separate roots. The crown of P_4 is straight, and the trigonid is substantially wider but somewhat shorter than the talonid. The conids are separated by a very wide external fold and a narrower internal fold that closely approach the crown base. M_1 and M_2 curve slightly anteriorly. The posterior end of the talonid has a relatively large hypoconulid bordered by a deep internal fold and a small external fold. The internal fold is filled with cement and descends to approximately one-fourth of the crown height from the occlusal surface (at the initial stages of wear). When the crown is slightly worn, this fold closely approaches the center of the occlusal surface of the talonid.

Measurements in mm. Upper cheek teeth (length × width): P^4, 3.0 × 5.0 (PIN, no. 4516/206) and

Explanation of Plate 4

All specimens come from the Aral Formation.

Figs. 1–5. *Desmatolagus veletus* Lopatin, 1998: (1) specimen PIN, no. 4516/206, left P^4; (2) specimen PIN, no. 4516/205, worn right P^4; (3) holotype PIN, no. 4516/208, left P_3; (4) specimen PIN, no. 4516/22, left M_1; and (5) specimen PIN, no. 4516/211, right M_1, ×9; Altynshokysu locality, Bone Bed 4.

Figs. 6–10. *Sinolagomys pachygnathus* Li et Qiu, 1980: (6) specimen PIN, no. 4516/2, right dentary fragment with P_4–M_2: (6a) labial and (6b) occlusal views, ×5; (7) specimen PIN, no. 4516/223, right P^3; (8) specimen PIN, no. 4516/244, right M^1; (9) specimen PIN, no. 4516/258, right M^2, ×9; and (10) specimen PIN, no. 4516/27, right P_3, ×15; Altynshokysu, Bone Bed 4.

Fig. 11. *Prosciurus daxnerae* Lopatin, 2000, holotype NMW, no. 1994/00271/0001/1, left M_1, ×15; Altynshokysu, Bone Bed 2.

Fig. 12. *Ansomys crucifer* Lopatin, 1997, holotype PIN, no. 4516/202, left P_4, ×15; Altynshokysu, Bone Bed 4.

Fig. 13. *Steneofiber kumbulakensis* (Lytschev, 1970), specimen PIN, no. 210/767, left dentary fragment with P_4 and M_1: (13a) labial view, ×3; (13b) P_4–M_1, occlusal view, ×6; Akespe locality.

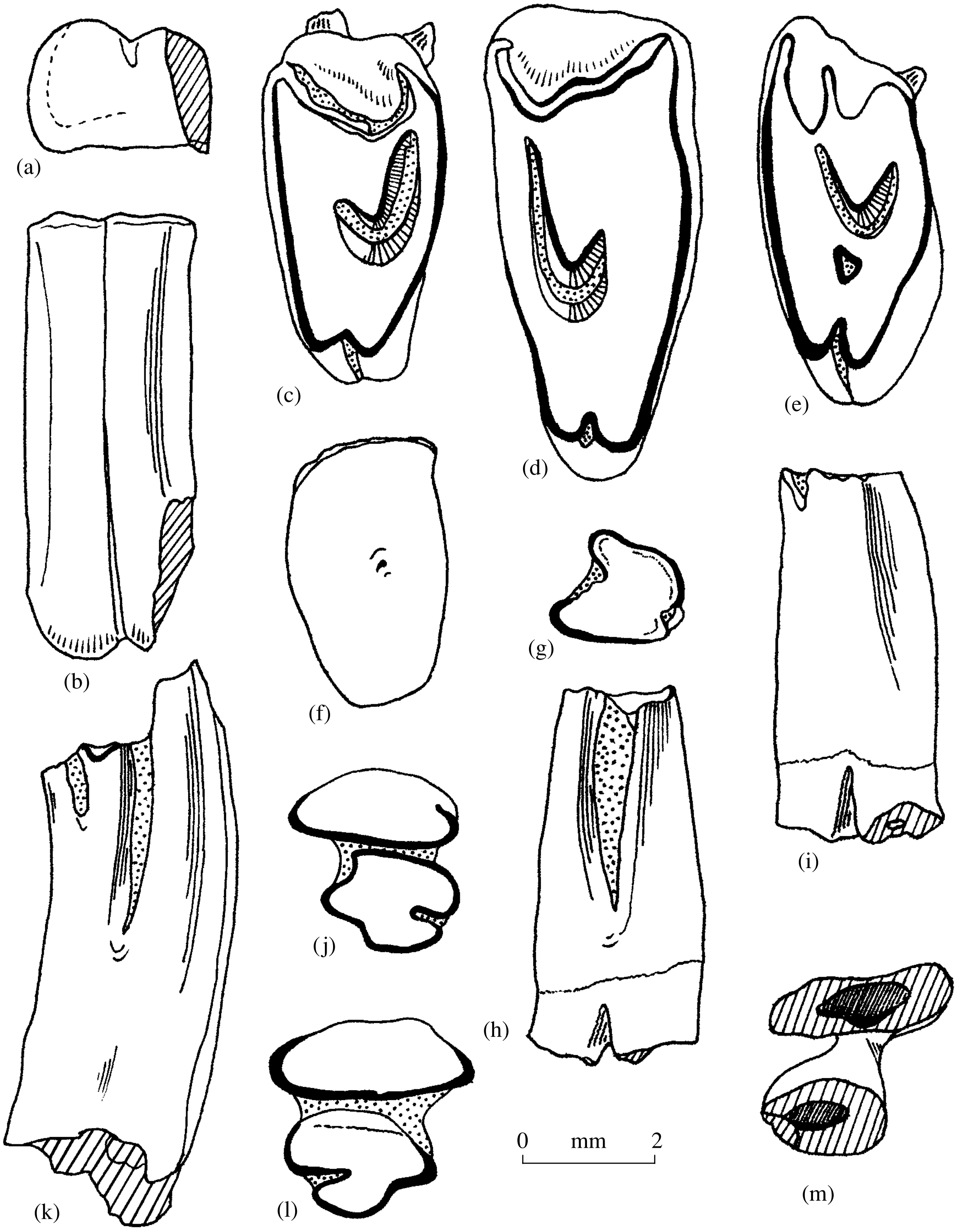


Fig. 20. *Desmatolagus veletus* Lopatin, 1998: (a, b) specimen PIN, no. 4516/213, right anterior upper incisor: (a) occlusal and (b) frontal views; (c) specimen PIN, no. 4516/206, left P^4; (d) specimen PIN, no. 4516/205, right P^4; (e) specimen PIN, no. 4516/207, left M^1; (f) specimen PIN, no. 4516/214, left lower incisor; (g–i) holotype PIN, no. 4516/208, left P_3: (g) occlusal, (h) labial, and (i) lingual views; (j, k) specimen PIN, no. 4516/22, left M_1: (j) occlusal and (k) lingual views; (l, m) specimen PIN, no. 4516/211, right M_1: (l) occlusal view and (m) root side; Altynshokysu locality, Aral Formation, Bone Bed 4.

3.3 × 6.6 (PIN, no. 4516/205); M^1, 2.6 × 5.25 (PIN, no. 4516/207).

Lower cheek teeth: P_3 (length × width), 1.75 × 2.3 (holotype); total length (talonid length) × trigonid width—talonid width: P_4, 3.5 (1.9) × ?—2.5 (PIN, no. 4516/212) and 3.0 (1.55) × 3.25—? (PIN, no. 4516/209); M_1, 3.0 (1.55) × 2.7—2.2 (PIN, no. 4516/22), 3.15 (1.55) × 3.15—2.35 (PIN, no. 4516/210), and 3.25 (1.75) ×

3.1—2.35 (PIN, no. 4516/211); and M_2, ? (?) × 3.55—? (PIN, no. 4516/215) and ? (1.5) × 3.4—? (PIN, no. 4516/209).

Measurements of the hypoconulid of M_1 (length × width): 0.6 × 1.1 (PIN, no. 4516/210), 0.6 × 1.3 (PIN, no. 4516/22), and 0.6 × 1.5 (PIN, no. 4516/211).

Comparison. *D. veletus* is distinguished from all known species of the genus by relatively large measurements, clearly differentiated hypoconulids, and the presence of cement in the anteroexternal fold of P_3 and the internal fold, which isolates the hypoconulid from the talonid. In addition, it differs from *D. simplex* in its well-developed roots of P_3–M_2 and from *D. gobiensis* and *D. periaralicus* in its double-rooted P_3.

Remarks. The available material does not contain P^3; however, the description provided by Bendukidze (1993, p. 26) suggests a close structural similarity between this tooth and P^3 of *D. robustus.* Bendukidze described the form in question as *Amphilagus* aff. *robustus* (Matthew et Granger, 1923) and proposed that *Desmatolagus robustus* be assigned to the genus *Amphilagus.* In my opinion, this is incorrect, because, in contrast to all species of the genus *Amphilagus*, *D. robustus* and *D. veletus* have double-rooted P_3 with a rather shallow anteroexternal groove, separate roots of P_4–M_2, and P^3 lacking the anteroexternal element. In addition, *D. robustus* has a talonid in M_3 and a well-developed M^3 and lacks cement in the anteroexternal fold of P_3 and internal talonid folds of P_4–M_2. *D. veletus* is probably closely related to *D. robustus* and represents its direct descendants. Apparently, the cement in the above-mentioned folds of P_3 and P_4–M_2 was acquired by *D. veletus* in parallel to *Amphilagus.*

Occurrence. North Aral Region; Lower Miocene, Aral Formation.

Material. In addition to the holotype, the collection stored at the PIN contains the following isolated teeth and tooth fragments from the type locality: an upper incisor (no. 4516/213), two P^4 (nos. 4516/205 and 206), M^1 (no. 4516/207), two lower incisors (nos. 4516/187 and 214), two P_4 (nos. 4516/209 and 212), three M_1 (nos. 4516/22, 210, and 211), and two M_2 (nos. 4516/215 and 216). The PIUZ collection contains M_1 from the type locality.

Family Ochotonidae Thomas, 1897

Subfamily Sinolagomyinae Gureev, 1960

Genus *Sinolagomys* Bohlin, 1937

Sinolagomys pachygnathus Li et Qiu, 1980

Plate 4, figs. 6–10

Sinolagomys pachygnathus: Li and Qiu, 1980, p. 198, pl. I, fig. 1, text-figs. 1 and 2; Lopatin, 1998, p. 86, pl. V, fig. 11, text-fig. 4.

Sinolagomys aff. *kansuensis*: Bendukidze, 1993, p. 37, pl. XIV, figs. 2–7.

Sinolagomys aff. *gracilis*: Bendukidze, 1993, p. 35, pl. XIII, figs. 3 and 4, pl. XIV, fig. 1.

Holotype. IVPP, no. 5985; fragmentary right dentary with P_3–P_4; China, Qinghai, Xiejia locality; Lower Miocene, Xiejia Formation.

Description (Fig. 21). A medium-sized member of the genus (P_3–M_3 are 8 mm long along the alveoli). The roots of P^3–M^2 are rudimentary. P^3 is wide and longitudinally short. Its anteroloph ranges from one-third to one-half of the occlusal surface of the crown. The anterior labial root is shaped into a small ridge that is fused with the lingual root. The posterior root projects strongly labially and looks like a sharp keel. The protocone and hypocone project lingually to approximately the same extent, and the protocone is somewhat more massive than the hypocone. They are separated from each other by a large hypostria with a depth and width that depend on the extent of wear. The hypostria reaches the crown base; occasionally, it is filled with cement. The anteroloph is relatively long, large, rounded, and separated from the protocone by a distinct groove, which is almost as long as the hypostria. The crescentic fold varies in depth, is asymmetrical, and its bottom is rounded or slightly pointed.

P^4, M^1, and M^2 are closely similar in structure and decrease in size from P^4 to M^2. The occlusal surface is rounded rectangular, and the protocone projects lingually to a substantially greater extent than the hypocone. The hypostria is narrow; at different stages of wear, it extends for one-third to one-half of the width of the occlusal surface. The labial roots are strongly reduced. The anterior root is slightly more massive than the posterior root.

The lower jaw is stout. At the level of P_4, the horizontal ramus has a characteristic thickening. The mental foramina are located in line with the middle of the diastema and under M_1. The alveolus of the incisor terminates under the talonid of M_1.

P_3 has anteroexternal and anterior reentrant folds and associated superficial grooves that extend to the crown base. The anteroexternal fold is filled with cement.

DP_3 is small, the anterior conid is relatively small, while the posterior conid is substantially wider than the middle conid.

P_4–M_2 are similar in structure and have transversely extended pentagonal trigonids and oviform talonids with slightly sharpened labial edges. The trigonid of P_4 differs from that of M_1 and M_2 in its less extended labial area and the more regular trapezoid outline.

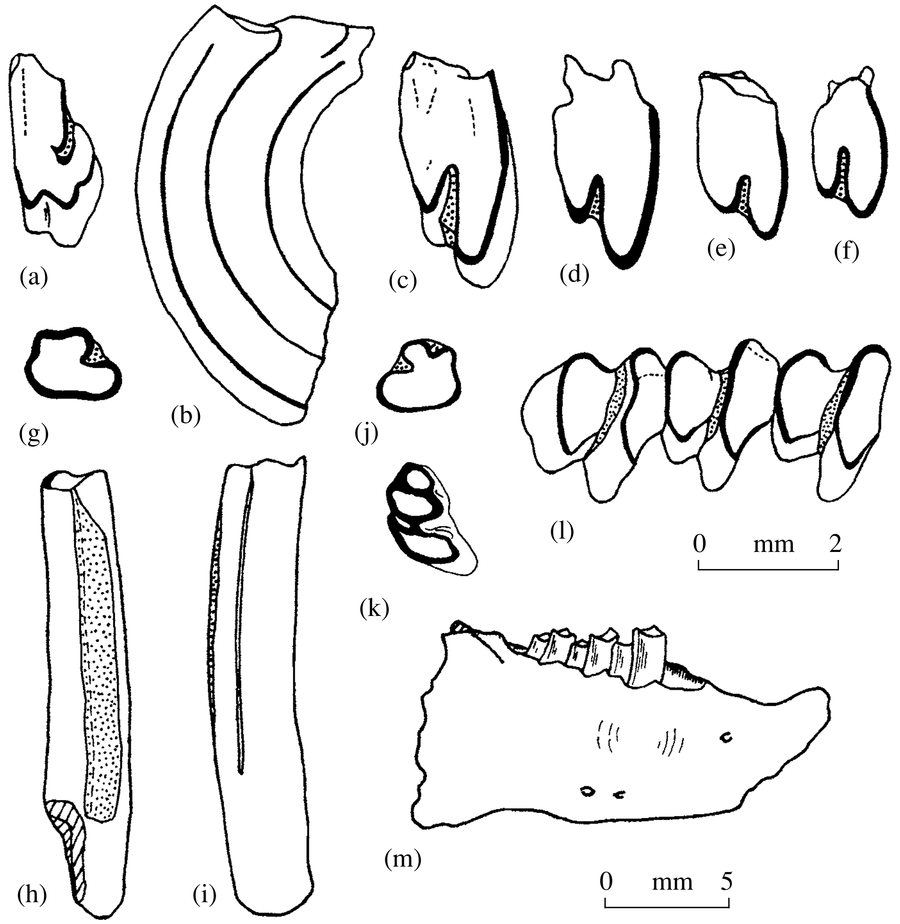


Fig. 21. *Sinolagomys pachygnathus* Li et Qiu, 1980 from the Aral Formation of the Altynshokysu locality: (a, b) specimen PIN, no. 4516/221, right P^3: (a) occlusal and (b) frontal views; (c) specimen PIN, no. 4516/33, right P^4; (d) specimen PIN, no. 4516/231, right P^4; (e) specimen PIN, no. 4516/243, right M^1; (f) specimen PIN, no. 4516/258, right M^2; (g–i) specimen PIN, no. 4516/27, right P_3: (g) occlusal, (h) labial, and (i) frontal views; (j) specimen PIN, no. 4516/269, left P_3; Bone Bed 4; (k) specimen PIUZ, ALT no. 158, right DP_3; Bone Bed 2; (l, m) specimen PIN, no. 4516/2, right dentary fragment with P_4–M_2: (l) P_4–M_2, occlusal view; and (m) general appearance of the labial side; Bone Bed 4.

Measurements in mm:

Tooth	Length			Width				
	n	limits	mean	*n*	limits		mean	
P^3	9	1.3–1.5	1.38	6	2.0–2.8		2.3	
P^4	14	1.45–1.7	1.55	13	2.8–3.5		3.05	
M^1	17	1.25–1.6	1.42	13	2.5–2.9		2.75	
M^2	12	1.1–1.35	1.23	10	2.0–2.25		2.13	
P_3	3	1.0–1.2	1.1	3	1.3–1.5		1.43	
					trigonid	talonid	trigonid	talonid
P_4	4	1.7–1.8	1.75	4	1.75–2.0	1.05–1.45	1.88	1.21
M_1	4	1.6–1.7	1.65	4	1.75–1.9	1.1–1.35	1.81	1.2
M_2	6	1.4–1.7	1.56	6	1.6–1.9	1.0–1.5	1.8	1.16

Comparison. *Sinolagomys pachygnathus* differs from *Sinolagomys major* Bohlin, 1937 in its considerably smaller measurements, shallower hypostriae of P^4–M^2, and relatively narrower talonids of P_4–M_2. The last character also distinguishes this species from *S. gracilis* Bohlin, 1942 and *S. ulungurensis* Tong,

1989. It differs from *S. kansuensis* Bohlin, 1937 in the reduced labial roots of the upper cheek teeth, long anteroloph of P^3, relatively deep hypostria and deep crescentic fold of this tooth, the presence of an anterior fold on P_3, the relatively shorter lower incisor, and the presence of thickening in the anterior region of the horizontal ramus.

Remarks. The length of the anteroloph and the depth of the hypostria and crescentic fold of P^3 of *S. pachygnathus* widely vary, depending on the degree of tooth wear. In a moderately worn tooth, these characters are especially well-pronounced. Bendukidze (1993) determined this form as *S.* aff. *gracilis* on the basis of measurements alone. In addition, this researcher described "*S.* aff. *kansuensis*" from Sayaken (northwestern coast of the Aral Sea). This form displays almost the same characters but has a longer anteroloph of P^3 and is somewhat larger. In my opinion, this form also belongs to *S. pachygnathus*. The difference in size agrees well with the variation ranges of this character in *S. pachygnathus* (Li and Qiu, 1980) and other species of the genus *Sinolagomys* (Bohlin, 1942; Tong, 1989).

Occurrence. China and Kazakhstan; Lower Miocene.

Material. The collection of the PIN contains a dentary fragment with P_4–M_2 (no. 4516/2), a dentary fragment with M_1 (no. 4516/217), and 70 isolated teeth from Bone Bed 4 of the Altynshokysu locality: 12 P^3 (nos. 4516/124, 218–228), 16 P^4 (nos. 4516/32, 33, 35, 229–241), 17 M^1 (nos. 4516/31, 34, 242–256), 12 M^2 (nos. 4516/257–268), two P_3 (nos. 4516/27 and 269), two P_4 (nos. 4516/26 and 42), four M_1 (nos. 4516/127, 128, 270, 271), and five M_2 (nos. 4516/272–276). The PIUZ collection contains three P^4, five M^1, two M^2, P_3, two P_4, one M_1, and two M_2 from Bone Bed 4 of Altynshokysu. The PIUZ, DK, and NMW collections contain 25 isolated teeth and tooth fragments, including nine P^3, three P^4, three M^1, one M^2, two M^3, two DP_3, and fragments of P_4 and molars from Bone Bed 2 of Altynshokysu; and a single P^3 from Akotau (collection DK). In addition, the collection of the PIN contains a dentary fragment with P_3 (no. 210/773) and isolated teeth (P^3, two M^1, three P_4, and four M_{1-2}) from the Akespe locality and three P^3, M^2, two P_4, and M_2 from the Zherlepes locality.

Order Rodentia Bowdich, 1821

Family Aplodontidae Brandt, 1855

Subfamily Prosciurinae Wilson, 1949

Genus *Prosciurus* Matthew, 1903

Prosciurus daxnerae Lopatin, 2000

Plate 4, fig. 11

Prosciurus daxnerae: Lopatin, 2000b, p. 81, text-figs. 1 and 2.

Holotype. NMW, no. 1994/00271/0001/1, left M_1; Kazakhstan, North Aral Region, Altynshokysu locality; Lower Miocene, Aral Formation, Bone Bed 2.

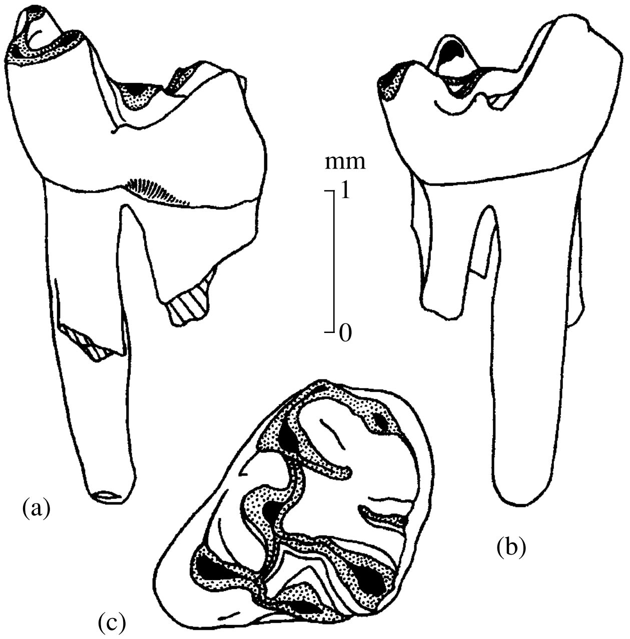


Fig. 22. *Prosciurus daxnerae* Lopatin, 2000, holotype NMW, no. 1994/00271/0001/1, left M_1: (a) labial, (b) lingual, and (c) occlusal views.

Description (Fig. 22). A medium-sized member of the genus. M_1 is four-rooted and low-crowned. The occlusal surface is triangular, the trigonid is substantially narrower than the talonid, and the protoconid and the metaconid are positioned close together. The hypoconid is strongly displaced labially. Metalophid I is well-developed and connects the protoconid to the weakly differentiated anteroconid and the metaconid. Metalophid II looks like a short posterior arm of the protoconid. The metaconid is higher than the protoconid and is weakly compressed transversely. The inner metaconid crest is undeveloped, while the metastylid crest is weakly developed. The mesostylid is small and rounded and separated from the metaconid and entoconid by distinct folds. The mesostylid crest is short, narrow, and weak. The mesoconid is large, low, and lacks an ectomesolophid. The ectolophid and the hypolophid are complete. The entoconid is strongly displaced posteriorly. The hypolophid is directed posterointernally and has a weak anterior projection in the middle. The hypoconulid is large and triangular. The posterolophid is complete and reaches the middle of the posterior wall of the entoconid.

Measurements in mm. Holotype: length, 1.80; trigonid width, 1.35; and talonid width, 1.75.

Comparison. *P. daxnerae* differs from the Asian *P. arboraptus* Shevyreva, 1971 in its narrow trigonid and the presence of the mesostylid and rudimentary mesostylid crest on M_1. It differs from all North American species in its narrower M_1. In addition, it differs from *P. relictus* (Cope, 1873) in its small mesostylid and from *P. vetustus* Matthew, 1903, *P. parvus* Korth,

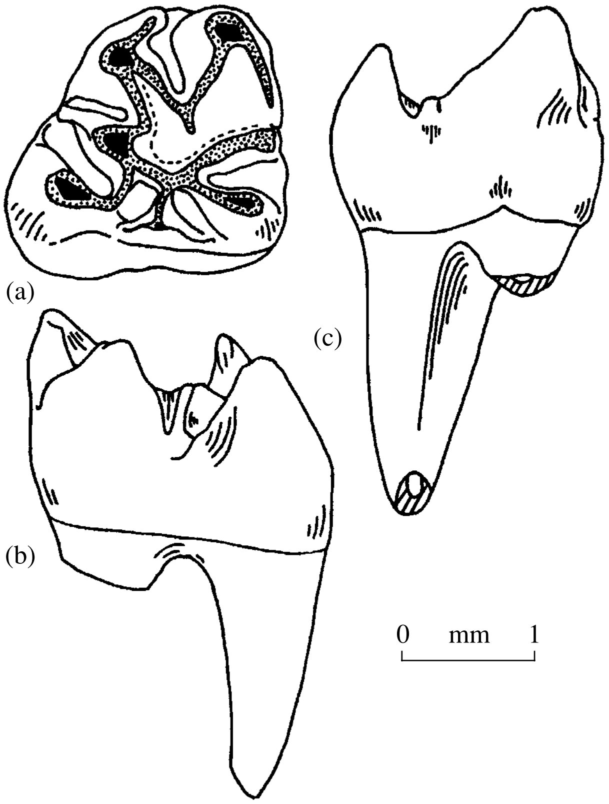


Fig. 23. *Ansomys crucifer* Lopatin, 1997, holotype PIN, no. 4516/202, left P_4: (a) occlusal, (b) labial, and (c) lingual views.

1989, and *P. magnus* Korth, 1989 in its long and complete hypolophid.

Remarks. *P. daxnerae* is assigned to *Prosciurus* because it is similar to this genus in the structure of M_1. The complete hypolophid and rudimentary mesostylid crest are also characteristic of some North American species of the genus *Prosciurus* (Rensberger, 1975; Korth, 1989).

Three species of the genus *Prosciurus* have been described from the Oligocene of Asia: *P. lohiculus* Matthew et Granger, 1923, *P. arboraptus* Shevyreva, 1971, and *P. ordosicus* Wang, 1987. On the basis of structural features of the upper and lower teeth, *P. lohiculus* is currently placed in a separate genus, *Anomoemys* Wang, 1986, of the family Cylindrodontidae (Wang, 1986; Huang, 1993). *P. ordosicus* is most likely a synonym for *P. arboraptus.* The idea proposed by Wang (1987) that *P. arboraptus* belongs to the genus *Haplomys* Miller et Gidley, 1918 is incorrect. This assumption was based on comparison of the sole M^2 from China (original material examined by Wang) with specimens obtained by Kowalski (1974) from the Oligocene of Mongolia, instead of comparison with the type material described by Shevyreva (1971) from Kazakhstan. In actual fact, *P. arboraptus* does belong to *Prosciurus,* because the structure of its P^4–M^3 fits into this genus (Shevyreva, 1971, 1976). *P. daxnerae* may well be a descendant of *P. arboraptus.*

Material. Holotype.

Subfamily Ansomyinae Qiu, 1987

Genus *Ansomys* Qiu, 1987

Ansomys crucifer Lopatin, 1997

Plate 4, fig. 12

Ansomys crucifer: Lopatin, 1997, p. 102, text-fig. 2.

Holotype. PIN, no. 4516/202, isolated left P_4; Kazakhstan, North Aral Region, Altynshokysu locality; Lower Miocene, Aral Formation, Bone Bed 4.

Description (Fig. 23). P_4 is double-rooted and low-crowned. The occlusal surface is trapezoid. The protoconid and metaconid are relatively massive and high, and the metaconid is somewhat higher than the protoconid. These cusps are separated from one another by a deep anterior valley. The protoconid has a short free anterior arm and a long posterior arm that is posterolingually directed and connected to a long inner crest of the metaconid; thus, the V-shaped metalophid II is formed. From the point of fusion between the inner crest of the metaconid and the posterior arm of the protoconid, a crest originates; it extends posteriorly, slightly curves lingually, and closely approaches the mesostylid crest. The mesostylid is low and weakly developed. It is separated from the entoconid by a deep lingual fold. The mesostylid crest is long and wide and connected to the middle region of the hypolophid. The crest of the metastylid is relatively weakly developed. A distinct shallow groove is noticeable between its posterior end and the cuspule of the mesostylid. The mesoconid is comparatively large, low, and flattened. A massive ectomesolophid is present. It reaches the labial edge of the occlusal surface and divides the external fold into anterior and posterior parts. The ectolophid is complete and abruptly curves inward both anterior and posterior to the mesoconid. The hypolophid deviates from the posterior region of the mesoconid and extends posterolingually. It is connected to the relatively small and longitudinally compressed entoconid. The hypoconid is stout, very large, and shifted somewhat labially. Its anterior arm is fused with the ectolophid. In the present stage of wear, the posterolophid is incomplete, since the segment of this crest between the hypoconid and hypoconulid is substantially lower than the posterior cusps. Apparently, a well-pronounced posterolophid is only formed in a considerably worn tooth. The hypoconulid is a triangle with a very wide base, which corresponds to the posterior side of the cusp. A relatively small additional crest (hypoconulid crest) diverges from its anterior side and adjoins the middle region of the hypolophid. Thus, a cruciform pattern composed of the hypolophid and crests of the mesostylid and hypoconulid is formed in the center of the talonid basin.

Measurements in mm. Holotype: length, 1.91; width, 2.05.

Comparison. *A. crucifer* differs from *A. shantungensis* (Rensberger et Li, 1986) in the presence of well-developed additional crests of the talonid basin, a distinct metaconid crest, and a stronger metastylid crest. It differs from *A. orientalis* Qiu, 1987 in its larger dimensions, the absence of bifurcation in the inner crest of the metaconid of P$_4$, the more weakly developed metastylid crest, the absence of the anterior spur of the mesoconid, and the more massive hypoconid. It differs from *A. shanwangensis* Qiu et Sun, 1988 in its lower metastylid crest, relatively smaller hypoconulid, absence of the anterior spur of the mesoconid, smaller mesostylid, and a different pattern of contacts between additional crests of the talonid basin, i.e., the mesostylid crest is connected to the hypolophid instead of the metaconid crest (as is observed in *A. shanwangensis*).

Remarks. In addition to *A. crucifer*, three species of the genus *Ansomys* have been described from Asia (all were originally established in China): the Late Oligocene *A. shantungensis* and the Miocene *A. orientalis* (ca. MN4) and *A. shanwangensis* (ca. MN5) (Qiu, 1987; Qiu and Sun, 1988; Qiu and Qiu, 1995). *A. orientalis* was also registered in the Early Miocene Ulan-Tologoi Fauna of Mongolia (Zazhigin and Lopatin, 2000a). The well-developed additional crests of the talonid basin and the complete ectolophid and hypolophid (Qiu and Sun, 1988) are characteristic of Miocene species. These characters draw *A. crucifer* together with *A. orientalis* and *A. shanwangensis.* On the other hand, this species has a relatively low metastylid crest, a massive hypoconid, and a small mesostylid; this is typical of the Late Oligocene *A. shantungensis.* Thus, regarding the evolutionary stage of its dental morphology, *A. crucifer* is intermediate between the Late Oligocene species and the more advanced Miocene forms.

A. crucifer is likely a direct descendant of *A. shantungensis*, since the lower teeth of this Late Oligocene species tend to acquire additional crests of the talonid basin that occur in the same specific combination (Rensberger and Li, 1986, text-figs. 1, 2), as is fully developed in P$_4$ of *A. crucifer.* At the same time, *A. crucifer* retains primitive features that are characteristic of *A. shantungensis*: a relatively stout hypoconid, an incomplete posterolophid, and a weakly developed mesostylid and metastylid crest.

Material. Holotype.

Family Castoridae Hemprich, 1820

Subfamily Castorinae Hemprich, 1820

Genus *Steneofiber* Geoffroy, 1833

Steneofiber kumbulakensis (Lytschev, 1970)

Plate 4, figs. 13; Plate 5, figs. 1–13

Propalaeocastor kumbulakensis: Lytschev, 1970, p. 84, text-fig. 1; 1987, p. 70, text-fig. 1.

Steneofiber cf. *viciacensis*: Lytschev and Aubekerova, 1971, p. 14, text-fig. 3.

Steneofiber aff. *kumbulakensis*: Bendukidze, 1993, p. 79, pl. XXIII, fig. 6; pl. XXIV, figs. 1–3.

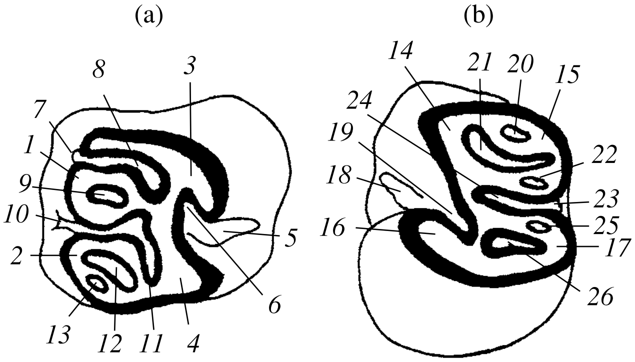


Fig. 24. Dental structure in the family Castoridae, using moderately worn premolars of *Steneofiber kumbulakensis* (Lytschev, 1970) as an example: (a) right P^4 and (b) left P$_4$. Designations: (*1*) paracone, (*2*) metacone, (*3*) protocone, (*4*) hypocone, (*5*) hypostria, (*6*) hypoflexus, (*7*) anterostria, (*8*) anteroflexus, (*9*) parafossette, (*10*) mesostria, (*11*) mesoflexus, (*12*) postmesofossette, (*13*) metafossette, (*14*) protoconid, (*15*) metaconid, (*16*) hypoconid, (*17*) entoconid, (*18*) hypostriid, (*19*) hypoflexid, (*20*) parafossettid, (*21*) metafossettid, (*22*) premesofossettid, (*23*) mesostriid, (*24*) mesoflexid, (*25*) postmesofossettid, and (*26*) entofossettid.

Capacikala sajakensis: Bendukidze, 1993, p. 92, pl. XXVII, figs. 1, 2, and 4.

Capacikala aff. *sajakensis*: Bendukidze, 1993, p. 94.

Steneofiber kumbulakensis: Lopatin, 2003, p. 15, text-figs. 1–3, 4A–4M, and 5.

Holotype. IZ, no. M-2020/66-Ag, skull fragment with $P^4/_4$–$M^3/_3$; Kazakhstan, North Aral Region, Kumbulak locality; Lower Miocene, Aral Formation.

Description (Figs. 24–26). The cheek teeth are relatively low-crowned (mesodont) and lack cement. P^4 is rectangular in outline; in the unworn state, its occlusal surface is finely tuberculate and divided by numerous folds (one specimen; Pl. 5, fig. 1). The hypostria extends for more than two-thirds of the lingual height of the crown, the mesostria extends for approximately two-thirds of the labial height, and the anterostria extends for a little less than one-third of the anterolabial height of the crown. The hypoflexus is shallow and directed abruptly anteriorly. It is connected by a narrow groove to the point where the anteroflexus and the anterior arm of the mesoflexus fuse (in the anterolingual corner of the occlusal surface). The posterior arm of the mesoflexus abruptly curves posteriorly. It is separated from the postmesofossette by a very narrow crest; in the space between them, there are two small fossettes. The parafossette (subparafossette after Hugueney, 1999a) consists of three isolated fossettes. The area of the metafossette is located dorsal to the main plane of the occlusal surface and isolated by a low crest from the postmesofossette. The walls of folds are irregular in shape and equipped with fine protrusions (plication).

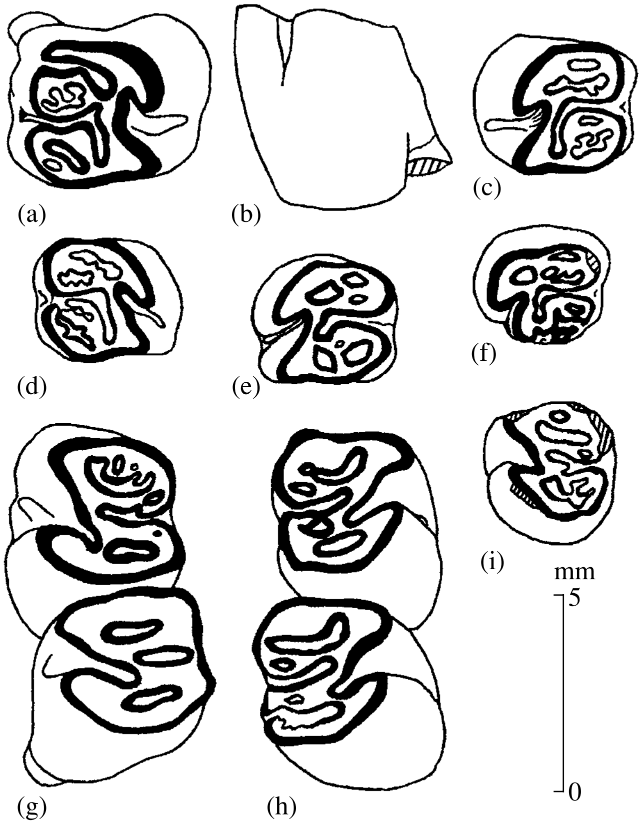


Fig. 25. *Steneofiber kumbulakensis* (Lytschev, 1970) from the Aral Formation: (a, b) specimen PIN, no. 4516/11, right P^4: (a) occlusal and (b) lingual views; (c) specimen PIN, no. 4516/312, left M^1; (d) specimen PIN, no. 4516/322, right M^2; Altynshokysu locality, Aral Formation, Bone Bed 4; (e) specimen PIN, no. 210/768, left M^2; Akespe locality; (f) specimen PIN, no. 4516/310, left M^3; Altynshokysu, Bone Bed 4; (g) specimen PIN, no. 210/767, left P_4–M_1; Akespe locality; (h) specimen PIN, no. 4516/320, right M_1–M_2; and (i) specimen PIN, no. 4516/333, left M_3; Altynshokysu, Bone Bed 4.

At the initial stage of wear, the plane of the occlusal surface becomes even (two specimens; Pl. V, fig. 2). The anteroflexus and the anterior arm of the mesoflexus remain in connection with each other and with the end of the hypoflexus. The posterior arm of the mesoflexus is connected to a small round lake that is located in the posterolingual corner of the occlusal surface. The flexi are almost as high as in unworn teeth. The metafossette may be shaped into a small flexus and have a weak metastria. The parafossette consists of two or three small lakes. Three small oval or teardrop-shaped lakes are arranged in a row located in place of the postmesofossette.

A slightly worn P^4 (two specimens; Pl. 5, fig. 3) has completely formed roots and a relatively deep hypoflexus, the end of which is neither connected to the posterior arm of the mesoflexus nor to the anteroflexus (these folds contact lingually). The anterostria is short. The posterior region of the mesoflexus adjoins or is fused with the postmesofossette, namely, with the largest fossette participating in the formation of the postmesofossette. A small supplementary lake is located between the labial region of the mesoflexus and the postmesofossette. The parafossette consists of two small lakes. The metafossette lies on a level with, or somewhat dorsal to, the main plane of the occlusal surface.

A moderately worn P^4 (two specimens; Pl. 5, figs. 4, 5; Fig. 25a) has a very small anterostria. The anteroflexus has a constriction in the middle and strongly expands lingually. The parafossette is shaped like a small and irregularly shaped lake. The anteroflexus and mesoflexus are isolated from each other; however, the mesoflexus has a small anterior process. The postmesofossette is isolated from the posteriorly curved mesoflexus; like the metafossette, it is shaped as a small oval lake. Subsequently, the hypoflexus becomes deeper, while its end turns more and more posteriorly; the anteroflexus is divided into two parts, the lingual anterofossette and the labial anteroflexus (the latter retains contact with a small anterostria); the anterior process of the mesoflexus disappears; and the parafossette tends to become round. At this stage, the depth of the hypostria ranges from one-half to one-fourth of the lingual crown height. The enamel walls increase in thickness.

In a heavily worn tooth (one specimen), the enamel walls of the fossettes strongly project above the dentin field and the mesoflexus becomes closed to form the mesofossette. The hypoflexus also closes.

An unworn M^1 (one specimen) is similar to P^4. The hypoflexus slightly juts out into the occlusal surface. The anterior lobe has three clearly differentiated transverse fossettes: a broad anterofossette (parafossette after Hugueney, 1999a), a relatively narrow parafossette (subparafossette after Hugueney, 1999a), and a small premesofossette, which are bordered by small tuberculate crests. Lingually, there is an isolated rounded longitudinal fossette. The lingual region of the mesoflexus abruptly curves posteriorly and almost reaches the posterior border of the occlusal surface. Behind it, there are an isolated postmesofossette (which has a poorly pronounced exit), the metafossette the lingual end of which curves posteriorly, and a small lake at the posterior border of the occlusal surface.

In a slightly worn tooth (two specimens; Pl. 5, fig. 6; Fig. 25c), the hypoflexus juts out into the occlusal surface to a greater extent, the anterofossette becomes shorter, and the parafossette is fused with the premesofossette and the anterolingual fossette. Three transversely elongated oval fossettes, i.e., the postmesofossette and the double metafossette, are located one after another posterior to the mesoflexus. The metafossette consists of two fossettes, which are connected to each other or isolated. At this stage of wear, the fossettes retain slightly crimped walls, the hypostria extends for one-half of the lingual crown height, and the mesostria extends for one-third of the lingual crown height.

In a moderately worn M^1 (one specimen), the same structural pattern is preserved; however, the lingual region again becomes isolated from the parafossette. In a heavily worn tooth (two specimens), the posterior region becomes isolated from the mesoflexus, the hypostria shortens to one-fifth of the lingual height, and the hypoflexus strongly juts out into the occlusal surface, which becomes broader in outline.

An unworn M^2 (one specimen) is similar in structure to M^1. The anteroflexus has a poorly pronounced exit on the anterolabial side and its lingual region is isolated (anterolingual fossette). The parafossette is closed. The mesoflexus abruptly curves posteriorly. Its extreme posterior part is shaped into a separate fossette. The long metafossette crosses the metacone and closely approaches this fossette. The hypostria extends for approximately two-thirds of the lingual crown height, while the mesostria extends for one-half to one-third of the labial crown height and contains a poorly pronounced premesofossette exit. Posteriorly, the mesoflexus is connected to a relatively small postmesofossette.

At the initial stage of wear (one specimen; Pl. 5, fig. 7), the crests acquire a clearly flat surface and the fossettes have slightly crimped walls. The anterofossette is connected to the anterolingual fossette, while the parafossette is separated from it by a distinct crest. The mesoflexus is connected to its posterior lobe. The postmesofossette and metafossette are closed.

The occlusal surface of a slightly worn M^2 (one specimen; Pl. 5, fig. 8; Fig. 25d) has a united dentin field. The hypostria extends for one-half or one-third of the lingual height, and the mesostria extends for one-third of the labial height. A long anterofossette is formed with a lingual region that expands and adjoins the end of the hypoflexus. The labial regions of the postmesofossette, mesoflexus, and metafossette are connected to each other.

At the moderate stage of wear, the occlusal surface of M^2 (two specimens; Pl. 5, fig. 9; Fig. 25e) is simplified. The anterofossette and metafossette are divided into two. The posterior region of the mesoflexus is detached. The parafossette and postmesofossette are small lenticular lakes.

M^3 is round in outline. The protocone projects lingually to a much greater extent than the hypocone. In the intact state (two specimens), the occlusal surface is tuberculate–plicate. The hypoflexus only slightly juts out into the crown. The anterofossette is isolated and, occasionally, has a poorly pronounced exit. Its lingual region is detached to form a separate fossette, which is sometimes connected to the parafossette or the lingual edge of the mesoflexus. At the labial edge, the parafossette is divided by a transverse ridge. The lingual region of the mesoflexus abruptly curves posteriorly and is occasionally connected to the hypoflexus. The postmesofossette is located behind the mesoflexus. The metaflexus has a poorly pronounced exit on the posterior side of the crown. It extends obliquely and is located substantially more dorsally than the main plane of the occlusal surface. A small ridge separates the metaflexus from the relatively close positioned labial region of the postmesofossette (Pl. 5, fig. 10).

A slightly worn M^3 (two specimens) has a united dentin field on the occlusal surface. The anteroflexus is oval. Its exit is shaped as a weak notch. Posterior to the anteroflexus, the parafossette is located (or two connected transverse fossettes), lingual to which there is a triangular or isolated oval fossette. The structure of the mesoflexus, postmesofossette, and metafossette is the same as in the preceding stage of wear.

In a moderately worn M^3 (one specimen), the expanded posterior region of the mesoflexus is detached, the anteroflexus and metaflexus are closed, and the fossettes are reduced.

P_4 in the unworn state displays a tuberculate–plicate pattern (two specimens; Pl. 5, fig. 11). At the initial wear stage (one specimen), the surface of the crests becomes flat. The hypostriid extends for approximately two-thirds or three-fourths of the labial crown height, while the mesostriid extends for one-third or half of the lingual height. At these stages, the main structural elements of the occlusal surface are masked by the crimped pattern of folds alternating with the tuberculate crests. It is possible to discern an isolated fossettid in the anterolabial corner of the occlusal surface (i.e., the labial region of the metafossettid), a small parafossettid (proparafossettid after Hugueney, 1999a), metafossettid (parafossettid after Hugueney, 1999a), premesofossettid (with a very small exit into the mesostriid), mesoflexid, postmesofossettid, and entofossettid (metafossettid after Hugueney, 1999a). The entofossettid is large, and its lingual region is detached to form the entoflexid.

The occlusal surface of a slightly worn P_4 (one specimen) displays a united dentin field. The hypoflexid deeply juts out into the occlusal surface and adjoins the entofossettid. The entoflexid is detached, short, and broad. Other structural elements are a short transverse parafossettid, long metafossettid, short lenticular premesoflexid, mesoflexid, and small teardrop-shaped postmesofossettid. The metafossettid is slightly inclined anteriorly, with an expanding labial region, and the lingual region curves. The mesoflexid is similar in shape to the metafossettid. The premesoflexid has a very narrow and small exit.

In a moderately worn P_4 (one specimen; Pl. 4, fig. 13b; Fig. 25g), the parafossettid, premesofossettid, and postmesofossettid are shaped as small lakes; the lingual region of the mesoflexid abruptly narrows; the entoflexid closes; and the entofossettid is formed. The hypoflexid deeply juts out into the occlusal surface and extends posteriorly. The hypostriid extends for about half of the labial height, while the mesostriid extends for approximately one-fifth of the lingual height of the crown.

A slightly worn M_1 (four specimens; Pl. 5, fig. 12) displays a relatively deep hypoflexid. The parafossettid is shaped as a round lake. The metafossettid curves abruptly anteriorly. The premesofossettid is small, oval, and located at the lingual border of the occlusal surface. The mesoflexid is straight or slightly curved anteriorly, and its posterior process is connected to a small postmesofossettid. The entoflexid has a narrow exit (which, sometimes, is completely closed) and, usually, a posteriorly oriented process. The hypostriid and mesostriid are relatively short and extend for half of the labial height and one-fifth of the lingual height of the crown, respectively.

At a moderate stage of wear (three specimens; Fig. 25h), the parafossettid disappears, the entoflexid becomes the entofossettid, the premesofossettid and postmesofossettid decrease in size, and the hypoflexid deepens.

In a heavily worn tooth (one specimen: Pl. 4, fig. 13b; Fig. 25g), the mesofossettid appears. Two other fossettids—the oval metafossettid (of the same width as the mesofossettid) and the entofossettid—are retained. The hypostriid extends for about a third of the labial height. In an extremely heavily worn tooth (one specimen), the crown is completely abraded down to the root. Only the hypofossettid, a short mesofossettid (extending to the center of the occlusal surface), and a round lake in place of the metafossettid are observed on the occlusal surface. The hypofossettid extends posteriorly, while its end abruptly curves anteriorly.

An unworn M_2 (one specimen) has a somewhat asymmetrical crown, because the posterior lobe of the tooth narrows. The hypostriid and mesostriid are deep and extend for two-thirds and one-third of the labial and lingual height of the crown, respectively. The occlusal surface is tuberculate–plicate, and individual structural elements become better pronounced at subsequent wear stages.

In a slightly worn M_2 (three specimens), the parafossettid is large and has crimped walls. The metaflexid (paraflexid after Hugueney, 1999a) is very long, gently curves posteriorly, and expands lingually. The premesofossettid is reduced; sometimes, it is connected to the mesoflexid. The mesoflexid is transversely extended and has crimped walls. The posterior process of this fold is sometimes connected to the postmesofossettid, which is smaller in size. The entoflexid is large and reaches the posterior termination of the hypoflexid; it has a constriction in the middle or is divided into the lingual flexid and the labial fossettid.

At a moderate stage of wear (two specimens; Fig. 25h), the parafossettid is shaped as a small lake and the metafossettid is formed. The premesofossettid and postmesofossettid become small lakes isolated from the mesoflexid or completely disappear. The entoflexid retains a very narrow exit or closes. The hypostriid extends for about half of the labial height, and the mesostriid extends for about one-fourth of the lingual height of the crown. The subsequent wear stages seem to be similar to those of M_1.

The anterior lobe of M_3 is slightly wider than the posterior lobe. A slightly worn tooth (one specimen) displays wide folds of the mesoflexid and entoflexid and has a small premesofossettid. At a moderate stage of wear (one specimen; Pl. 5, fig. 13; Fig. 25i), the tooth has a relatively shallow hypoflexid, small oval parafossettid, anteriorly curved metafossettid, superficial lingual lake of the premesofossettid, mesoflexid with a posterior arm, and lake of the postmesofossettid connected to a large and posteriorly concave entofossettid. The hypostriid extends for about one-half of the labial height, while the mesostriid extends for about one-fourth of the lingual height of the crown.

Measurements in mm. Length of P_4–M_1 (PIN, no. 210/767), 7.7; length of M_1–M_2 (PIN, no. 4516/320), 8.0.

Measurements of isolated teeth (occlusal surface):

Tooth	Length			Width		
	n	limits	mean	*n*	limits	mean
P^4	6	3.7–4.2	4.0	5	2.7–3.5	3.1
M^1	5	3.0–3.3	3.2	5	2.7–4.1	3.1
M^2	3	2.9–3.2	3.0	3	2.3–3.0	2.6
M^3	5	2.7–3.0	2.8	7	2.4–3.2	2.7
P_4	4	3.7–4.0	3.9	5	2.9–3.6	3.2
M_1	4	3.5–3.7	3.65	5	3.1–3.7	3.4
M_2	6	3.0–3.7	3.3	6	2.7–3.4	3.05
M_3	1	3.0	–	2	2.5–2.6	–

Comparison. *S. kumbulakensis* differs from *S. minimus* Filhol, 1891, *S. wenzensis* Sulimski, 1964, *S. butselensis* Misonne, 1957, and *S. dehmi* Freudenberg, 1941 in the presence of the postmesofossettid on P_4–M_2. In addition, it differs from the first two species in the presence of anteroflexi and parafossettids on these teeth. From *S. shevyrevae* Lytschev et Shevyreva, 1994 and *S. zaissanensis* Lytschev et Shevyreva, 1994, it differs in the longer and crimped mesoflexus of P^4 and, from *S. kazakhstanicus* (Borissoglebskaya, 1967), in the larger measurements. It differs from *S. depereti* Mayer, 1908, *S. anderssoni* (Schlosser, 1924), *S. broilii* (Teilhard de Chardin et Young, 1931), *S. jaegeri* (Kaup, 1832), *S. minutus* (Meyer, 1838), and *S. eseri* Meyer, 1846 in its smaller measurements.

Remarks. Study of ontogenetic variation in the dental structure of *S. kumbulakensis* has shown that the pattern of the occlusal surface gradually simplifies, depending on the extent of wear (Fig. 26; see also Lopatin, 2003). The structure and measurements of P_4 and M_1 in the holotype of *Capacikala sajakensis* Bendukidze, 1993 (Bendukidze, 1993, pl. XXVII, figs. 1, 2) fit into those of heavily worn teeth of *S. kumbulakensis*, and M^1 of this form is identical to a worn M^1 of *S. kumbulakensis*. Consequently, the name *Capacikala sajakensis* should be regarded as a junior synonym for *S. kumbulakensis.*

Occurrence. Kazakhstan; Lower Miocene.

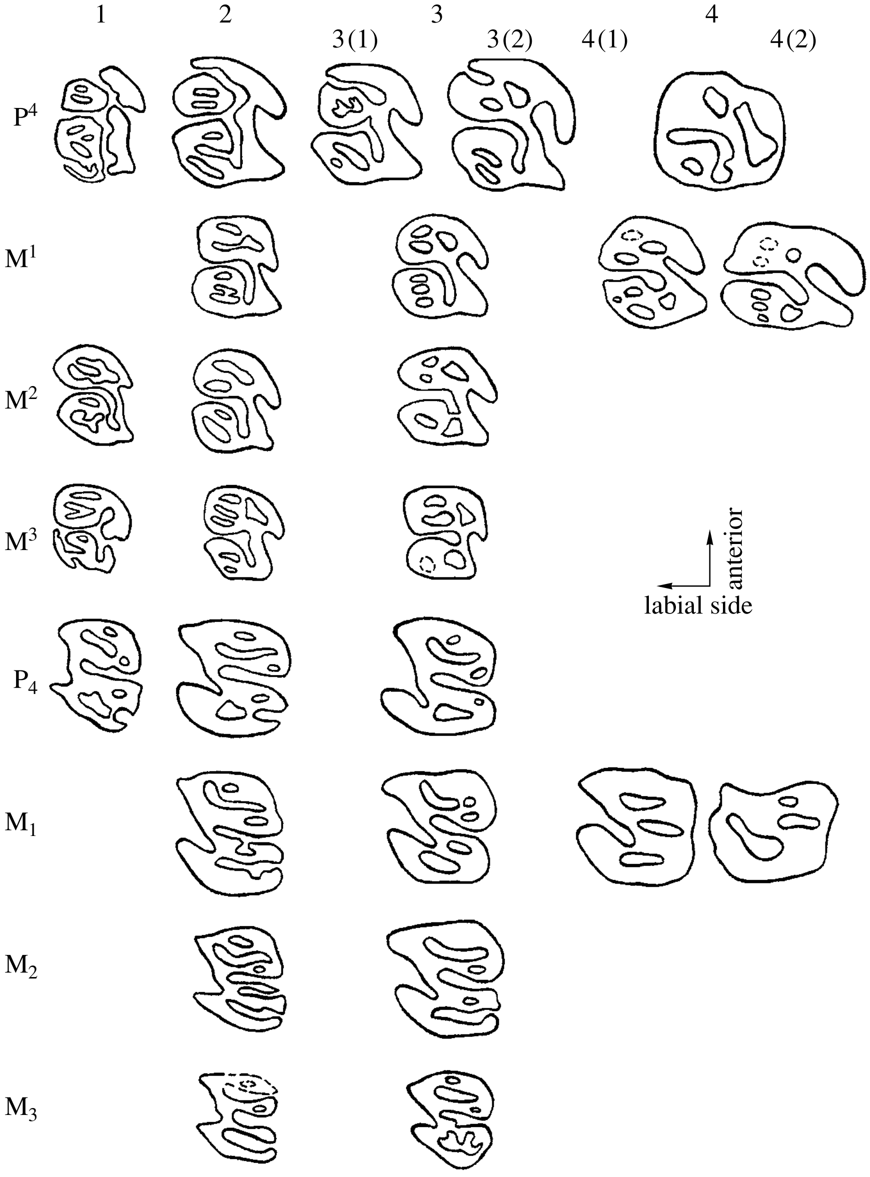


Fig. 26. The changes in the occlusal surface pattern of the cheek teeth of *Steneofiber kumbulakensis* (Lytschev, 1970) as a result of wear. Designations: (1–4) stages of wear: (1) initial stage, the presence of three or four flexi (flexids) and crimped enamel walls; (2) slight wear, three flexi (flexids) are usually present; (3) moderate wear, two flexi (flexids) are usually present; and (4) heavy wear, as a rule, only the hypoflexus (hypoflexid) is present, while other folds are closed; 3(1)–3(2) and 4(1)–4(2), successive phases of wear within the same stage.

Material. The collection stored at the PIN contains a fragment of the left dentary with P_4 and M_1 (no. 210/767) and two isolated teeth, M^2 (no. 210/768) and M_2 (no. 210/769), from the Akespe locality; isolated M_2 (no. 4516/122) and M_3 (no. 4516/121) from Bone Bed 1 of Altynshokysu; a fragment of the right dentary with M_1 and M_2 (no. 4516/320) and 38 isolated teeth and tooth fragments: eight P^4 (nos. 4516/10–12, 307, 308, 315, 316, and 339), six M^1 (nos. 4516/24, 312, 313, 323, 330, and 331), three M^2 (nos. 4516/314, 317, and 322), six M^3 (nos. 4516/29, 310, 319, 332, 336, and 337), four P_4 (nos. 4516/23, 37, 38, and 309), seven M_1 (nos. 4516/39, 324, 326, 328, 329, 334, and 338), four M_2 (nos. 4516/301, 318, 326, and 335), and M_3 (no. 4516/333) from Bone Bed 4 of Altynshokysu.

Steneofiber schokensis (Bendukidze, 1993)

Plate 5, fig. 14

Palaeocastor sp.: Bendukidze, 1993, p. 84, pl. XXV, fig. 8.

Capatanka schokensis: Bendukidze, 1993, p. 85, pl. XXVI, figs. 1–4.

Capatanka aff. *schokensis*: Bendukidze, 1993, p. 91.

Steneofiber schokensis: Lopatin, 2003, p. 21, figs. 4N, 6A–6D.

Plate 5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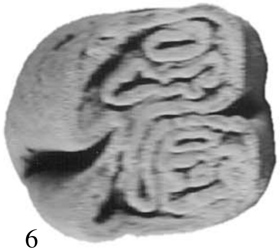
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Holotype. IP, no. 15/48, horizontal ramus of the lower jaw with a fragmentary incisor and P_4–M_3; Kazakhstan, North Aral Region, Altynshokysu locality; Lower Miocene, Aral Formation.

Description (Fig. 27). The cheek teeth are relatively low-crowned (mesodont) and lack cement in the flexi and flexids. P^4 is large and massive and has a rounded square crown outline and three roots, i.e., a

Explanation of Plate 5

All specimens come from the Aral Formation.

Figs. 1–13. *Steneofiber kumbulakensis* (Lytschev, 1970): (1) specimen PIN, no. 4516/10, left P^4; (2) specimen PIN, no. 4516/316, right P^4; (3) specimen PIN, no. 4516/308, left P^4; (4) specimen PIN, no. 4516/11, right P^4; (5) specimen PIN, no. 4516/12, right P^4; (6) specimen PIN, no. 4516/312, left M^1; (7) specimen PIN, no. 4516/314, right M^2; (8) specimen PIN, no. 4516/322, right M^2; Altynshokysu locality, Bone Bed 4; (9) specimen PIN, no. 210/768, left M^2; Akespe locality; (10) specimen PIN, no. 4516/332, right M^3; (11) specimen PIN, no. 4516/38, right P$_4$; (12) specimen PIN, no. 4516/329, left M$_1$; and (13) specimen PIN, no. 4516/333, left M$_3$, ×9; Altynshokysu, Bone Bed 4.

Fig. 14. *Steneofiber schokensis* (Bendukidze, 1993), specimen PIN, no. 4516/321, left P$_4$, ×9; Altynshokysu, Bone Bed 4.

Fig. 15. *Asiacastor* sp., specimen PIN, no. 4516/13, right M^2, ×12; Altynshokysu, Bone Bed 4.

broad and stout lingual root and two small labial roots. The enamel walls of the crown and fossettes are very thick. The hypostria extends for approximately half of the lingual crown height, and the anterostria is shaped as a small fold. The hypoflexus is clearly anteriorly directed. The anteroflexus is relatively shallow. The lingual region of this fold adjoins a relatively large parafossette. The parafossette is rounded triangular, and its relatively wide lingual end deviates posteriorly and closely adjoins the labial wall of the hypoflexus. The mesoflexus deviates posteriorly at a small angle. At the posterior end of its lingual region, there is a small enamel eminence that likely represents a reduced lake. The exact number and arrangement of the fossettes in the posterior region of the occlusal surface and the shape of the labial region of the mesoflexus are uncertain, because the posterolabial corner of the occlusal surface has been broken off.

A heavily worn P^4 has a closed hypoflexus (hypofossette). The mesoflexus is divided into two regions: the labial region is shaped as a short and straight flexus, while the lingual region is shaped as a large fossette in the center of the occlusal surface. The anterofossette is small, round, and positioned close to the anterolabial corner of the tooth. The parafossette is large with a posteriorly curved lingual end. Two small, round fossettes (arranged in one transverse row) are located posterior to the mesoflexus.

P$_4$ has two stout roots. The crown is rounded rectangular, and its anterior region is narrower than the posterior region. The hypostriid descends for two-thirds of the labial height of the crown. An additional columella that is located inside the hypostriid (observed in the middle third of the height of this side) divides this fold into two portions; the anterior portion descends along the anterior side of the columella to the level of the proper hypostriid. The mesostriid extends for about one-fifth of the lingual height of the crown. The hypoflexid deeply juts out into the occlusal surface. Its exit is very narrow, so that enamel walls approach each other closely. The lingual region of the hypoflexid is broad and directed to the posterior wall of the tooth and deviates only slightly to the inner side. The large metafossettid is located in the center of the anterior lobe of the occlusal surface. It is inclined anteriorly, while its lingual end curves posteriorly. Lingually, there is a small round lake, which is apparently a reduced premesofossettid. The mesoflexid is long, and its labial region expands and curves anteriorly. Behind this fold, there is a small oval lake of the postmesofossettid. The entofossettid is divided into two fossettids. The lingual entofossettid is shaped as a round lake that is smaller than the postmesofossettid. The labial entofossettid is relatively large and rounded triangular in shape; it closely adjoins the lingual region of the hypoflexid. Its anterior wall is slightly crimped. The available fragment of a slightly worn P$_4$ (collection PIUZ) displays a long

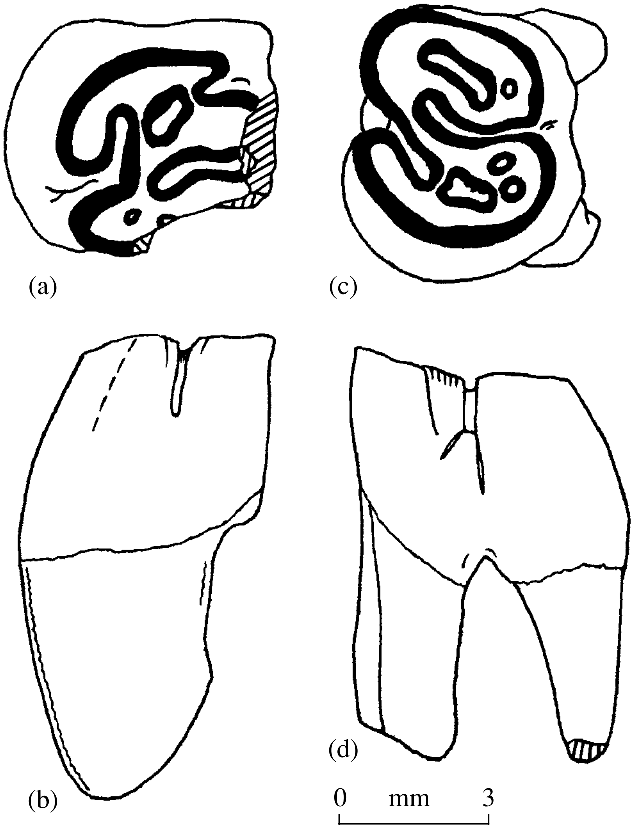


Fig. 27. *Steneofiber schokensis* (Bendukidze, 1993): (a, b) specimen PIN, no. 4516/306, fragmentary left P^4: (a) occlusal and (b) lingual views; (c, d) specimen PIN, no. 4516/321, left P$_4$: (c) occlusal and (d) labial views; Altynshokysu locality, Aral Formation, Bone Bed 4.

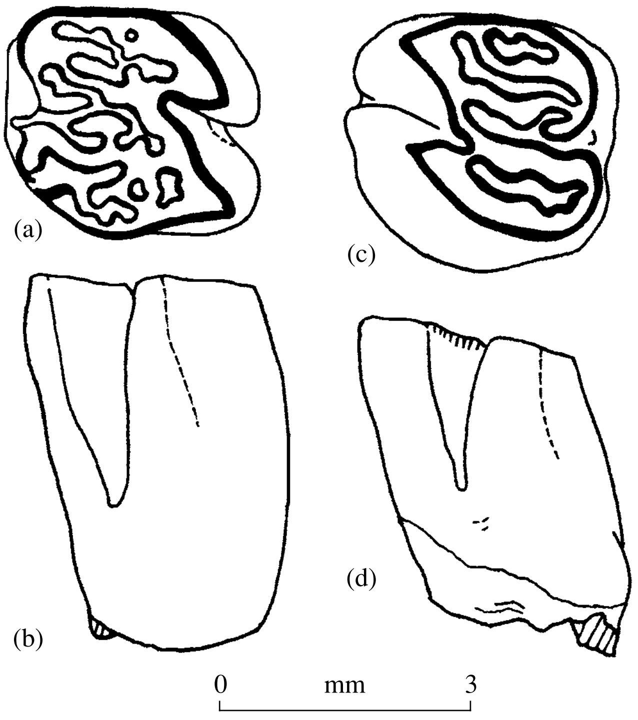


Fig. 28. *Asiacastor* sp.: (a, b) specimen PIN, no. 4516/13, right M^2: (a) occlusal and (b) lingual views; (c, d) specimen PIN, no. 4516/302, left M_3: (c) occlusal and (d) labial view; Altynshokysu locality, Aral Formation, Bone Bed 4.

hypostriid with an additional columella at the base and a relatively short hypoflexid as well as the metafossettid, mesoflexid with crimped walls, and labial entofossettid, which are similar in shape to the elements described above. Two small round lakes are located between the mesoflexid and the entofossettid.

A significantly worn M_2 has a subsquare occlusal surface. The hypostriid is shaped as a small notch. The hypoflexid deeply juts out into the occlusal surface and reaches its center. The mesofossettid is long and almost straight, only slightly deviating posteriorly. The small, round metafossettid is located ahead of the labial end of the mesofossettid. Another very small enamel hollow is located lingually to the metafossettid. The entofossettid is equal in size to the metafossettid and positioned close to the lingual end of the hypoflexid. Two small enamel hollows are located lingually to the entofossettid.

Measurements in mm. Length × width: P^4 (PIN, no. 4516/306), 4.5 × 5.2 (at the crown base); P_4 (PIN, no. 4516/321), 4.7 × 4.0 (at the occlusal surface) and 5.6 × 4.8 (at the crown base).

Comparison. *S. schokensis* differs from *S. kazakhstanicus*, *S. kumbulakensis*, and the majority of other species in its larger measurements and the absence of the metaflexid and entoflexid. In addition, it differs from *S. minimus* and *S. wenzensis* in the presence of the anteroflexus on P^4 and from *S. shevyrevae* and *S. zaissanensis* in the slightly crimped walls of the mesoflexi.

Remarks. Bendukidze (1993) placed this species in the North American genus *Capatanka* Macdonald, 1963. In my opinion, the presence of the anterostria on P^4 at the moderate wear stage, of the mesoflexus at the advanced wear stage (where the hypofossette is closed), and of many additional fossettes and fossettids conflicts with the assignment of this species to *Capatanka* (see Macdonald, 1963). At the same time, the lower jaw and teeth of the form in question display a significant similarity to various Oligocene and Early Miocene species of the genus *Steneofiber*, in particular, to the Oligocene *S. shevyrevae* from the Zaisan Depression (a relatively short mesoflexus of P^4, the presence of the anteroflexus, and the absence of metaflexids and entoflexids [Lytschev and Shevyreva, 1994, text-figs. 3, 4]) and the Early Miocene European *S. eseri* Meyer, 1846 (the presence of two mental foramina and the structure of P_4 [Hugueney, 1975, pl. 1, fig. 12; pl. 2, fig. 4]). On this basis, I assigned this species to the genus *Steneofiber.* Bendukidze (1993) compared this species to "*Capatanka*" *kazakhstanicus* (Borissoglebskaya, 1967). However, Lytschev and Shevyreva (1994) have conclusively shown that the species established by Borissoglebskaya (1967) and assigned to the genus *Propalaeocastor* in actual fact belongs to *Steneofiber.*

Occurrence. North Aral Region; Lower Miocene, Aral Formation.

Material. Two isolated premolars housed at the PIN (specimen PIN, no. 4516/306, fragmentary P^4; and PIN, no. 4516/321, P_4) and four tooth fragments (two P^4, P_4, and M_2) housed at the PIUZ from Bone Bed 4 of the Altynshokysu locality.

Subfamily Castoroidinae Trouessart, 1880

Tribe Trogontheriini Lytschev, 1973

Genus *Asiacastor* Lytschev, 1971

Asiacastor sp.

Plate 5, fig. 15

Description (Fig. 28). The cheek teeth are high-crowned (semihypsodont). M^2 is rounded square in shape with pointed lingual protocone and hypocone edges. The enamel walls of the crown, flexi, and fossettes are thin. The fossette walls are multiplicate. Cement is absent. The hypostria extends for two-thirds of the lingual height of the crown. The mesostria is shaped as a small fold at the ventral edge of the labial side. The hypoflexus extends anterolabially and juts into the occlusal surface for approximately one-fourth of its width. The anterofossette extends across the whole of the anterior lobe of the occlusal surface. A small round lake is located ahead of the anterofossette near the center. The central region of the posterior wall of the anterofossette adjoins the lingual region of a relatively short parafossette that is located in the middle of the occlusal surface of the anterior lobe of the tooth. The mesoflexus is long, and its lingual end curves posterolingually and bifurcates. Anteriorly, the middle region of this fold is connected to the lingual end of a relatively long premesofossette; posteriorly, it is connected to a small postmesofossette. The occlusal surface of the posterior lobe of the tooth contains a large metafossette with four processes and, lingual to the metafossette, three relatively small lakes. The labial end of the metafossette closely approaches the tooth wall, which has a depression (i.e., a closed exit of the metaflexus) in this area.

The occlusal surface of M_3 is rectangular, with pointed projections of the protoconid and hypoconid. The protoconid projects to a substantially greater extent than the hypoconid. The hypostriid descends for three-fourths of the labial height of the crown, and the mesostriid is shaped into a short and small fold. The hypoflexid juts out into the occlusal surface for approximately one-fourth of its width and slightly deviates posteriorly. The walls of the fossettids and mesoflexid are slightly crimped. The parafossettid is medium-sized, and its labial region curves anteriorly. The metafossettid is very long and narrow; its labial region curves anteriorly, and its extreme lingual region is slightly inclined posteriorly. The mesoflexid is somewhat shorter than the metafossettid, inclined anteriorly, and slightly curved. The labial end of a small premesofossettid is connected to the middle region of the posterior wall of the mesoflexid. The broad and undulating entofossettid entirely occupies the central area of the posterior lobe of the occlusal surface and closely approaches the hypoflexid.

Measurements in mm. Length × width: M^2 (no. 4516/13), 2.8×2.2; M_3 (no. 4516/302), 2.75×2.5 (at the occlusal surface).

Comparison and remarks. The form in question differs from *A. baschanovi* Lytschev, 1971 and *A. major* Lytschev, 1971 in the absence of cement in the flexi and flexids and from *A. antecedens* Lytshev, 1982 in the presence of the postmesofossette in the upper cheek teeth and the premesofossettid in M_3. These valleys are observed in *A. orientalis* Lytschev, 1987. The last species was described on the basis of isolated P^4, M^3, and P_4 (Lytschev, 1987) from the Lower Miocene of the Akzhar (=Zhamangora) Formation in eastern Kazakhstan [however, Lytschev and Shevyreva (1994) indicated that these specimens were only tentatively assigned to this stratigraphic level]. The PIN collection lacks material on the appropriate teeth from the North Aral Region; however, the structural pattern of the upper cheek teeth (lingual fusion between the anterofossette and the parafossette and the presence of the postmesofossette) and the measurements suggest an affinity between the form from the Aral Formation and *A. orientalis*. Bendukidze (1993) described isolated P^4, M^2, P_4, and M_3 from the North Aral Region under the name *Asiacastor* aff. *orientalis*. Subsequently, Bendukidze (1997) designated this form as *Anchitheriomys* aff. *orientalis* (Lytschev, 1987). In addition, in my opinion, the isolated teeth Bendukidze (1993) determined as *Capacikala* cf. *sciuroides* (Matthew, 1907) and subsequently (Bendukidze, 1997) referred to as *C. antecedens* (Lytschev, 1982), in fact belong to the same small beaver. However, the structure of these teeth differs from that of *A. orientalis*, which conflicts with the assignment of the form in question to *A. orientalis* from the Akzhar Formation.

The so-called *Asiacastor* dental pattern is characteristic of four genera: *Asiacastor, Youngofiber, Trogontherium*, and *Anchitheriomys* (Xu, 1994). Xu (1994) believes that these genera compose a monophyletic group and that the large *Youngofiber* originates from an early member of the genus *Asiacastor* that had relatively low-crowned teeth. Korth (2002) combines *Asiacastor, Youngofiber*, and *Trogontherium* together in the tribe Trogontheriini of the subfamily Castoroidinae and places *Anchitheriomys* in the tribe Anchitheriomyini of the subfamily Agnotocastorinae. This researcher believes that the later Miocene species of the genus *Asiacastor* are direct descendants of *Youngofiber*. I share the phylogenetic hypothesis proposed by Xu and consider the form from the Aral Formation to be the earliest member of *Asiacastor* with a precise stratigraphic assignment.

Material. The collection of the PIN contains M^2 (no. 4516/13) and M_3 (no. 4516/302) from Bone Bed 4 of the Altynshokysu locality.

Family Eomyidae Deperet et Douxami, 1902

Subfamily Eomyinae Deperet et Douxami, 1902

Genus *Eomyodon* Engesser, 1987

Eomyodon bolligeri Lopatin, 2000

Plate 6, figs. 1–4

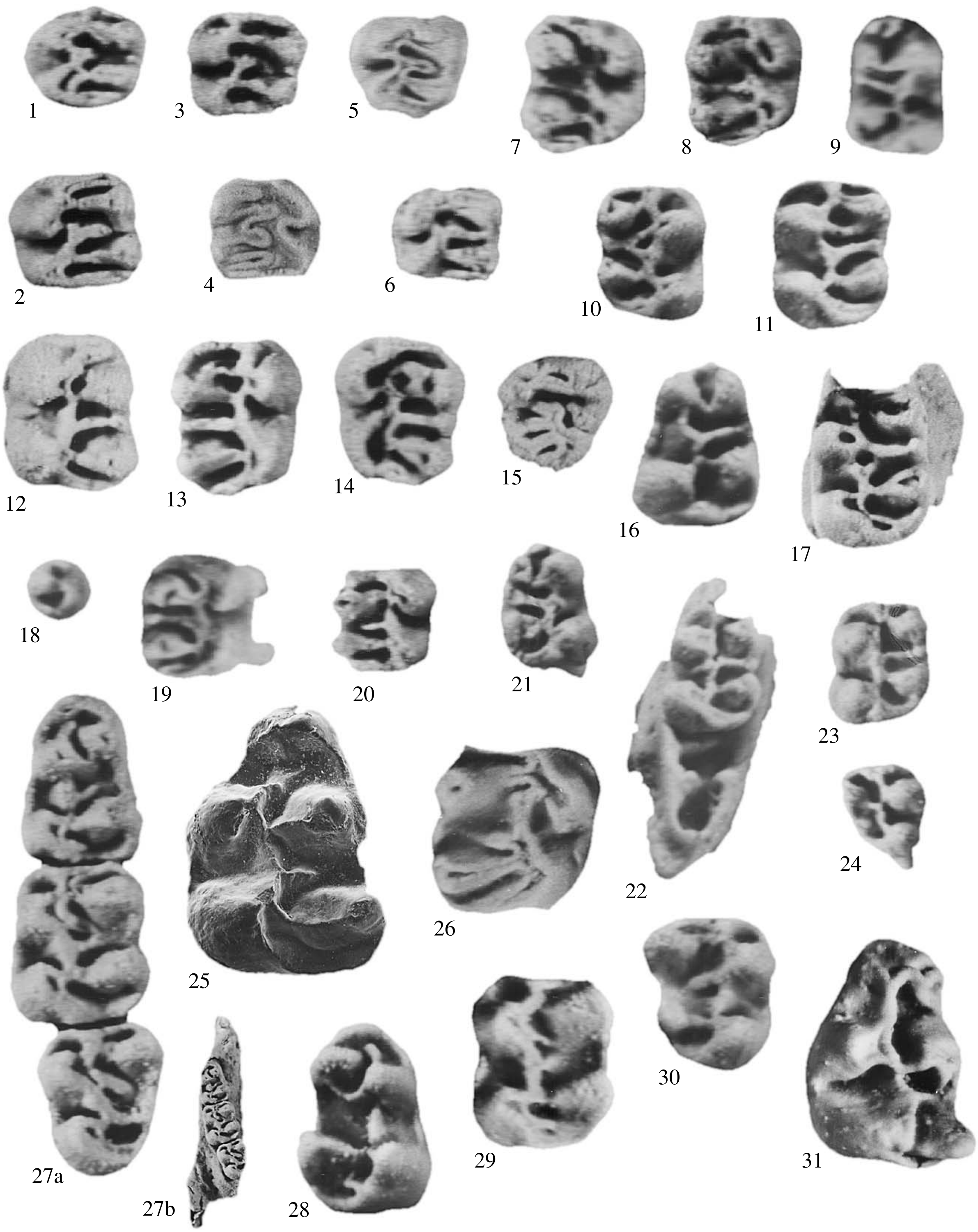
Eomyodon bolligeri: Lopatin, 2000b, p. 82, text-figs. 2b, 3a–3l.

Holotype. PIN, no. 4516/466, left M^2; Kazakhstan, North Aral Region, Altynshokysu locality; Lower Miocene, Aral Formation, Bone Bed 1.

Description (Fig. 29). A small-sized member of the genus. The cheek teeth are brachyodont–lophodont with well-pronounced main cusps and high transverse crests.

The occlusal surface of P^4 is a rounded trapezoid, and the anterior lobe is substantially wider than the posterior lobe. The anteroloph and syncline I are absent. The anterior region of the tooth has two narrow ridges; the first is connected to the middle of the protoloph, while the second is isolated and occupies a more labial position. These elements are probably a rudimentary anteroloph. The protoloph curves anteriorly. The metaloph is connected to the anterior arm of the hypocone. The mesoloph is very short. The mesostyle is well-pronounced and relatively large; however, it does not close the exit of the central syncline. The entoloph is complete and curved labially. The sinus is straight. Syncline IV is open, its lingual part is wide and deep, and the exit is extremely narrow.

Plate 6



M^1 is relatively large and subsquare in outline. The main cusps are equal in massiveness, the transverse crests are straight. All synclines are open, and their exits are very narrow. The anteroloph has a long labial arm and a short lingual arm. The metaloph is connected to the anterior arm of the hypocone. The mesoloph is relatively long and reaches the lingual region of the paracone. The mesostyle is fused with the paracone and appears to be a small posterior projection of this cusp (the posterior crest of the paracone). The entoloph is

Explanation of Plate 6

All specimens come from the Aral Formation of the Altynshokysu locality.

Figs. 1–4. *Eomyodon bolligeri* Lopatin, 2000: (1) specimen PIUZ, ALT no. 301, left P^4; (2) specimen PIUZ, ALT no. 302, left M^1, ×20; Bone Bed 2; (3) holotype PIN, no. 4516/466, left M^2, ×20; Bone Bed 1; and (4) specimen PIUZ, ALT no. 303, right M^2, ×20; Bone Bed 2.

Figs. 5 and 6. *Pseudotheridomys yanshini* Lopatin, 2000: (5) holotype IAUU, ALT no. 44, left P^4, ×20; Bone Bed 2; and (6) specimen PIUZ, ALT no. 6, left M^2, ×20; Bone Bed 4.

Figs. 7–11. *Plesiosminthus tereskentensis* Lopatin, 1999: (7) specimen PIN, no. 4516/461, right M^1; (8) holotype PIN, no. 4516/479, right M^2; (9) specimen PIN, no. 4516/472, right M_1; (10) specimen PIN, no. 4516/375, right M_2, and (11) specimen PIN, no. 4516/462, left M_2, ×20; Bone Bed 1.

Figs. 12–17. *Parasminthus debruijni* Lopatin, 1999: (12) specimen PIN, no. 4516/585, left M^1; (13) holotype IAUU, ALT no. 49, right M^2; (14) specimen PIN, no. 4516/586, left M^2; (15) specimen PIN, no. 4516/587, right M^3; (16) specimen PIN, no. 4516/588, left M_1; and (17) specimen PIN, no. 4516/589, left dentary fragment with M_2, ×20; Bone Bed 2.

Figs. 18–24. *Bohlinosminthus cubitalus* Lopatin, 1999: (18) specimen PIN, no. 4516/590, left P^4; (19) specimen PIN, no. 4516/591, right M^1; (20) specimen PIN, no. 4516/592, right M^2; (21) specimen PIN, no. 4516/593, right M_1; (22) holotype IAUU, ALT no. 115, left dentary fragment with M_2; (23) specimen PIN, no. 4516/594, left M_2; and (24) specimen PIN, no. 4516/595, right M_3, ×20; Bone Bed 2.

Figs. 25–30. *Eucricetodon occasionalis* Lopatin, 1996: (25) specimen PIN, no. 4516/198, left M^1, ×25; Bone Bed 4; (26) specimen PIN, no. 4516/497, right M^2, ×20; Bone Bed 1; (27) holotype PIN, no. 4516/196, left dentary fragment with M_1–M_3: (27a) M_1–M_3, ×20; (27b) general appearance, ×5; Bone Bed 4; (28) specimen PIN, no. 4516/68, right M_1; (29) specimen PIN, no. 4516/500, left M_2; and (30) specimen PIN, no. 4516/501, right M_3, ×20; Bone Bed 1.

Fig. 31. *Eumyarion* sp., specimen PIN, no. 4516/502, left M^1, ×20; Bone Bed 1.

complete. The sinus slightly curves anteriorly. Syncline IV is long and equal to syncline II.

M^2 is relatively small and subsquare. It is similar in structure to M^1 and differs in its reduced mesostyle. In a worn tooth, the lingual arm of the anteroloph is absent.

Measurements in mm. Length × anterior lobe width—posterior lobe width: P^4, 0.825 × 0.95—0.775 (PIUZ, ALT no. 301); M^1, 0.9 × 0.9—0.875 (PIUZ, ALT no. 302); and M^2 (holotype), 0.8 × 0.9—0.85.

Comparison. *E. bolligeri* differs from the type species *E. volkeri* Engesser, 1987 and all other European species in the narrow posterior lobe of P^4. In addition, it differs from *E. pusillus* (Fahlbush, 1969) in its much smaller measurements and from *E. mayoi* Engesser, 1990 and *E. wiedmanni* Engesser, 1990 in the low crowns of the upper cheek teeth, the absence of syncline I on P^4, and the shorter mesoloph of P^4–M^2. It differs from *E. dangheensis* Wang, 2002 (Upper Oligocene of Gansu, China) in the shorter mesoloph and open syncline II of M^1 and M^2 and from *E. asiaticus* (Wang et Emry, 1991) (Upper Oligocene of Inner Mongolia, China) in the presence of a well-developed posterior crest of the paracone on M^1 and M^2.

Remarks. *Eomyodon* was registered in Europe in the Late Oligocene–Early Miocene, Mammal Zones MP28–MN1 (Engesser, 1987, 1990, 1999; Werner, 1994). Regarding the level of evolutionary advantage of dental morphology, *E. bolligeri* is closely similar to *E. volkeri* (MP28–MP29)—*E. mayoi* (MP30–MN1). Within central Asia, *Eomyodon* was discovered in the Upper Oligocene of China (Wang and Emry, 1991; Wang, 2002).

Occurrence. North Aral Region; Lower Miocene, Aral Formation.

Material. In addition to the holotype, five isolated upper teeth: P^4, M^1, and M^2 (stored at the PIUZ); a fragmentary P^4 (DK); and P^4 (IAUU) from Bone Bed 2 of the Altynshokysu locality.

Genus *Pseudotheridomys* Schlosser, 1926

Pseudotheridomys yanshini Lopatin, 2000

Plate 6, figs. 5 and 6

Pseudotheridomys yanshini: Lopatin, 2000b, p. 84, text-figs. 1c, 3m–3q.

Holotype. IAUU, ALT no. 44, left P^4; Kazakhstan, North Aral Region, Altynshokysu locality; Lower Miocene, Aral Formation, Bone Bed 2.

Description (Fig. 30). A medium-sized member of the genus. The cheek teeth are low-crowned. The main cusps are well-pronounced, and the transverse crests are narrow and well-developed.

The occlusal surface of P^4 is trapeziform. The labial side of the crown is longer than the lingual side, and the anterior lobe of the tooth is slightly wider than the posterior lobe. The main cusps are approximately equal in size. The protoloph, mesoloph, and metaloph are equal in height; each of these transverse crests is substantially higher than the anteroloph and posteroloph. The anteroloph is weak, with only its labial arm being developed, and it adjoins the anterolabial side of the paracone and forms closed syncline I. This labial fold is extremely small and oval. The anterior arm of the protocone is connected to the lingual end of the anteroloph and extends to the paracone to form the protoloph. The

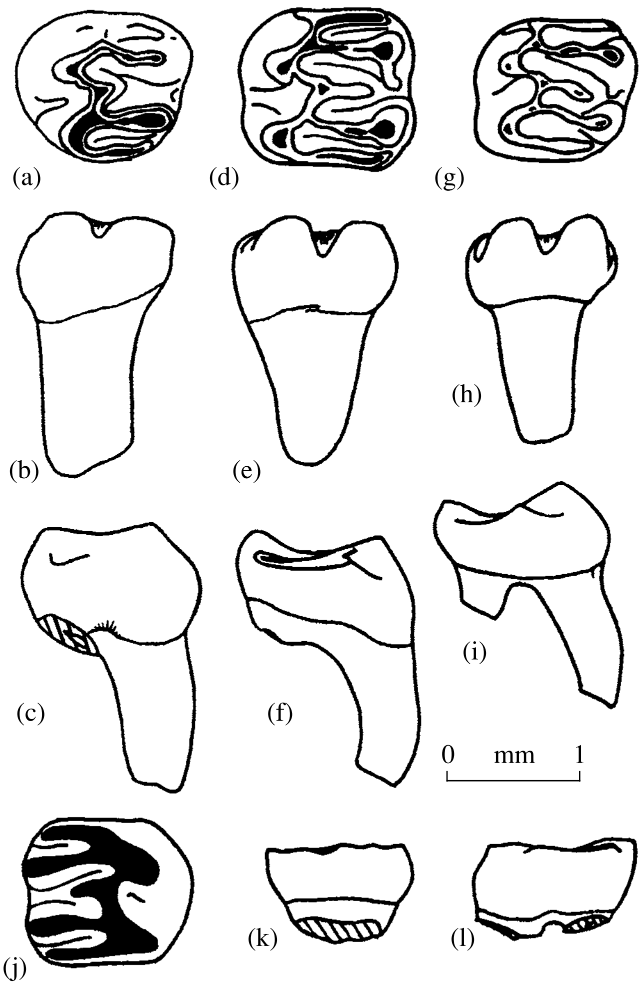


Fig. 29. *Eomyodon bolligeri* Lopatin, 2000 from the Aral Formation of the Altynshokysu locality: (a–c) specimen PIUZ, ALT no. 301, left P^4: (a) occlusal, (b) lingual, and (c) frontal views; (d–f) specimen PIUZ, ALT no. 302, left M^1: (d) occlusal, (e) lingual, and (f) frontal views; Bone Bed 2; (g–i) holotype PIN, no. 4516/466, left M^2: (g) occlusal, (h) lingual, and (i) frontal views; Bone Bed 1; (j–l) specimen PIUZ, ALT no. 303, right M^2: (j) occlusal, (k) lingual, and (l) frontal views; Bone Bed 2.

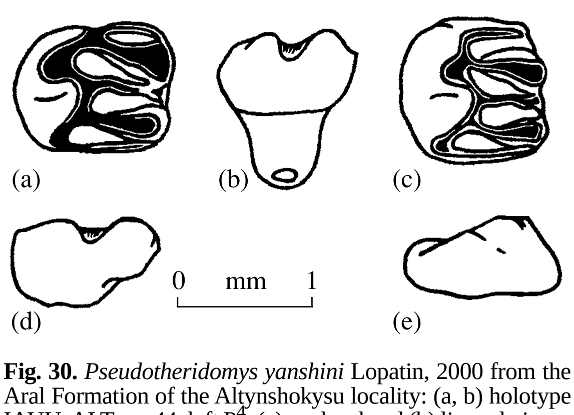


Fig. 30. *Pseudotheridomys yanshini* Lopatin, 2000 from the Aral Formation of the Altynshokysu locality: (a, b) holotype IAUU, ALT no. 44, left P^4: (a) occlusal and (b) lingual views; Bone Bed 2; (c–e) specimen PIUZ, ALT no. 6, left M^2: (c) occlusal, (d) lingual, and (e) frontal views; Bone Bed 4.

entoloph is complete; it forms a labially directed elbow, which curves around the internal fold (sinus) directed to the anterolabial angle of the tooth. A long mesoloph deviates from the central part of the entoloph, curves in a wavy manner anteriorly, and adjoins the posterior side of the paracone to form closed syncline II. This is the longest labial fold, and it extends for approximately two-thirds of the occlusal surface. Syncline III is open, has a narrow exit, and is slightly shorter than syncline IV. The metaloph adjoins the posterior end of the entoloph at the point of fusion with the hypocone. The posteroloph is long and narrow, extends from the hypocone along the posterior border of the occlusal surface, and reaches the posterolabial side of the metacone to form closed syncline IV.

M^2 is subsquare in outline. The main cusps are approximately equal in size, but the paracone is somewhat more massive. All the crests are narrow and low. The transverse crests are almost straight. The anteroloph lacks a lingual arm. The protoloph and metaloph are connected to the anterior arms of the protocone and hypocone, respectively. The mesoloph is long and straight and extends to the border of the occlusal surface. The low mesostyle completely closes the exit of the central syncline. Synclines I and IV are also closed. The entoloph is complete. The sinus is straight. Syncline IV is equal in length to syncline II.

Measurements in mm. Length × anterior lobe width—posterior lobe width: P^4, 0.75×0.82—0.75 (holotype); M^2, 0.8×0.8—0.75 (PIUZ, ALT no. 6).

Comparison. *P. yanshini* differs from *P. parvulus* (Schlosser, 1884), *P. schaubi* Lavocat, 1951, and the majority of other species in the reduced anteroloph of P^4 and the complete entoloph of the upper cheek teeth. From *P. feifari* Alvarez Sierra et Daams, 1987, *P. lacombai* Alvarez Sierra, 1987, *P. bernensis* Engesser, 1990, *P. rolfoi* Engesser, 1990, and *P. bouziguensis* Escarguel, 1995, it differs in its substantially smaller measurements and low tooth crowns.

Remarks. The genus *Pseudotheridomys* was widespread in the Late Oligocene (beginning with MP28) and the Early Miocene of Europe and in the Early–Middle Miocene of North America. It was represented in Asia by *P. asiaticus* Wang et Emry, 1991, *?Pseudotheridomys* sp. (Upper Oligocene of China, Saint-Jaques: Wang and Emry, 1991), and *Pseudotheridomys* sp. (Middle Miocene of Kazakhstan, Kentyubek: Bendukidze, 1993). At present, *P. asiaticus* is commonly assigned to the genus *Eomyodon*, while *?Pseudotheridomys* sp. is unquestionably considered to be *Pseudotheridomys* sp. (Wang, 2002). In its crown height, the extent to which the labial folds of the upper molars are closed, and the anteroloph structure of P^4, the species from the Aral Formation is probably similar to the evolutionary stage of the European *P. schaubi* (MP30) and *P. bernensis* (MN1).

Occurrence. North Aral Region; Lower Miocene, Aral Formation.

Material. In addition to the holotype, M^2 (stored at the PIUZ) from Bone Bed 4 of the Altynshokysu locality.

Family Zapodidae Coues, 1875

Subfamily Sicistinae Allen, 1901

Genus *Plesiosminthus* Viret, 1926

Plesiosminthus tereskentensis Lopatin, 1999

Plate 6, figs. 7–11

Plesiosminthus tereskentensis: Lopatin, 1999b, p. 94, text-figs. 1a and 2.

Holotype. PIN, no. 4516/479, right M^2; Kazakhstan, North Aral Region, Altynshokysu locality; Lower Miocene, Aral Formation, Bone Bed 1.

Description (Fig. 31). M^1 and M^2 are three-rooted. M^1 is rounded square in outline, the anterior and posterior lobes of the tooth are approximately equal in width; sometimes, the anterior lobe is somewhat narrower than the posterior lobe. In the majority of specimens, the anterior arm of the protocone is connected to the anteroloph, or, less often, a small fold can be observed between them. Only the labial arm of the anteroloph is developed. The central part of the anterior arm of the protocone is usually distinctly expanded. The posterior arm of the protocone is connected to the paracone and forms protoloph II. The mesocone and mesostyle are relatively small but distinctly pronounced. The mesoloph is narrow and straight (occasionally, it has curved and expanded segments) and extends from the mesocone to the mesostyle. The metaloph is connected to the central part of the hypocone. The posteroloph is well-developed but, frequently, incomplete, i.e., it terminates at the base of the hypocone. The entosinus is deep and slightly curves anteriorly.

The occlusal surface of M^2 is subsquare in outline, and the posterior lobe is somewhat narrower than the anterior lobe. The labial anteroloph extends parallel to the anterior border of the crown. A distinct protoloph I is present and connects the paracone with the anterior arm of the protocone. Protoloph II diverges posterolingually from the paracone and comes into contact with the mesocone. The protocone is separated from the mesocone by an extensive entosinus, so that the entoloph originates behind the mesocone. The mesocone and mesostyle are small; and the mesoloph is long, straight, relatively narrow, and low. The metaloph is connected to the central region of the hypocone. The posteroloph is distinctly developed.

M^3 and M_3 are absent from the material.

M_1 is rounded rectangular in outline and expands posteriorly. The protoconid and hypoconid are slightly displaced posteriorly with reference to the metaconid and entoconid, respectively. The anteroconid is strongly reduced and shaped like a small cuspule irregular in outline, which is located at the anterior border of the occlusal surface. In some cases, it has a small spur that stretches posterointernally. Metalophid II is located between the protoconid and the metaconid and is more or less arched posteriorly. The ectolophid originates from the posterolabial part of the protoconid, extends obliquely, and does not come into contact with metalophid II. The mesoconid is medium-sized, while the mesostylid is small. The ectosinusid occasionally contains a small ectostylid shaped as a longitudinally extended cusp at the labial border of the occlusal surface. The mesolophid is well-developed, long, and narrow; it extends anterolingually from the mesoconid to the mesostylid. The ectomesolophid is absent. The hypolophid is connected to the anterior projection of the hypoconid at the point of its fusion with the ectolophid. The posterolophid has a relatively small expansion in the area of the hypoconulid; it reaches the posterointernal side of the entoconid and forms a closed posterosinusid.

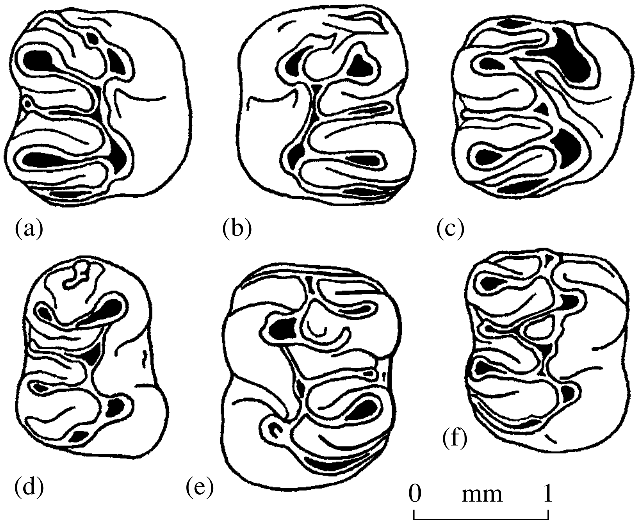


Fig. 31. *Plesiosminthus tereskentensis* Lopatin, 1999: (a) specimen PIN, no. 4516/461, right M^1; (b) specimen PIN, no. 4516/471, left M^1; (c) holotype PIN, no. 4516/479, right M^2; (d) PIN, no. 4516/472, right M_1; (e) PIN, no. 4516/462, left M_2; and (f) PIN, no. 4516/375, right M_2.

M_2 is rectangular in outline. The anterior and posterior lobes of the tooth are of approximately the same width. The anterolophid has two arms, the lingual arm is developed to a greater extent than the labial arm. The protoconid is slightly displaced posteriorly relative to the metaconid. The protoconid and metaconid are separated from the anterolophid by small and narrow folds. The metaconid and the anterior arm of the protoconid are connected to a longitudinal crest that is fused with the middle of the anterolophid; thus, metalophid I is slightly curved anteriorly. The mesoconid and mesostylid are small. In most cases, the mesostylid closely adjoins the posterolingual border of the metaconid, but, in some cases, a small inflection occurs between them. The mesolophid is usually long, narrow, straight or slightly curved, directed anterolingually, and reaches the mesostylid. Two variants of its combination with the posterior arm of the protoconid are observable: (1) the posterior arm of the protoconid is connected to the metaconid and forms metalophid II; the mesolophid reaches the mesostylid (four specimens; Fig. 31e); in some cases (one specimen), the mesolophid and metalophid II are connected by a very small and low additional crest; and (2) within a certain segment, the posterior arm of the protoconid and the mesolophid are connected to each other or fused to form a common transverse crest that extends to the mesostylid; the interval from the contact of the crests to the lingual border of the crown is approximately one-third of the crown width (two specimens, Fig. 31f). The structural details of the posterior part of M_2 are the same as those of M_1.

Measurements in mm. Length × width: M^1, 1.05 × 1.0 (PIN, nos. 4516/447, 461), 1.07 × 1.0 (PIN, no. 4516/460), 1.1 × 1.0 (PIN, no. 4516/471), 1.15 × 1.05 (PIN, no. 4516/484), and 1.2 × 1.05 (PIN, no. 4516/469); M^2, 1.0 × 0.93 (holotype); M_1, 1.1 × 0.78 (PIN, no. 4516/472), 1.1 × 0.8 (PIN, no. 4516/405), and ? × 0.9 (PIN, no. 4516/473); M_2, 1.05 × 0.9 (PIN, no. 4516/485), 1.1 × 0.875 (PIN, no. 4516/444), 1.125 × 0.875 (PIN, no. 4516/375), 1.15 × 0.825 (PIN, no. 4516/480), 1.15 × 0.87 (PIN, no. 4516/465), 1.2 × 0.9 (PIN, no. 4516/462), and ? × 0.8 (PIN, no. 4516/481).

Comparison. *P. tereskentensis* differs from *P. winistoerferi* Engesser, 1987 in its considerably smaller measurements, less developed crests, the absence of an additional transverse crest between the metalophid and mesolophid, a more lingual position of the ectolophid on M_1, and the presence of contact between the protoconid and anterolophid of M_2. It differs from *P. moralesi* Alvarez Sierra, Daams et Lacomba Andueza, 1996 in the absence of an anterolingual cingulum on M^1 and M^2, the double protoloph and incomplete entoloph on M^2, the complete mesolophid on M_2, and a generally more bunodont occlusal molar surface. It differs from *P. schaubi* Viret, 1926 in its smaller measurements, the reduced lophodont structure of the occlusal surface of molars, more strongly developed posteroloph of M^1, more strongly developed posterior arm of the protoconid on M_2, and the presence of a double protoloph and incomplete entoloph on M^2. It differs from *P. myarion* Schaub, 1930 in its substantially smaller measurements, the better developed posteroloph on M^1, the absence of a lingual arm of the anteroloph on M^2, the more lingual position of the ectolophid of M_1, and the more strongly developed posterior arm of the protoconid on M_2. It differs from *P. promyarion* Schaub, 1930 in the better developed posteroloph of M^1 and the absence of an anterior spur of the hypoconulid on M_2. It differs from *P. admyarion* Compte, 2000 in the presence of a double protoloph on M^2; relatively shorter M^1, M^2, M_1, and M_2; and somewhat smaller measurements.

Remarks. *P. tereskentensis* is most similar in dental structure and measurements to the Oligocene European *P. promyarion* and is obviously related to the lineage *P. promyarion–P. admyarion–P. myarion.* Such *P. tereskentensis* characters as only partial isolation of the posteroloph from the hypocone on M^1, the incomplete entoloph combined with the double protoloph on M^2, and the combination of metalophid II with the mesolophid on M_2 are often observed in *P. promyarion* (Engesser and Hugueney, 1982, p. 71, text-fig. 9e; Engesser, 1987, pp. 975, 976, text-figs. 19, 20; Kristkoiz, 1992, pp. 110–112, text-figs. 73, 74). *P. tereskentensis* apparently represents a primitive local lineage of the genus *Plesiosminthus*, which is probably related to *P. promyarion.*

Material. In addition to the holotype, 16 isolated teeth from the type locality (stored at the PIN): six M^1 (nos. 4516/447, 460, 461, 469, 471, and 484); three M_1 (nos. 4516/405, 472, and 473); and seven M_2 (nos. 4516/375, 444, 462, 465, 480, 481, and 485).

Genus *Parasminthus* Bohlin, 1946

Parasminthus debruijni Lopatin, 1999

Plate 6, figs. 12–17

Parasminthus aff. *tangingoli*: Bendukidze, 1993, p. 43, pl. XVI, figs. 4 and 5.

Parasminthus debruijni: Lopatin, 1999b, p. 96, text-figs. 1b, 3a–3k.

Holotype. IAUU, ALT no. 49, right M^2; Kazakhstan, North Aral Region, Altynshokysu locality; Lower Miocene, Aral Formation, Bone Bed 2.

Description (Fig. 32). P^4 is small and round in outline. M^1 and M^2 are four-rooted (available material includes only one three-rooted M^1). M^1 is rounded rectangular in outline, and its posterior lobe is slightly wider than the anterior lobe. The anterior arm of the protocone is connected to the labial anteroloph, while the posterior arm is connected to a projection of the paracone (protoloph II). The mesocone is only slightly detached and connected to a small mesostyle by a long and narrow mesoloph. The metaloph adjoins the central (metaloph I) or posterior (metaloph II) region of the hypocone. A complete posteroloph gently curves and extends along the posterior border of the occlusal surface, reaches the metacone, and forms a closed posterosinus.

M^2 is extended rectangular in outline. Its posterior lobe is somewhat narrower than the anterior lobe. The labial anteroloph extends parallel to the anterior border of the occlusal surface. The lingual arm of the anteroloph is only weakly developed or completely reduced. Two well-developed protolophs are present. Protoloph I curves anteriorly and adjoins the anterior cusps at the point of fusion between the protocone and anteroloph. Protoloph II is formed by the posterior arms of the protocone and paracone and curves posteriorly. At the point of fusion between these arms, an almost straight entoloph diverges from protoloph II. The mesocone is only partially detached. The mesostyle is relatively well-developed and is larger than the mesostyle of M^1. These cusps are connected by a distinct straight mesoloph. The metaloph and the anterior or central region of

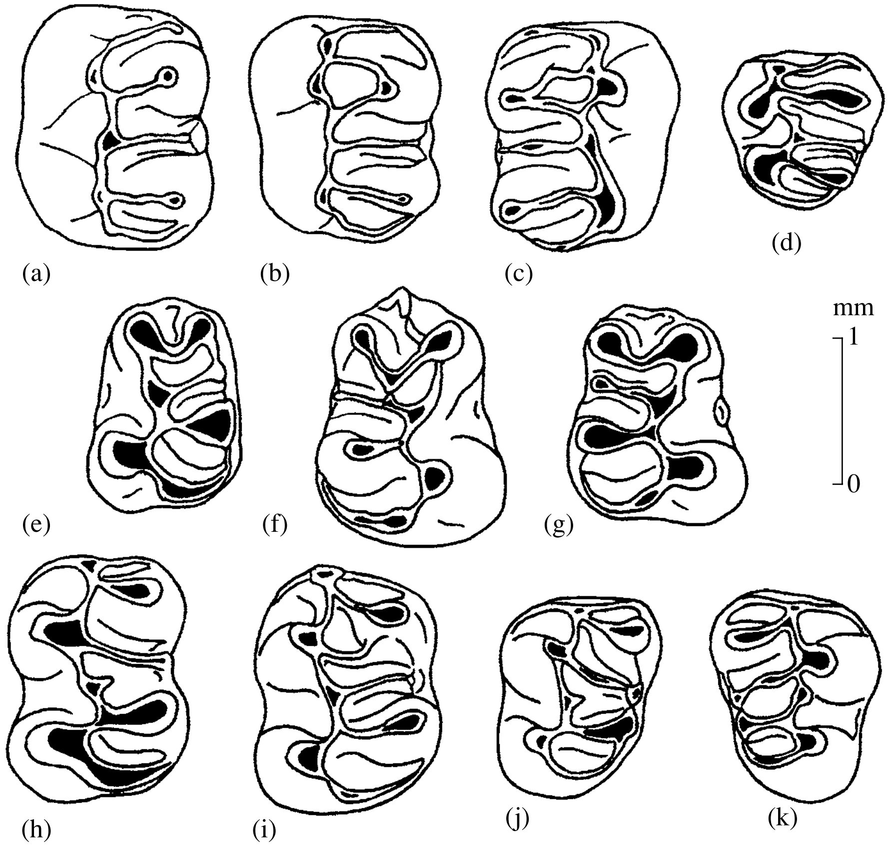


Fig. 32. *Parasminthus debruijni* Lopatin, 1999 from the Aral Formation of the Altynshokysu locality (Bone Bed 2): (a) specimen IAUU, ALT no. 45, left M^1; (b) specimen IAUU, ALT no. 48, left M^2; (c) holotype IAUU, ALT no. 49, right M^2; (d) specimen PIUZ, ALT no. 232, left M^3; (e) specimen IAUU, ALT no. 56, left M_1; (f) specimen IAUU, ALT no. 59, right M_1; (g) specimen IAUU, ALT no. 62, right M_1; (h) specimen IAUU, ALT no. 69, left M_2; (i) specimen IAUU, ALT no. 70, left M_2; (j) specimen IAUU, ALT no. 74, left M_3; and (k) specimen IAUU, ALT no. 75, right M_3.

the hypocone are fused, the fusion is usually observed at the point of contact with the entoloph. The structure of the posteroloph and posterosinus are similar to those of M^1.

M^3 is three-rooted, and its occlusal surface is rounded triangular in outline. The posterior lobe is significantly narrower than the anterior lobe. The anteroloph possesses only one labial arm. Protoloph I, a distinct mesocone, and a long mesoloph extending to the labial border of the occlusal surface are developed. The metaloph adjoins the anterior region of the hypocone. The posterosinus is closed. The entosinus is open, and the protocone and hypocone are connected by the labially curved entoloph.

M_1 is rectangular in outline. Its anterior part is somewhat narrower than the posterior part. The protoconid and metaconid are located within the same transverse section and are connected by metalophid II, which strongly curves posteriorly. An extensive anterior fold isolating the central parts of the protoconid and the metaconid is observed anterior to this crest. The fold is usually open; occasionally, it is bordered anteriorly by a small cingulid. A rudimentary anteroconid occurs in approximately 60% of specimens, it looks like a small crest or a small and flattened cuspule. The ectolophid deviates from the posterolabial region of the protoconid at a small angle to the longitudinal tooth axis. The anterior end of this crest is located at a certain distance from the contact point of the metalophid and the protoconid. The relatively large mesoconid is connected to a small mesostylid by a long and straight or slightly curved mesolophid. Sometimes, the mesolophid and metalophid are connected by an additional longitudinal crest. The ectostylid is frequently present. The hypolophid is short. The posterolophid is long, closes the posterosinusid posteriorly and lingually, and has an expansion in place of the hypoconulid.

M_2 is extended rectangular in outline. Its anterior and posterior lobes are approximately equal in width and connected to each other by a clear constriction that looks like a relatively abrupt narrowing in the middle of the crown. Both anterolophid arms are usually present; however, the labial arm is shorter and weaker; in some specimens, it is completely be absent. Occasionally, the anterior border of the tooth in the region of the lingual arm of the anterolophid strongly slants internally. The anterior arm of the protoconid and a projection of the metaconid form metalophid I, which is connected to the central part of the anterolophid. The mesoconid is distinct, while the ectomesolophid is absent. The mesostylid is small. The posterior arm of the protoconid and, usually, the mesolophid are well-developed. The following three combinations are recognized: (1) the posterior arm of the protoconid is connected to the base of the metaconid and forms metalophid II, and the mesolophid is long and reaches the mesostylid (10% of specimens; Fig. 32i); (2) the posterior arm of the protoconid forms a long pseudomesolophid, while the mesolophid is reduced and shaped into a short and free crest or is connected to the pseudomesolophid (75%; Fig. 32h); and (3) only the pseudomesolophid is present (15%). The ectolophid, hypolophid, and posterolophid are of the same structure as in M_1.

M_3 is rounded triangular in outline. Its posterior lobe is significantly narrower than the anterior lobe. Both arms of the anterolophid are well-developed. The main elements of the occlusal surface are of the same structure as in M_2. The mesoconid and mesostylid are weakly developed. The posterior arm of the protoconid is long and reaches the mesostylid (70% of specimens) or only approaches it. The middle of the posterior arm of the protoconid is frequently connected to metalophid I by a supplementary transverse crest (25%). The mesolophid is strongly reduced (15%) or completely absent.

Measurements in mm:

Tooth	Length			Width		
	n	limits	mean	*n*	limits	mean
M^1	15	1.125–1.30	1.24	13	0.90–1.05	1.00
M^2	13	1.00–1.25	1.18	14	0.90–1.10	0.985
M^3	7	0.75–0.85	0.81	7	0.75–0.90	0.825
M_1	21	1.10–1.35	1.21	24	0.75–1.10	0.88
M_2	17	1.15–1.45	1.285	18	0.85–1.025	0.94
M_3	12	0.975–1.225	1.08	12	0.75–0.90	0.84

Comparison. *P. debruijni* differs from *P. asiaecentralis* Bohlin, 1946 and *P. tangingoli* Bohlin, 1946 in its smaller measurements, the absence of contact between metaloph II and the posteroloph on M^1 and M^2, reduced anteroconid on M_1 and reduced mesolophid on M_2, and almost invariably four-rooted M^1 and M^2. *P. debruijni* is smaller than *P. huangshuiensis* (Li et Qiu, 1980) and differs from it in the double protoloph of M^2.

Remarks. Judging from the structure of M_1 and M_2, the specimens assigned by Bendukidze (1993) to *P.* aff. *tangingoli* Bohlin, 1946 belong in actuality to *P. debruijni.*

The Oligocene *P. parvulus* Bohlin, 1946 and *P. quartus* (Shevyreva, 1970) and the Early Miocene *P. xiningensis* (Li et Qiu, 1980) and *P. lajeensis* (Li et Qiu, 1980) were previously assigned to the genus *Parasminthus* (Li and Qiu, 1980; Wang, 1985; Wang *et al.*, 1995). On the basis of the molar structure, I proposed referring these Oligocene species to a separate genus, *Bohlinosminthus* (Lopatin, 1999b), while the Miocene forms should be assigned to the genera *Shamosminthus* and *Gobiosminthus*, respectively (see Huang, 1992).

Judging by the dental structure, *P. debruijni* is most probably a late member of the *P. tangingoli* lineage. It is likely that, in the course of evolution of this presumptive lineage, the anteroconid of M_1 became reduced, and such characters as the doubled protoloph of M^2, well-developed pseudomesolophid of M_2, and presence of four roots in M^1 and M^2 stabilized (increased in the frequency of manifestation).

Occurrence. North Aral Region; Lower Miocene, Aral Formation.

Material. In addition to the holotype, 117 isolated teeth from Bone Bed 2 of the Altynshokysu locality: 31 at the IAUU (three M^1, ALT nos. 45–47; eight M^2, ALT nos. 48–55; 12 M_1, ALT nos. 56–68; five M_2, ALT nos. 69–73; and three M_3, ALT nos. 74–76); 37 at the PIUZ (fragmentary P^4, six M^1, seven M^2, two M^3, eight M_1, six M_2, and eight M_3); 27 at the DK (seven M^1, six M^2, three M^3, five M_1, five M_2, and one M_3); 11 at the NMW (two M^1, one M^3, four M_1, and four M_2); and five at the PIN (M^1, no. 4516/585; M^2, no. 4516/586; M^3, no. 4516/587; M_1, no. 4516/588; and M_2, no. 4516/589); and M^3 and M_3 from Bone Bed 4 of the Altynshokysu locality stored at the PIUZ.

Genus *Bohlinosminthus* Lopatin, 1999

Bohlinosminthus cubitalus Lopatin, 1999

Plate 6, figs. 18–24

Bohlinosminthus cubitalus: Lopatin, 1999b, p. 99, text-figs. 1c, 3l–3v.

Holotype. IAUU, ALT no. 115, fragmentary left dentary with M_2; Kazakhstan, North Aral Region, Altynshokysu locality; Lower Miocene, Aral Formation, Bone Bed 2.

Description (Fig. 33). P^4 is small and round. The sole small cuspule is developed at the anterior border of the occlusal surface. An extensive round valley bordered by a narrow circular crest is located behind it. In some cases, it is divided into two by a short longitudinal crest that connects the cuspule to the posterior wall of the valley.

M^1 and M^2 are four-rooted. M^1 is rounded square in outline; its anterior and posterior lobes are approximately equal in width, and the lingual side of the crown is somewhat longer than the labial side. The anterior arm of the protocone is connected to the anteroloph (occasionally, a very small fold is observed between them). Protoloph II is present. The mesocone is almost undeveloped, and the middle point of the entoloph is connected to a small mesostyle by a long and narrow mesoloph. The metaloph adjoins the central or anterior region of the hypocone (metaloph I). The posteroloph extends to the posterolabial side of the metacone and forms a closed posterosinus, which is occasionally partitioned by a small additional ridge connecting the posteroloph and the metacone.

M^2 is rounded rectangular in outline. Its posterior lobe is markedly narrower than the anterior lobe, and the labial and lingual sides of the crown are approximately equal in length. Only the labial arm of the anteroloph is developed, extending in parallel to the anterior border of the tooth. Protoloph I is formed by the projections of the anterior cusps and connected to the lingual end of the anteroloph. Protoloph II is absent. The mesoloph is long and well-developed. The metaloph is connected to the anterior region of the hypocone at the point of fusion with the entoloph.

M^3 is round in outline and three-rooted. The hypocone and metacone are strongly reduced. The anteroloph has a long labial arm, the lingual end of which is connected to a large and straight protoloph. The hypocone and metacone are connected by the anteriorly curved metaloph. The short entoloph connects the central parts of the protoloph and metaloph; occasionally, it is incomplete or absent (Fig. 33). The entosinus is closed. The posterior region of the protocone is fused with the anterolingual region of the hypocone. The mesoloph connects the mesostyle to the entoloph or metaloph; in some specimens, it is absent. The posteroloph reaches the metacone and forms a narrow and closed posterosinus.

M_1 is elongated rectangular, and its anterior lobe is significantly narrower than the posterior lobe. The anterior cusps are located within the same transverse plane. The hypoconid is displaced posteriorly with reference to the entoconid. The anteroconid is distinct and is shaped as a small cuspule at the anterior border of the tooth (this conid is registered in 85% of specimens). It is either completely isolated from the anterior cusps (70%) or connected by a small crest to the anterior arm of the protoconid (13%) or to the base of the metaconid (17%). The almost straight ectolophid and posteriorly curved metalophid II are connected to the protoconid at the same point. The mesoconid and mesostylid are small and connected to each other by a narrow and long mesolophid, which extends anterolingually. The posterolophid reaches the entoconid and borders an extensive posterosinusid posteriorly and lingually.

M_2 is rectangular in shape. Its anterior and posterior lobes are approximately equal in width. Both arms of the anterolophid are present. A crest deviates posteriorly from the central part of the anterolophid and adjoins metalophid I. Metalophid II is frequently absent. The following four structural variants are recognized: (1) the posterior arm of the protoconid forms a distinct metalophid II, and the mesolophid reaches the mesostylid (one specimen); (2) a long posterior arm of the protoconid and the mesolophid are fused to form an integrated transverse crest that reaches the mesostylid (5% of specimens); (3) the posterior arm of the protoconid reaches the mesostylid and forms the pseudomesolophid, while the mesolophid is strongly reduced or absent (12%); and (4) the posterior arm of the protoconid is absent, while the mesolophid is well-developed and reaches the mesostylid (83%). Occasionally, the mesolophid and protoconid have short projections, which are most likely rudiments of the posterior arm of the protoconid (Fig. 33h). Other structural details are the same as in M_1.

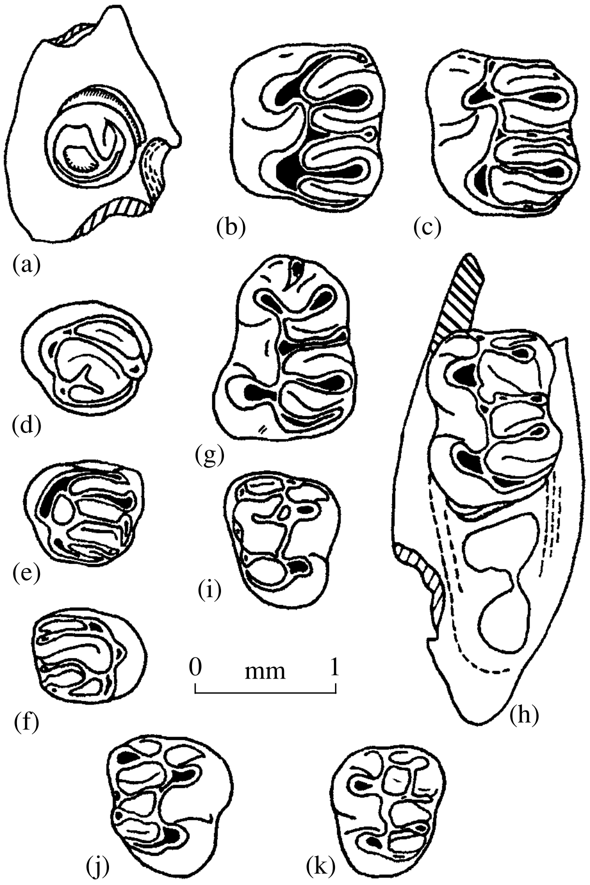


Fig. 33. *Bohlinosminthus cubitalus* Lopatin, 1999 from the Aral Formation of the Altynshokysu locality (Bone Bed 2): (a) specimen PIUZ, ALT no. 113, fragmentary left maxilla with P^4; (b) specimen IAUU, ALT no. 83, left M^1; (c) specimen IAUU, ALT no. 95, left M^2; (d) specimen IAUU, ALT no. 101, left M^3; (e) specimen PIUZ, ALT no. 154, left M^3; (f) specimen PIUZ, ALT no. 152, right M^3; (g) specimen IAUU, ALT no. 104, left M_1; (h) holotype IAUU, ALT no. 115, left dentary fragment with M_2; (i) specimen IAUU, ALT no. 123, right M_3; (j) specimen PIUZ, ALT no. 207, right M_3; and (k) specimen PIUZ, ALT no. 211, left M_3.

M_3 is relatively small and rounded triangular in outline. Its posterior lobe is significantly narrower than the anterior lobe. The tooth is similar in structure to M_2 and differs in the absence of the mesoconid, distinctly reduced posterior cusps, and the relatively large mesostylid, which is positioned close to the posterolingual region of the metaconid and the anterior side of the

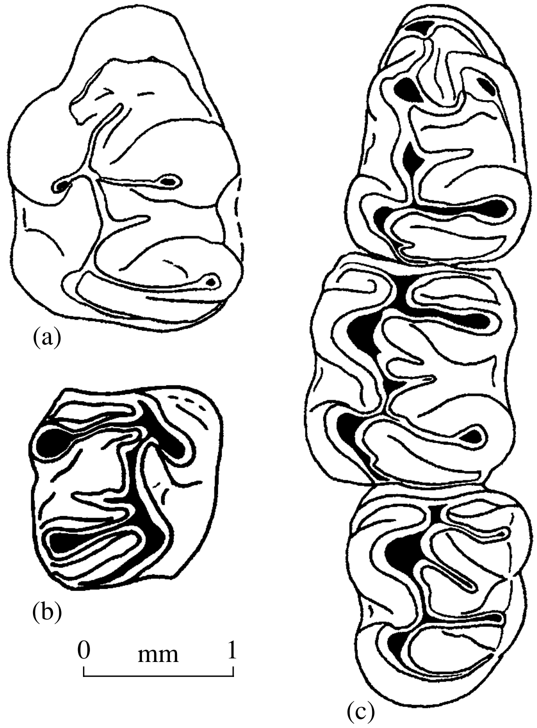


Fig. 34. *Eucricetodon occasionalis* Lopatin, 1996 from the Aral Formation of the Altynshokysu locality: (a) specimen PIN, no. 4516/198, left M^1; Bone Bed 4; (b) PIN, no. 4516/497, right M^2; Bone Bed 1; and (c) holotype PIN, no. 4516/196, left M_1–M_3; Bone Bed 4.

entoconid. The posterior arm of the protoconid is present; it is usually short and does not come into contact with the mesostylid (75% of specimens).

Measurements in mm:

Tooth	Length			Width		
	n	limits	mean	*n*	limits	mean
P^4	7	0.40–0.55	0.49	7	0.40–0.55	0.48
M^1	40	0.825–1.00	0.93	39	0.80–0.92	0.85
M^2	25	0.75–0.90	0.85	26	0.65–0.825	0.78
M^3	12	0.50–0.60	0.56	12	0.50–0.725	0.61
M_1	30	0.80–1.05	0.95	30	0.625–0.80	0.70
M_2	45	0.85–1.00	0.94	45	0.675–0.80	0.75
M_3	12	0.675–0.775	0.72	12	0.60–0.70	0.65

Comparison. *B. cubitalus* differs from *B. quartus* (Shevyreva, 1970) in its smaller dental measurements and different structure of the mesolophid of M_2 (connected to the mesostylid instead of the protoconid). It is similar in size to *B. parvulus* (Bohlin, 1946) and differs in the predominant development of the mesolophid, combined with the absence of the posterior arm of the protoconid on M_2 and the obligatory development of four roots in M^1 and M^2.

Remarks. The molar structure of *B. cubitalus* suggests that it is a descendant of the Oligocene *B. parvulus*. The differences between these forms consist in the stabilization of characters that widely vary in *B. parvulus*, such as the four-rooted M^1 and M^2, the pronounced anteroconid on M_1, and distinct mesolophid on M_2.

Material. In addition to the holotype, 252 isolated teeth from the type locality: 46 at the IAUU (17 M^1, ALT nos. 77–94; six M^2, ALT nos. 95–100; one M^3, ALT no. 101; seven M_1, ALT nos. 102–108; 14 M_2, ALT no. 109–122; and one M_3, ALT no. 123); 102 at the PIUZ (five P^4, 20 M^1, ten M^2, ten M^3, 21 M_1, 28 M_2, and eight M_3); 80 at the DK (two P^4, 25 M^1, ten M^2, five M^3, 17 M_1, 15 M_2, and six M_3); 18 at the NMW (five M^1, three M^2, one M^3, three M_1, five M_2, and one M_3); and six at the PIN (P^4, no. 4516/590; M^1, no. 4516/591; M^2, no. 4516/592; M_1, no. 4516/593; M_2, no. 4516/594; and M_3, no. 4516/595).

Family Cricetidae Fischer von Waldheim, 1817

Subfamily Eucricetodontinae Mein et Freudenthal, 1971

Genus *Eucricetodon* Thaler, 1966

Eucricetodon occasionalis Lopatin, 1996

Plate 6, figs. 25–30

Eucricetodon aff. *caducus*: Bendukidze, 1993, p. 44, pl. XVII, figs. 1–3.

Eucricetodon occasionalis: Lopatin, 1996, p. 77, pl. I, figs. 4 and 5, text-figs. 5g and 5h.

Holotype. PIN, no. 4516/196; left dentary fragment with M_1–M_3; Kazakhstan, North Aral Region, Altynshokysu locality; Lower Miocene, Aral Formation, Bone Bed 4.

Description (Fig. 34). A small-sized member of the genus, M_1–M_3 are approximately 5 mm long. In M^1, the anterior lobe is aligned centrally; the anterocone is small, very low, and unicuspid and only slightly projects anteriorly. The anterior projection of the protocone (spur of the protocone) is free and terminates short of reaching the anterocone base. The protolophule and metalophule are almost straight. The entoloph is slightly inclined. The mesoloph is short and straight. The posteroloph is narrow and poorly pronounced. The posterosinus is narrow and long.

M^2 is rounded square in outline, and its posterior lobe slightly narrows. The labial arm of the anteroloph is well-developed, while the lingual arm is somewhat reduced. The longitudinal and transverse crests are almost straight. The mesoloph is wide, flat, and short and extends in parallel to transverse crests. The posteroloph is weak. The posterosinus is long and narrow.

M^3 is small and round in outline. Its hypocone and metacone are strongly reduced. The mesoloph is short and terminates short of the labial border of the occlusal surface.

M_1 is rounded triangular in outline and expands posteriorly. The anteroconid is low and connected to the anterior arm of the protoconid (anterolophulid). The arms of the anterolophid are weakly developed. The long posterior arm of the protoconid forms a U-shaped metalophulid. The ectolophid is straight and displaced to the labial side of the tooth. The mesolophid is well-developed and directed anterolingually. The hypoconid and entoconid are widely spaced. The hypolophulid is straight. The posterior arm of the hypoconid is short but well-pronounced. The posterolophid is weak. The posterosinusid is shallow but relatively wide and long.

M_2 is extended rectangular. Both arms of the anterolophid are present. The transverse crests are slightly curved. The ectolophid is slightly inclined and has a clear short mesolophid. The posterior arm of the protoconid is short and free. The posterolophid is weak. Occasionally, a weak posterior arm of the hypoconid is present.

M_3 is rounded triangular in shape, short, and tapers posteriorly. Both arms of the anterolophid are well-developed. The protoconid and metaconid are widely spaced, and the posterior arm of the protoconid terminates at one-fourth of the crown width from the lingual border of the occlusal surface. The mesolophid is absent. The hypoconid and posterolophid are well-pronounced, while the entoconid is relatively strongly reduced. The posterior arm of the hypoconid is absent. The posterosinusid is wide and closed.

Measurements in mm. Length of M_1–M_3, 4.9; dentary depth under M_1, 3.8; under M_3, 4.0 (holotype).

Measurements of isolated teeth from Bone Bed 1:

Tooth	n	Length		Width	
		limits	mean	limits	mean
M^1	5	1.70–2.05	1.80	1.10–1.50	1.16
M^2	2	–	1.45	1.25–1.30	1.275
M^3	1	–	1.00	–	1.00
M_1	5	1.50–1.75	1.61	1.00–1.20	1.12
M_2	2	1.40–1.60	1.50	1.15–1.35	1.25
M_3	3	1.25–1.40	1.30	1.00–1.25	1.13

Comparison. The small and unicuspid anterocone distinguishes *E. occasionalis* from *E. gerandianus* (Gervais, 1848), *E. infralactorensis* (Viret, 1930), *E. aquitanicus* Baudelot et Bonis, 1968, *E. occitanicus* Bonis, 1970, *E. huerzeleri* Vianey-Liaud, 1972, *E. cetinensis* Daams, 1976, and *E. margaritae* Daams *et al.*, 1989. The species considered differs from *E. collatus* (Schaub, 1925), *E. dubius* (Schaub, 1925), and *E. longidens* Hugueney, 1969 in the short mesoloph and weak posteroloph of M^1 and M^2 and the absence of the mesolophid in M_3. It is distinguished from *E. asiaticus* (Matthew et Granger, 1923) and *E. caducus* (Shevyreva, 1967) by the absence of the ectomesolophid on M_1 and the absence of a mesolophid on M_3. It differs from *E. robustus* Agusti et Arbiol, 1989, *E. quadratus* Viret, 1930, and *E. martinensis* Freudenthal, 1994 in its small measurements and less massive cusps. It differs from *E. gergovianus* (Gervais, 1848) in the more strongly reduced posterior lobe of M^3. From *E. hochheimensis* (Schaub, 1925), *E. haslashensis* (Schaub, 1925), *E. leptaleos* Wang et Meng, 1986, and *E. sajakensis* Bendukidze, 1993, it differs in the small anterocone and short mesolophs and mesolophids. It differs from *E. schaubi* (Zdansky, 1930) in the more strongly developed anteroconid of M_1. It differs from *E. meridionalis* Wang et Meng, 1986 in the absence of mesostyles and from *E. youngi* Li et Qiu, 1980 in the long posterosinuses, straight protolophule, and better developed lingual arm of the anteroloph on M^2. It differs from *E. hesperius* Engesser, 1985 in the small anterocone of M^1, a weaker posteroloph on M^1 and M^2, and a better developed mesolophid and posterior arm of the hypoconid on M_1. It differs from *E. praecursor* (Schaub, 1925) in the short mesoloph on M^1 and M^2 and the better developed connection between the anteroconid and the protoconid on M_1. It differs from *E. thezelensis* Comte, 2000 in the smaller mean measurements, shorter mesolophs of M^1 and M^2, better developed metalophulid of M_1, better developed mesolophids of M_1 and M_2, more weakly developed posterior arm of the hypoconid of M_1 and M_2, and absence of this arm in M_3.

Remarks. *E. incertus* (Schlosser, 1884) is currently referred to the genus *Allocricetodon* (Freudenthal, 1994); *E. murinus* (Schlosser, 1884), *E. huberi* (Schaub, 1925), *E. atavus* (Misonne, 1957), and *E. nanus* Pelaez-Campomanes, 1995 are assigned to the genus *Atavocricetodon* (Freudenthal, 1996). Therefore, *E. occasionalis* is not compared with these species.

E. occasionalis is closely related to the European lineage *E. praecursor* (MP29)—*E. thezelensis* (MP30)—*E. hesperius* (MN1)—*E. gerandianus* (MN2)—*E. infralactorensis* (MN3). Regarding the level of evolutionary advantage of dental morphology, it is similar to *E. hesperius*. *E. sajakensis*, another species of the genus *Eucricetodon* from the Aral Formation, is related to the European lineage *E. hochheimensis—E. haslashensis* and approaches *E. haslashensis* (MN2) in the level of evolutionary advantage.

Occurrence. North Aral Region; Lower Miocene, Aral Formation.

Material. In addition to the holotype, the PIN collection contains a fragmentary left dentary with M_1 (PIN, no. 4516/197) and isolated M^1 (no. 4516/198) from Bone Bed 4 of the Altynshokysu locality and 12 isolated teeth from Bone Bed 1 (five M^1, nos. 4516/47, 49, 494–496; two M^2, nos. 4516/497, 498; one M^3, no. 4516/492; two M_1, nos. 4516/68, 499; one M_2, no. 4516/500; and one M_3, no. 4516/501); and five teeth from Bone Bed 2 (one M^1 housed at the NMW and three M_1 and one M_3 at the PIUZ).

Subfamily Cricetinae Fischer von Waldheim, 1817

Genus *Eumyarion* Thaler, 1966

Eumyarion tremulus Lopatin, 1996

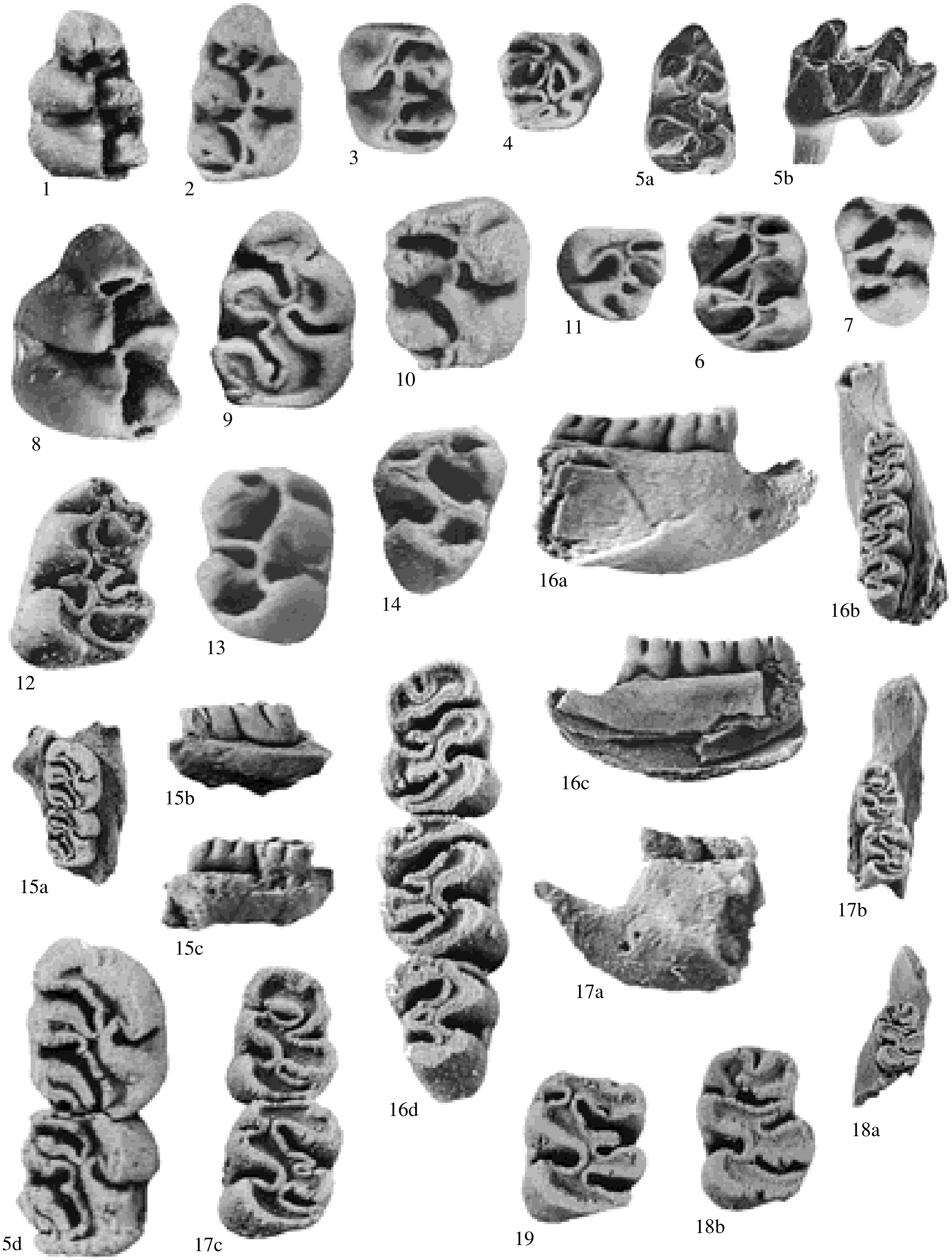
Plate 7, figs. 1–7

Eucricetodon aff. *youngi*: Bendukidze, 1993, p. 51.

Eumyarion tremulus: Lopatin, 1996, p. 75, pl. I, figs. 1–3, text-figs. 5a–5f.

Holotype. PIN, no. 4516/70, right M_1; Kazakhstan, North Aral Region, Altynshokysu locality; Lower Miocene, Aral Formation, Bone Bed 1.

Plate 7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18b
18a

Description (Fig. 35). A medium-sized member of the genus, M_1 is 1.5–1.85 mm long. M^1 has a large anterior lobe. The anterocone is transversely extended, slightly bifurcates, and occupies the central position with reference to the longitudinal axis of the tooth or is displaced somewhat labially. The protosinus and anterosinus are separated from each other by the anterolophule, which is connected to the anterior projection of the protocone. A well-pronounced spur of the anterocone is located labially to the anterolophule; its end abruptly curves labially and sometimes reaches the cingulum to form the anteromesoloph. Sometimes, the spur is straight or forked. It is frequently connected to the anterior projection of the protocone. The paracone almost invariably has a posterior spur. The metalophule is formed by a projection of the metacone that is connected to the anterior arm of the hypocone. The entoloph is oblique or nearly straight. The mesoloph is well-differentiated and short and extends in parallel to the transverse crests. The posteroloph is separated from the metacone by a narrow and deep posterosinus.

M^2 is rounded square in outline. The labial arm of the anteroloph is well-developed, while the lingual arm is almost completely reduced. The cusps are massive, and the transverse crests are almost straight. The paracone has a clear spur. The mesoloph is narrow, sharp, and usually long; it reaches the spur of the paracone. The posteroloph is well-developed. The posterosinus is deep, wide, and long.

M^3 is small and round; the anterior elements of its occlusal surface (the labial arm of the anteroloph, protocone, paracone, and mesoloph) are well-developed, while the metacone and hypocone are reduced. The mesoloph is long and usually reaches the labial border of the occlusal surface. The protocone and hypocone contact lingually, so that the entosinus is closed.

M_1 is extended triangular in outline, and its posterior lobe slightly expands. The anteroconid is relatively small, well-differentiated, and connected to the metaconid. The anterior arm of the protoconid reaches the base of the anteroconid. The posterior arm of the protoconid forms the metalophulid, which slightly curves posteriorly. The hypolophulid slightly curves anteri-

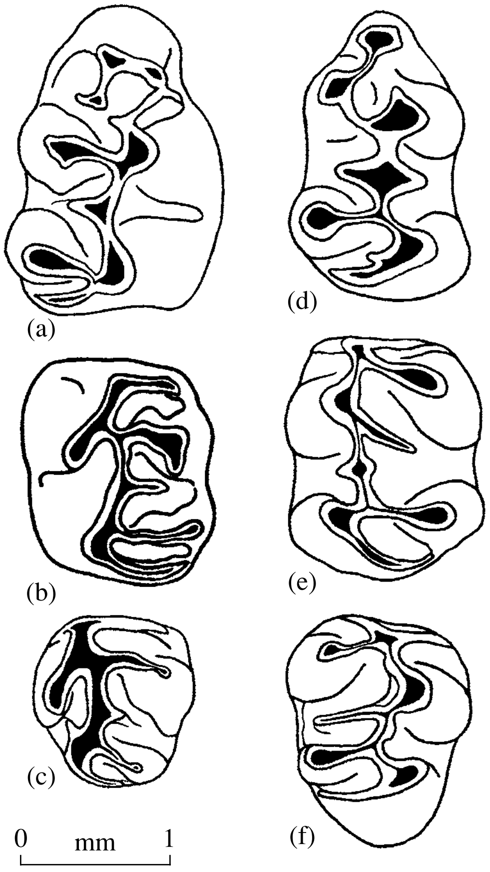


Fig. 35. *Eumyarion tremulus* Lopatin, 1996: (a) specimen PIN, no. 4516/60, right M^1; (b) specimen PIN, no. 4516/350, left M^2; (c) specimen PIN, no. 4516/389, left M^3; (d) holotype PIN, no. 4516/70, right M_1; (e) specimen PIN, no. 4516/15, left M_2; and (f) specimen PIN, no. 4516/402, right M_3; Altynshokysu locality, Aral Formation, Bone Bed 1.

Explanation of Plate 7

All specimens come from the Aral Formation.

Figs. 1–7. *Eumyarion tremulus* Lopatin, 1996: (1) specimen PIN, no. 4516/408, left M^1; (2) specimen PIN, no. 4516/60, right M^1; (3) specimen PIN, no. 4516/350, left M^2; (4) specimen PIN, no. 4516/389, right M^3; (5) holotype PIN, no. 4516/70, right M_1: (5a) occlusal and (5b) labial views; (6) specimen PIN, no. 4516/51, right M_2; and (7) specimen PIN, no. 4516/402, right M_3, ×15; Altynshokysu locality, Bone Bed 1.

Figs. 8–14. *Aralocricetodon schokensis* Bendukidze, 1993: (8) specimen PIN, no. 4516/539, left M^1; (9) specimen PIN, no. 4516/536, right M^1; (10) specimen PIN, no. 4516/541, right M^2; (11) specimen PIN, no. 4516/548, left M^3; (12) specimen PIN, no. 4516/550, left M_1; (13) specimen PIN, no. 4516/560, right M_2; and (14) specimen PIN, no. 4516/577, left M_3, ×15; Altynshokysu, Bone Bed 1.

Figs. 15–19. *Argyromys aralensis* (Argyropulo, 1939): (15) specimen PIN, no. 210/260 (holotype of *?Protalactaga borissiaki* Argyropulo, 1939), fragmentary right maxilla with M^1 and M^2: (15a) occlusal, (15b) lingual, and (15c) labial views, ×5; (15d) M^1 and M^2, occlusal view, ×12; (16) holotype PIN, no. 210/261, right dentary fragment with M_1–M_3: (16a) labial, 16b) occlusal, (16c) lingual views, ×5; (16d) M_1–M_3, occlusal view, ×12; (17) specimen PIN, no. 210/262 (holotype of *Schaubeumys woodi* Argyropulo, 1939), left dentary fragment with M_1 and M_2: (17a) labial and (17b) occlusal views, ×5; (17c) M_1 and M_2, occlusal view, ×12; (18) specimen PIN, no. 210/766, left dentary fragment with M_1, occlusal view: (18a) general appearance, ×5; (18b) M_1, ×12; and (19) specimen PIN, no. 210/765, left M_2, ×12; Akespe locality.

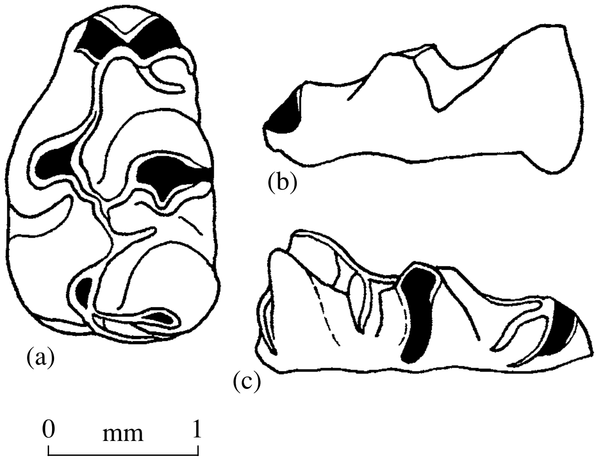


Fig. 36. *Eumyarion* sp., specimen PIN, no. 4516/502, left M^1: (a) occlusal, (b) lingual, and (c) labial views; Altynshokysu locality, Aral Formation, Bone Bed 1.

orly. The ectolophid is oblique. The mesolophid and ectomesolophid are well-developed. Occasionally, the posterior arm of the hypoconid has a rudimentary ridge. The posterolophid is long and arched. The posterosinusid is large.

M_2 is rectangular. The anterolophid is well-developed and forked. The metalophulid is connected to the anteroconid. The posterior arm of the protoconid is long and free. The hypolophulid is straight. The ectolophid is short and oblique. A weakly developed mesolophid and (or) the ectomesolophid are occasionally present. The posterolophid is long and straight, and the posterosinusid is deep.

M_3 is elongated triangular in outline, and its posterior lobe is narrow. The anterolophid forms two well-developed arms. The metaconid and protoconid are connected to the anteroconid. The free posterior arm of the protoconid is long and usually reaches the border of the occlusal surface of the tooth. A rudimentary mesolophid is extremely scarcely observed.

Measurements in mm:

Tooth	*n*	Length		Width	
		limits	mean	limits	mean
M^1	29	1.75–2.05	1.90	1.10–1.35	1.25
M^2	13	1.35–1.55	1.45	1.20–1.40	1.30
M^3	6	1.00–1.20	1.10	1.05–1.25	1.15
M_1	18	1.50–1.85	1.70	1.00–1.15	1.10
M_2	20	1.40–1.65	1.50	1.05–1.30	1.20
M_3	13	1.40–1.50	1.45	1.10–1.20	1.15

Comparison. *E. tremulus* differs from *E. latior* (Schaub et Zapfe, 1953) in the presence of a massive posterior spur of the paracone of M^1 and M^2, relatively weakly forked anterocone of M^1, and closed entosinus of M^3. If differs from *E. bifidus* (Fahlbush, 1964) in the less developed anterocone of M^1 and from *E. medius* (Lartet, 1851) and *E. leemanni* (Hartenberger, 1966) in the smaller and low-crowned teeth. *E. tremulus* is substantially larger than *E. microps* Bruijn et Sarac, 1991 and *E. intercentralis* Bruijn et Sarac, 1991 and, in contrast to these species, it lacks a well-developed posterior arm of the hypoconid on the lower molars. It differs from *E. montanus* Bruijn et Sarac, 1991 in the massive posterior spur of the paracone of M^1 and M^2; it differs from *E. carbonicus* Bruijn et Sarac, 1991 in the absence of the posterior arm of the hypoconid in M_2 and M_3, the rudimentariness of this arm in M_1, the longer posterior arm of the protoconid in M_3, and less developed mesolophid and ectomesolophid in M_2.

Remarks. In *E. tremulus*, a generally primitive dental structure (similar to that of *E. carbonicus* from the Harami 1 locality, Turkey; Early Miocene, MN1) is combined with the complete loss of the posterior arm of the hypoconid of M_2 and M_3, while M_1 has an extremely reduced ridge only rarely, which is characteristic of later (Middle Miocene) species of the genus *Eumyarion*. This suggests an independent development of this lineage of *Eumyarion* and corroborates the Asian origin of the genus (Bruijn and Sarac, 1991).

Occurrence. North Aral Region; Lower Miocene, Aral Formation.

Material. In addition to the holotype, the PIN collection contains 139 teeth and tooth fragments from Bone Bed 1 of the Altynshokysu locality; they include 36 M^1 (PIN, nos. 4516/60, 408–441, 468), 15 M^2 (nos. 4616/46, 340–344, 347, 348, 350–356), seven M^3 (nos. 4516/389–395), 31 M_1 (nos. 4516/357–366, 368–374, 376–380, 382–388, 403, 404), 30 M_2 (nos. 4516/15, 51–59, 71–79, 277–287), and 18 M_3 (nos. 4516/61, 62, 87–96, 395–401); and 22 isolated teeth from Bone Bed 2 of Altynshokysu (stored at the IAUU, PIUZ, DK, and NMW) and one M^1 (PIN, no. 210/764) from the Akespe locality.

Eumyarion sp.

Plate 6, fig. 31

Description (Fig. 36). M^1 is small and relatively low-crowned. The anterocone is broad, very short, and low; it is only slightly detached and weakly forked. Wear facets on the anterocone ascend dorsolabially and dorsolingually. Clear cingulids are absent. The protosinus is shallow. The well-developed anterolophule and the labial spur of the anterocone deviate from the anterocone. The anterolophule is fused with the anterior arm of the protocone to form an integrated crest that extends longitudinally. The spur of the anterocone abruptly curves labially. The protocone and paracone are relatively low and massive and are connected by a short posterior protolophule (protolophule II). The paracone has a large posterior spur. The wear facet of the paracone occupies an apical position; however, on the labial region, it extends onto the lateral side of this cusp (Fig. 36c). The entoloph curves labially. The entosi-

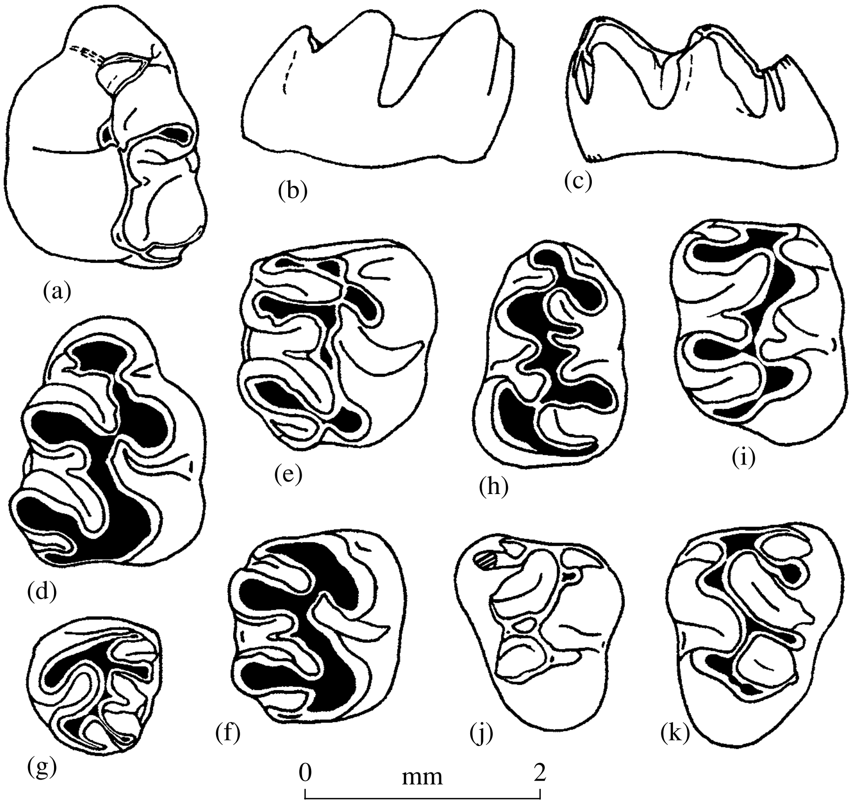


Fig. 37. *Aralocricetodon schokensis* Bendukidze, 1993: (a–c) specimen PIN, no. 4516/539, left M^1: (a) occlusal, (b) lingual, and (c) labial views; (d) specimen PIN, no. 4516/535, right M^1; (e) specimen PIN, no. 4516/541, right M^2; (f) specimen PIN, no. 4516/544, right M^2; (g) specimen PIN, no. 4516/548, left M^3; (h) specimen PIN, no. 4516/550, left M_1; (i) specimen PIN, no. 4516/561, right M_2; (j) specimen PIN, no. 4516/581, right M_3; and (k) specimen PIN, no. 4516/577, left M_3.

nus is transverse. The mesoloph is well-developed and closely approaches the spur of the paracone. The apices of the hypocone and metacone are strongly displaced labially and slightly inclined posteriorly, while the cusps themselves are located close to the posterior border of the tooth. The metalophule is connected to the posterior region of the hypocone. The metacone is strongly longitudinally compressed. The posteroloph is small. The posterosinus is reduced, short, and very narrow.

Measurements in mm. Length × width: M^1, 1.6 × 1.1.

Comparison and remarks. The structural pattern of the occlusal surface of M^1 suggests that it belongs to *Eumyarion*. This tooth differs from M^1 of *E. tremulus* and other currently known species of the genus *Eumyarion* in the structure of the anterior lobe (anterocone) and the reduced posterosinus. The tooth is smaller than M^1 of *E. tremulus*. Because the material is fragmentary, it is impossible to estimate the taxonomic significance of these distinctive features; therefore, a new species is not established.

Material. M^1 (PIN, no. 4516/502) from Bone Bed 1 of the Aral Formation of the Altynshokysu locality.

Subfamily Cricetodontinae Stehlin et Schaub, 1951

Genus *Aralocricetodon* Bendukidze, 1993

Aralocricetodon schokensis Bendukidze, 1993

Plate 7, figs. 8–14

Aralocricetodon schokensis: Bendukidze, 1993, p. 54, pl. XIX, figs. 2 and 3.

Holotype. IP, no. 15/27; isolated left M^1; Kazakhstan, North Aral Region, Altynshokysu locality; Lower Miocene, Aral Formation.

Description (Fig. 37). The molar crowns are relatively high. M^1 is asymmetrically pear-shaped with massive cusps. The apices of the protocone and hypocone are inclined posteriorly. In the majority of specimens, the anterocone only slightly bifurcates or lacks bifurcation; it is relatively small and weakly differentiated. The apex of the anterocone is displaced labially. Sometimes, the anterocone has two apices: the labial apex is the true apex of the anterocone, while the lingual apex is the origin of the anterolophule. The anterolophule is narrow and connected to the anterior arm of the protocone or its anterior side. The labial spur of the anterocone is usually present. It may be straight or curved labially or lingually; frequently, it is connected to the anterior arm of the protocone. The anterosinus is bordered by a low labial cingulum. The labial region of the entosinus slightly curves anteriorly. The protolophule curves posteriorly. The entoloph is oblique. The paracone has a weak posterior projection or a well-developed spur. The mesoloph is usually short and looks like a small projection; less often, this crest is relatively long and reaches the line of the paracone center. The metalophule is connected to the posteroloph. The posterosinus is short and shallow.

M^2 is rectangular. In the majority of specimens, only the labial arm of the anteroloph is present; less often, it also has a rudimentary lingual arm. The anterosinus and mesosinus are bordered by low labial cingula. The labial region of the entosinus abruptly curves anteriorly. The anterior arm of the protocone is connected to the anteroloph. The paracone has a posterior spur. The protolophule, entoloph, and mesoloph are similar in structure to those of M^1. The metalophule is connected to the posteroloph or the center of the labial side of the hypocone.

M^3 is rounded triangular. The anteroloph is labial. A large protocone is connected to its lingual part. The entosinus faces anteriorly; initially, it is open and closes in a heavily worn tooth. The mesoloph is usually long and reaches the labial edge of the occlusal surface (in some specimens, it is short or absent). The hypocone and metacone are strongly reduced. The metalophule is connected to the anterior region of the hypocone. The posterosinus is closed and displaced to the middle of the posterior side of the occlusal surface.

M_1 is subrectangular. The anteroconid is relatively large and well-pronounced. It is connected to the metaconid by a short anterolophulid. The anterior arm of the protoconid is connected to the anteroconid or anterolophulid; sometimes, it is free or absent. The posterior arm of the protoconid is free or connected to the metaconid to form metalophulid II. The mesolophid and ectomesolophid are usually well-developed (or only a short mesolophid is present). The hypolophulid adjoins the central region of the hypoconid. The posterolophid is long. The posterosinusid is large and bordered by a small lingual cingulid.

M_2 is rounded rectangular. Both arms of the anterolophid are present. The anterior arm of the protoconid and the protrusion of the metaconid connect to the middle of the anterolophid at the same point. The posterior arm of the protoconid is free and long; sometimes, it forms a pseudomesolophid and is often connected to the metaconid. The mesolophid is absent; occasionally, a weak ectomesolophid is present. The structure of the posterior region of the tooth is similar to that of M_1.

M_3 is rounded triangular, and its posterior part is significantly narrower than the anterior part. The anterolophid has two arms. Its middle part is connected to the anterior arm of the protoconid and the projection of the metaconid (in different points). The posterior arm of the protoconid is usually long and reaches the lingual border of the occlusal surface near the anterior side of the entoconid and forms the pseudomesolophid (sometimes, it is absent). The ectolophid is inclined and crosses the occlusal surface diagonally from the protoconid to the point of fusion between the projections of the hypoconid and entoconid. The posterior cusps are strongly reduced. The posterosinusid is broad but short. All folds are bordered by low cingulids.

Measurements in mm:

Tooth	Length			Width		
	n	limits	mean	*n*	limits	mean
M^1	29	2.10–2.50	2.31	29	1.60–1.90	1.73
M^2	16	1.65–2.00	1.78	16	1.45–1.80	1.65
M^3	13	1.15–1.50	1.30	13	1.20–1.50	1.37
M_1	25	1.90–2.25	2.08	25	1.20–1.60	1.43
M_2	28	1.75–2.10	1.91	31	1.35–1.70	1.52
M_3	13	1.55–1.95	1.75	16	1.35–1.60	1.49

Comparison. The sole species of the genus.

Remarks. Bendukidze (1993) described the new genus and species *Aralocricetodon schokensis* on the basis of a sole heavily worn M^1 and placed it in the subfamily Cricetodontinae. The study of additional specimens has corroborated the assignment of this form to the Cricetodontinae and that it represents a separate primitive genus.

Occurrence. North Aral Region; Lower Miocene, Aral Formation.

Material. Isolated teeth and tooth fragments: 61 from Bone Bed 1 (collection of the PIN: 17 M^1, nos. 4516/524–540; seven M^2, nos. 4516/541–547; two M^3, nos. 4516/548, 549; nine M_1, nos. 4516/550–558; 17 M_2, nos. 4516/559–575; and nine M_3, nos. 4516/576–584) and 116 from Bone Bed 2 of Altynshokysu: 31 at the IAUU (six M^1, four M^2, three M^3, six M_1, seven M_2, and five M_3); 33 at the PIUZ (two M^1, six M^2, seven M^3, eight M_1, six M_2, and four M_3); 15 at the DK (nine M^1, two M^2, one M_1, two M_2, and one M_3); and 36 at the NMW (seven M^1, three M^2, five M^3, eight M_1, nine M_2, and four M_3).

Family Spalacidae Gray, 1821

Genus *Argyromys* Schaub, 1958

Argyromys aralensis (Argyropulo, 1939)

Plate 7, figs. 15–19

Schaubeumys aralensis: Argyropulo, 1939b, p. 206, text-figs. a and d.

Schaubeumys woodi: Argyropulo, 1939b, p. 208, text-figs. b and c.

Schaubeumys (?) aralensis: Gromov, 1962, p. 158, text-figs. 148 and 149.

?Protalactaga borissiaki: Argyropulo, 1939c, p. 174, text-fig. b.

Protalactaga borissiaki: Gromov, 1962, p. 149, text-fig. 126.

Argyromys aralensis: Schaub, 1958, p. 807, text-fig. 268; Vorontzov, 1982, p. 197, text-fig. 159b.

Argyromys woodi: Vorontzov, 1982, p. 197, text-fig. 159c.

Holotype. PIN, no. 210/261, fragmentary right dentary with M_1–M_3; Kazakhstan, North Aral Region, Akespe locality; Lower Miocene, Aral Formation.

Description (Fig. 38). The posterior base of the zygomatic process of the maxilla is in line with the boundary between M^1 and M^2. The posterior border of the incisive foramina is located slightly anterior to M^1. The hard palate is very narrow; judging from the preserved right half, the total width of the palate is only slightly wider than M^1.

The cheek teeth are mesodont, relatively high-crowned compared to myomorph rodents, but too low for mole rats.

The upper molars are stout and inclined posteriorly. M^1 is round in occlusal view. The cusps are well-pronounced. The anterocone is unicuspid and distinct, although it projects only slightly. The anterior fold (anterolingual sinus) is well-pronounced, and the anterocone is only partially included in the anteroloph (the anterior arm of the protocone is recognized). The protocone is strongly compressed anterolabially, and its posterolingual part abruptly narrows. The lingual fold (lingual sinus, or entosinus) curves anteriorly; the labial folds (except for the posterosinus) abruptly curve and are directed posterolingually. The paracone is massive. The protoloph and the posterior arm of the protocone are short and connected to each other just anterior to a small mesocone. The mesoloph is very short. The hypocone is lophate. The metacone is connected to the posteroloph near the point of its fusion with the posterior side of the hypocone. The posteroloph is short and the posterosinus is weak.

M^2 is rounded square in outline. The anteroloph is labial. The protocone and paracone are connected in much the same manner as in M^1; however, behind the point where they contact, there is a short entoloph, which is connected to the mesocone. The paracone has a small posterior spur. The posterior lobe of the occlusal surface is similar in structure to that of M^1.

The diastema of the dentary ranges from relatively shallow to rather deep. The mental foramen (sometimes double) is located anterior to M_1 and at a distance of approximately 1.5–2 crown heights below the anterior alveolus. The lower masseteric ridge is distinctly developed, and its anterior edge is in line with the talonid of M_1. The incisor is large.

M_1–M_3 are lophodont, relatively high-crowned, and double-rooted. All the main cusps are well-developed, and the folds are deep.

M_1 is subrectangular. The anteroconid is large, round in outline, displaced posteriorly, and opposed to the anterior half of the metaconid. The anteroconid and metaconid are connected by a short and subtransversely positioned crest (anterolophulid + arm of the metaconid); anteriorly, they are separated from each other by a clear anterolingual fold (anterosinusid). These cusps are separated from the rest of the occlusal surface by a well-developed and deep transverse fold (holotype), which is formed by the anterolabial sinusid (protosinusid) fused with the anterior mesosinusid. In other specimens, these folds are separated from each other by close contact (PIN, no. 210/262) or fusion (PIN, no. 210/766) between the anteroconid and the protoconid. The anterior mesosinusid tends to close, because the long posterior arm of the protoconid (pseudomesolophid) closely adjoins or is fused with the posterior spur of the metaconid and forms a complete metalophid II. The protoconid is round and at least as massive as the anteroconid and metaconid. The mesoconid is undeveloped. The labial sinusid is almost transverse and only slightly inclined posteriorly. The lingual folds are deep. The ectolophid is short and oblique and oriented posterolingually. Its posterior end is connected to the anterior arm of the hypoconid and the projection of the entoconid. The entoconid occasionally has a small posterior spur. The hypoconid is massive. The posterolophid is long and gently curved; sometimes, it has a small thickening at the anterior border. The base of the lingual end of the posterolophid is positioned close to the posterior wall of the entoconid.

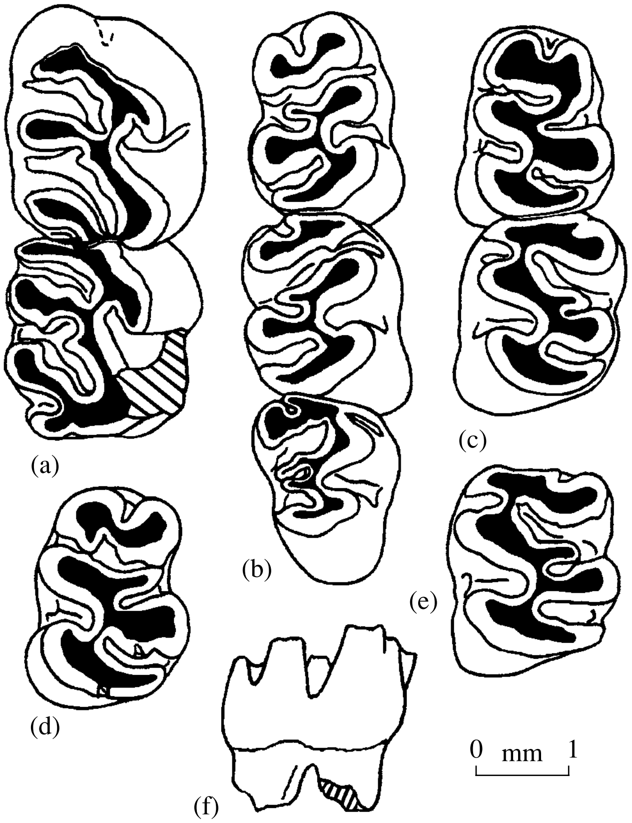


Fig. 38. *Argyromys aralensis* (Argyropulo, 1939): (a) specimen PIN, no. 210/260 (holotype of *?Protalactaga borissiaki* Argyropulo, 1939), right M^1 and M^2; (b) holotype PIN, no. 210/261, right M_1–M_3; (c) specimen PIN, no. 210/262 (holotype of *Schaubeumys woodi* Argyropulo, 1939), left M_1 and M_2; (d) specimen PIN, no. 210/766, left M_1; and (e, f) specimen PIN, no. 210/765, left M_2: (e) occlusal and (f) labial views; Akespe, Aral Formation.

The occlusal surface of M_2 is rounded rectangular or subsquare in outline. The anterolophid has two arms, the lingual arm is strongly reduced. The anterosinusid is small. The metaconid is transversely extended and has a small posterior spur. The metalophid is wide, short, and connected to the central part of the anterolophid. The protoconid is separated from the anterolophid by an oblique transverse fold or is connected to it by a short and narrow bridge of the anterior arm of the protoconid, which isolates the anterosinusid from the protosinusid. The mesoconid is undeveloped. The posterior arm of the protoconid is straight and relatively short, and its end is located far from the lingual border of the occlusal surface. The structural details of the posterior region of the occlusal surface are similar to those of M_1.

M_3 is longitudinally substantially shorter than M_2 and has a narrow posterior lobe. The anteroloph has two arms, the anterosinusid is short, and the protosinusid is long. The metacone and protocone are similar in structure to those of M_2. The protoconid is connected to the anterolophid. The anterior mesosinusid is large. The entoconid is strongly reduced. The lingual end of the posterior arm of the protoconid is connected to the anterior side of the entoconid; therefore, the posterior mesosinusid is closed and strongly reduced. The posteroloph is wide. The posterosinusid is large.

Measurements in mm. Length of M^1–M^2 (PIN, no. 210/260), 4.25; length of M_1–M_3 (holotype), 6.45; and length of M_1–M_2, 4.35 (holotype) and 4.0 (PIN, no. 210/262).

Measurements of teeth (length × width): M^1, 2.3 × 2.0 (PIN, no. 210/260); M^2, 1.95 × 2.0 (PIN, no. 210/260); M_1: 2.45 × 1.75 (holotype), 2.4 × 1.65 (PIN, no. 210/766), and 2.05 × 1.6 (PIN, no. 210/262); M_2: 2.3 × 1.85 (holotype), 2.05 × 1.75 (PIN, no. 210/766), and 2.1 × 1.7 (PIN, no. 210/262); M_3, 2.0 × 1.65 (holotype).

Comparison. The sole species of the genus.

Remarks. *A. woodi* (Argyropulo, 1939) is a junior synonym for *A. aralensis*. The differences in measurements, dental structure, shape of the diastema, and position of the mental foramen between *A. woodi* and *A. aralensis* should be regarded as intraspecific variation. Initially, only two jaw fragments of *Argyromys* were discovered and described as the holotypes of the two species. In specimen PIN, no. 210/766 (M_1), the metaconid and the lingual end of the mesolophid are positioned close to one another. In M_1 of the holotype of *A. aralensis*, these structures are clearly separated by a fold; in M_1 of the holotype of *A. woodi*, they are fused. In specimen PIN, no. 210/765 (M_2), the protoconid is connected to the anterolophid by a narrow anterior arm, whereas in M_2 of the holotype of *A. aralensis*, these structures are completely isolated; in M_2 of the holotype of *A. woodi*, they are connected by a wider and more massive crest. Newly found M_1 and M_2 are larger than the respective teeth of the holotype of *A. woodi* but smaller than the teeth of the holotype of *A. aralensis*. Thus, all the above structural variants are morphotypes of M_1 and M_2 of one and the same species. According to the Principle of Priority, the species name *A. aralensis* is retained.

In the original description, Argyropulo (1939b) assigned the two species to the genus *Schaubeumys* Wood, 1935, primarily on the basis of the specific division of the occlusal surface of the lower molars by the transverse fold and the general primitive dental pattern of the cricetoid–zapodid type. Currently, the generic name *Schaubeumys* is considered a junior synonym for *Plesiosminthus* (Martin, 1994). Schaub (1958) established *"Schaubeumys" aralensis* as a new genus, *Argyromys*, which was assigned to Cricetidae incertae sedis. The researcher noticed that certain characters of the dental structure of *Argyromys* resemble those of *Anomalomys* (Schaub, 1958, p. 807). Developing this viewpoint, some researchers placed *Argyromys* in the subfamily Anomalomyinae (Shevyreva, 1983). Klein Hofmeijer and Bruijn (1985) rejected the hypothesis of close relationships between the Anomalomyidae and *Argyromys* and placed this genus, together with *Eumysodon, Aralomys*, and *Tachyoryctoides*, in the family Tachyoryctoididae. Lindsay (1994) was of the opinion that *Argyromys, Eumysodon*, and *Aralomys* may be more closely related to the Zapodidae than to the Cricetidae. Bendukidze (1993) proposed that *Argyromys aralensis* is a primitive member of the family Dipodidae that is closely related to *Protalactaga*. Moreover, he initially suggested that the specimens identified as *A. woodi* and *"?Protalactaga" borissiaki* belong to the same rodent species from the subfamily Cricetodontinae (Cricetidae); subsequently, he considered *A. aralensis* (= *?Protalactaga borissiaki*) to be the ancestor of the subfamily Allactaginae (Bendukidze, 2001).

?Protalactaga borissiaki is also a junior synonym for *A. aralensis*. The species *?Protalactaga borissiaki* was originally described by Argyropulo (1939c) from the Akespe locality on the basis of a fragmentary maxilla with M^1 and M^2. It was assigned to the genus *Protalactaga* only tentatively, since the upper teeth of the type species *P. grabaui* Young, 1927 were not known, while the differences from the upper molars of *P. tunggurensis* Wood, 1936 were rather significant. It is worth noting that, based on the structure of P^4–M^2, *"Protalactaga" tunggurensis* is presently assigned to the subfamily Lophocricetinae (Martin, 1994) and considered a synonym for *Heterosminthus orientalis* Schaub, 1930 (Qiu, 1996; Zazhigin and Lopatin, 2000a). However, *"?Protalactaga" borissiaki* should not be referred to either Lophocricetinae or Allactaginae (or any other group of the superfamily Dipodoidea) (Lopatin, 2000a; Zazhigin and Lopatin, 2000b). The differences from the Miocene Dipodoidea include the presence of a very narrow hard palate, the absence of P^4, the high-crowned molars, the presence of a distinct anterocone in M^1, the pattern of connection between the metaloph and posteroloph in M^1 and M^2, and the shape of the labial sinus and the structure of the anterior region of M_1 (Lopatin, 2000a). The main distinction from the Cricetidae is the reduced anterocone of M^1.

On the basis of the structure of the zygomatic process in *?P. borissiaki* (which suggests small infraorbital foramen dimensions), Argyropulo concluded that this species is the earliest and most primitive member of the family Dipodidae. However, as he noted the absence of P^4 and the presence of a weak anterocone on M^1, the taxonomic position of this species remained uncertain for a long time (Gromov, 1962; *Catalogue…*, 1981) and it was commonly assigned to Cricetidae sensu lato (Carroll, 1988; Bendukidze, 1993). In my opinion, the general structural pattern and tooth measurements in the holotype of *P. borissiaki* suggest that it is conspecific to *A. aralensis.*

I believe that *Argyromys* may be regarded as the earliest genus of the family Spalacidae (Lopatin, 2000a). With respect to the structure of the upper and lower molars, *A. aralensis* is very similar to *Heramys eviensis* from MN4 of Greece (Klein Hofmeijer and Bruijn, 1985) and *Debruijnia arpati* from MN3 of Turkey (Ünay, 1996, 1999). These genera combine semihypsodont crowns and well-developed crests with an occlusal surface structure that is primitive for the Spalacidae and resembles the Cricetidae (Fig. 39). The common characters of *Argyromys* and *Debruijnia* consist of lophodont dental structure, presence of the cuspate anterocone and a short mesoloph on M^1, position of the anteroconid, and presence of an anterolingual fold between the anteroconid and the protoconid of M_1. In regard to the structure of M_2 and M_3 and the posterior region of M^1 and M^2, *Argyromys* is more similar to *Heramys* than to *Debruijnia. Argyromys* is a more advanced form than *Debruijnia* in the degree of consolidation between the anterocone and protocone of M^1. It is more advanced than both *Heramys* and *Debruijnia* in the extent of the reduction of the mesolophid and the posterior arm of the hypoconid of M_1 and the mesoloph of M^2. The Mio-Pliocene genus *Pliospalax* also displays certain similar features in the structure of M^1, M^2, and M^3. The sole structural distinction of *Argyromys* from *Debruijnia* and *Heramys* is the presence of protoloph II instead of protoloph I on M^2. However, this parameter widely varies in myomorph rodents (even at the intraspecific level). In addition, the presence of protoloph II was registered in some species of *Pliospalax* (see Ünay, 1999). The hard palate of the Spalacidae is also relatively narrow.

Thus, the set of morphological traits observed in the dentition and jaws characterize *A. aralensis* as the earliest member of the family Spalacidae. Close relationships between it and the Tachyoryctoididae and Rhizomyidae are less probable, since, in the dental evolution of these groups, simplification of the occlusal surface preceded the trend toward an increase in the crown height (Ünay, 1999), whereas the Spalacidae displayed the opposite succession. *Argyromys* apparently belongs to a special Asian lineage of this family, since it combines general primitiveness with an advanced (derived) state of certain characters, as compared with the later eastern Mediterranean genera discussed above.

Argyropulo (1939b, 1939c) assigned no. 210/1 to the holotype of *Schaubeumys aralensis*, no. 210/2 to the holotype of *Schaubeumys woodi*, and no. 210/8 to the holotype of *?Protalactaga borissiaki*. However, they were later replaced by nos. 210/261, 262, and 260, respectively (see Vorontzov, 1982, p. 197), because Gromova (1959) used the same numbers for other specimens.

Occurrence. North Aral Region; Lower Miocene, Aral Formation.

Material. In addition to the holotype, the PIN collection contains the following specimens from the type locality: a fragmentary maxilla with M^1 and M^2 (holotype of *?Protalactaga borissiaki*, no. 210/260); dentary fragment with M_1 and M_2 (holotype of *Schaubeumys woodi*, no. 210/262); dentary fragment with M_1 (no. 210/766); and isolated M_2 (no. 210/765).

Family Tachyoryctoididae Schaub, 1958

Genus *Tachyoryctoides* Bohlin, 1937

Tachyoryctoides glikmani (Vorontzov, 1963)

Plate 8, fig. 1

Aralomys glikmani: Vorontzov, 1963, p. 151, text-fig. 1; 1982, p. 196, text-fig. 158a.

Tachyoryctoides aff. *obrutshewi*: Bendukidze, 1993, p. 71, pl. XXII, figs. 1–4.

Holotype. PIN, no. 1971/1, left dentary fragment with M_1 and M_2; Kazakhstan, North Aral Region, Zherlepes locality; Lower Miocene, middle part of the Aral Formation.

Description (Fig. 40). The lower jaw is stout; the masseteric fossa is extensive and deep, and its anterior border is located in line with the posterior region of M_2. The lower molars are relatively high-crowned and have long lingual folds.

M_1 is slightly elongated and wide. The anteroconid is transversely widened, displaced labially, and fused with the arms of the anterior cingulid to form a united arched anterolophid, the labial arm of which is connected to the protoconid and the lingual arm of which is connected to the metaconid (hence, the protosinusid and anterosinusid are closed). The protoconid extends posterolingually. The anterior arm of the protoconid looks like a small projection; its posterior arm is long and connects to the projection of the metaconid to form metalophid II, which curves posteriorly. The long and posterolingually inclined anterolophulid is connected to the middle of metalophid II at the point of fusion between the posterior arm of the protoconid and the projection of the metaconid. The ectolophid is short and slightly oblique. The external fold (ectosinusid) extends posterolingually. The mesolophid is long. The mesosinusid is double. The entoconid is transversely extended and connected to the posterior end of the ectolophid at the same point as the arm of the hypoconid. The arm of the hypoconid deviates from the central part of this cusp.

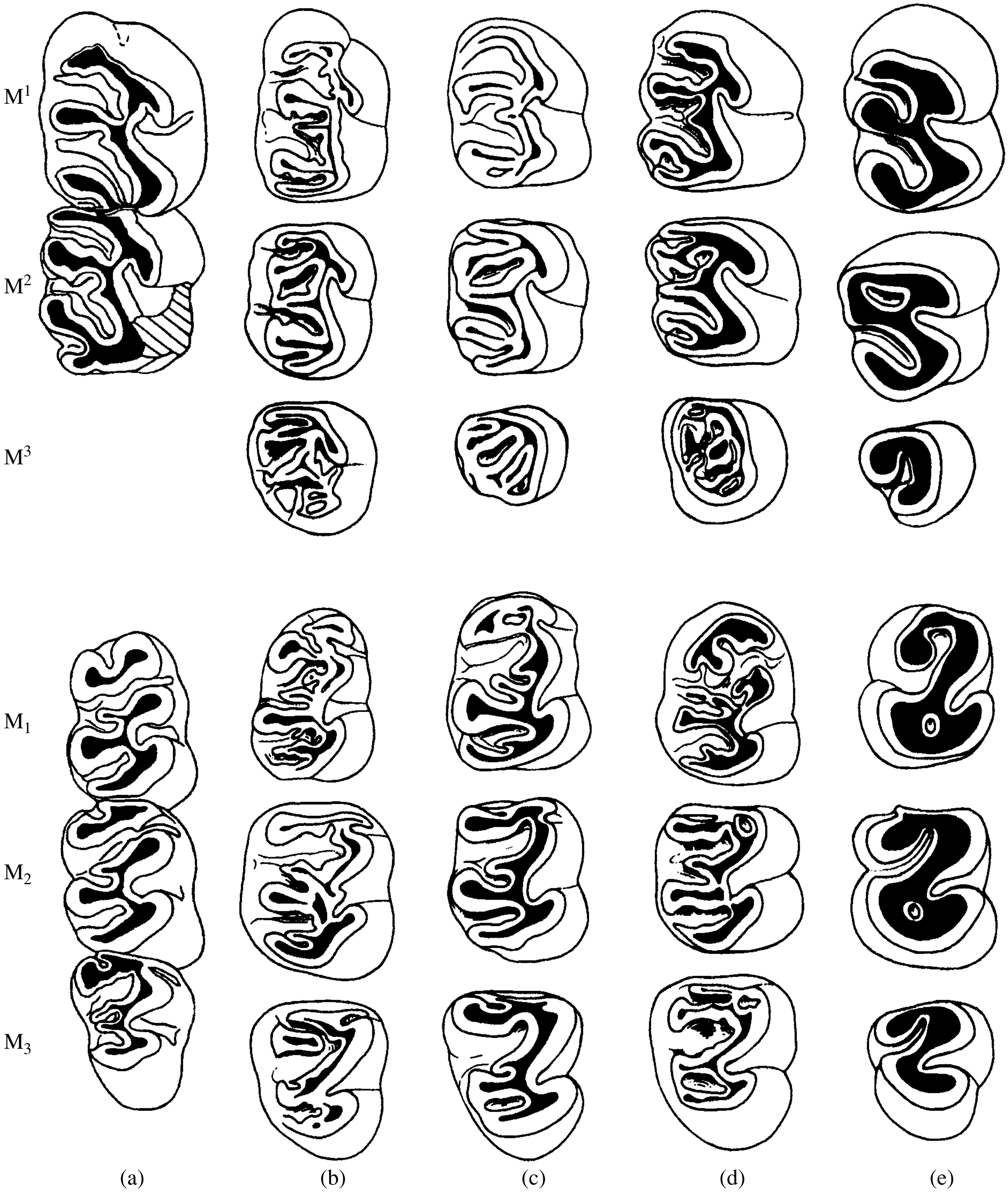


Fig. 39. Dental structure in members of the family Spalacidae: (a) *Argyromys*, (b) *Debruijnia*, (c) *Heramys*, (d) *Pliospalax*, and (e) *Spalax*; (b–e) after Ünay (1999).

The posterolophid is long and wide. The posterosinusid is long, deep, and closed lingually.

M_2 is massive, wide, and rounded quadrangular in outline. The anterolophid has two long arms. The anterosinusid and protosinusid are closed. The anterior arm of the protoconid and the projection of the metaconid are connected directly to the middle of the anterolophid without the participation of the anterolophulid and do not form metalophid I. The metaconid and entoconid are transversely extended. The protoconid, ectolophid, hypoconid, and posterolophid are similar in structure to those of M_1. The posterosinusid is closed. The external fold is slightly inclined posteriorly. The posterolabial region of the metaconid has a small spur that occupies an opposite position to the rudimentary mesolophid.

Measurements in mm. Holotype: length of M_1–M_2, 7.4; teeth (length × width): M_1, 3.7 × 3.0; and M_2, 3.9 × 3.5.

Comparison. *T. glikmani* differs from *T. obrutshewi* Bohlin, 1937, *T. intermedius* Bohlin, 1937, and *T. pachygnathus* Bohlin, 1937 in the substantially smaller measurements.

Remarks. Bendukidze (1993) identified this form as *Tachyoryctoides* aff. *obrutshewi* Bohlin, 1937 and proposed that *Aralomys glikmani* is a junior synonym for *Eumysodon spurius* Argyropulo, 1939 and the genus *Eumysodon* Argyropulo, 1939 is a synonym for the genus *Tachyoryctoides*. In addition, this researcher described a smaller member of *Tachyoryctoides* (see below) under the name *T. spurius* (= *A. glikmani*). However, it is impossible to concur with this point of view. First, the name *"Aralomys" glikmani* was given to the largest tachyoryctoidid from the Aral Formation, which corresponds to *"Tachyoryctoides* aff. *obrutshewi"* (after Bendukidze, 1993). Second, it is evident that *Eumysodon spurius* does not fit into *Tachyoryctoides*, since it strongly differs in dental morphology from all species of this genus (see below).

However, Bendukidze (1993) is correct in assuming that *"Aralomys" glikmani* belongs to *Tachyoryctoides* instead of to *Aralomys*. Bendukidze conclusively substantiated the presence of significant differences between the two genera and disproved the idea proposed by some researchers (Mellett, 1968; Dashzeveg, 1971; Kowalski, 1974) that *Aralomys* and *Tachyoryctoides* are synonyms. In the genus *Tachyoryctoides*, the teeth are more high-crowned, the folds are closed and form fossettes at later stages of tooth wear, M_1 has a relatively large mesolophid, and M_3 is only slightly reduced and always has a posterosinusid. This genus includes the Oligocene *T. obrutshewi* (= *T. tatalgolicus* Dashzeveg, 1971), *T. intermedius,* and *T. pachygnathus* and the Early Miocene *T. glikmani*, while *Aralomys* includes two Early Miocene species, *A. gigas* Argyropulo, 1939 and *A. kokonorensis* (Li et Qiu, 1980).

The Tachyoryctoidinae were placed in the family Cricetidae (Schaub, 1958; Dashzeveg, 1971; Vorontzov, 1982), Rhizomyidae (Bohlin, 1937, 1946; Kowalski, 1974; Li and Qiu, 1980; Bendukidze, 1993), Spalacidae (Flynn *et al.*, 1985) or were regarded as a separate family, the Tachyoryctoididae (Klein Hofmeijer and Bruijn, 1985; Russell and Zhai, 1987). Flynn *et al.* (1985) noted that *Tachyoryctoides* (and *Aralomys*) should not be assigned to the Rhizomyidae, because members of this genus are characterized by such advanced characters as short mesolophs and mesolophids, narrow crests of molars, and projecting masseteric crest of the lower jaw. In my opinion, the dental and jaw structure of these rodents suggests that they have close relationships with the family Spalacidae; consequently, they should be ranked as a separate family of the superfamily Spalacoidea.

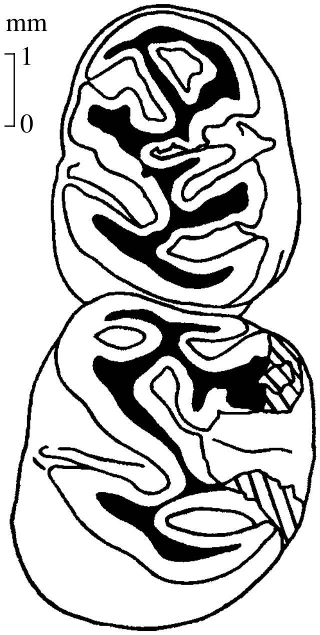


Fig. 40. *Tachyoryctoides glikmani* (Vorontzov, 1963), holotype PIN, no. 1971/1, left M_1 and M_2; Zherlepes locality, Aral Formation.

Occurrence. North Aral Region; Lower Miocene, Aral Formation.

Material. Holotype.

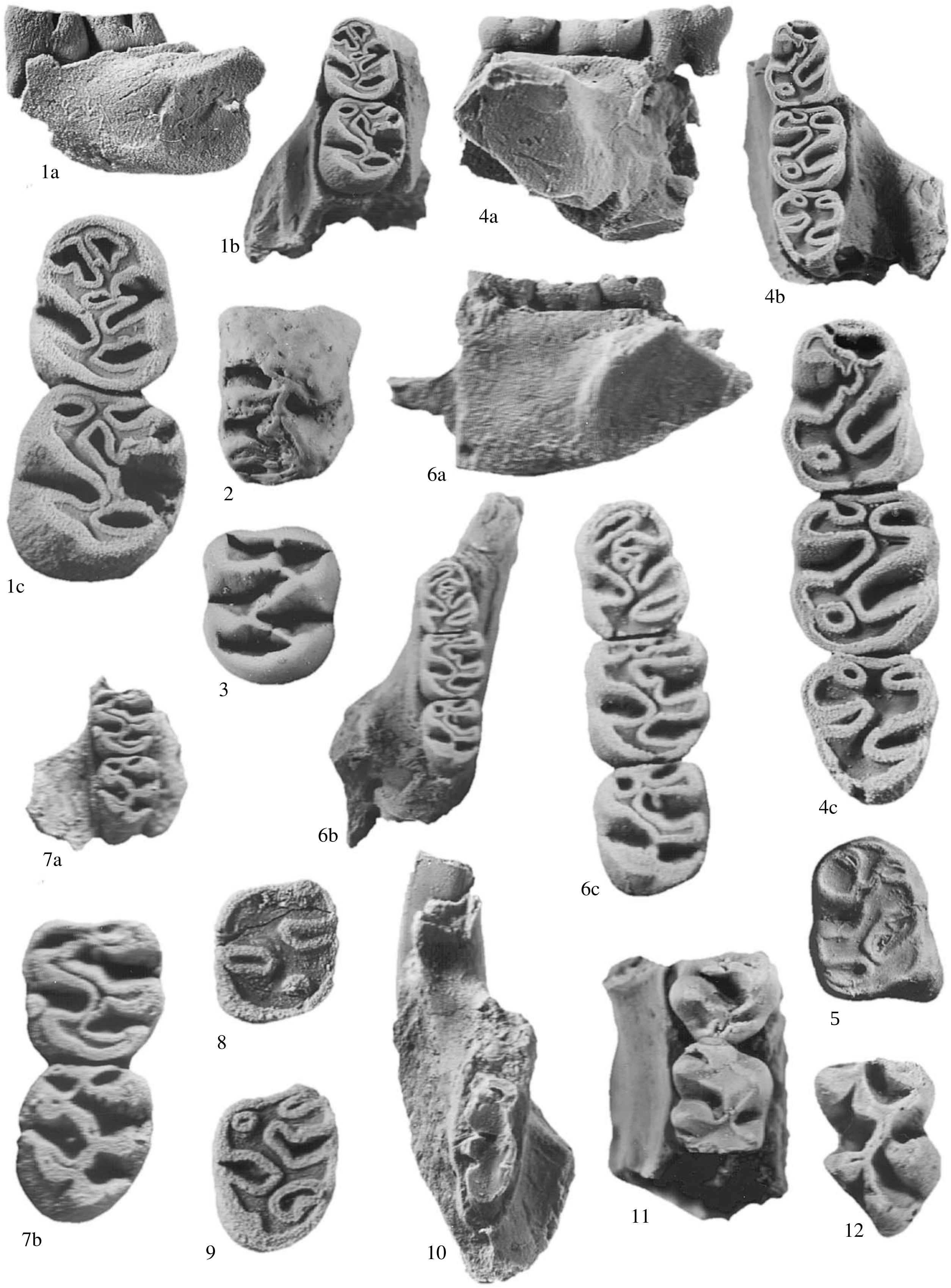
Tachyoryctoides sp.

Plate 8, figs. 2 and 3

Tachyoryctoides spurius: Bendukidze, 1993, p. 73, pl. XXII, figs. 5 and 6.

Description (Fig. 41). The crown of M^1 is relatively high, and the occlusal surface is rounded rectangular in outline. The folds are narrow, deep, and long. The cusps are massive. The anteroloph is well-developed, straight, and connected to the anterior arm of the protocone, which extends anterolabially. The anterosinus slightly curves posteriorly, and a small cingulum is located at its exit. The protocone extends anterolabially. The paracone is transversely elongated. The protoloph is connected to the oblique entoloph. The entosinus is deep and curves anteriorly. A short mesoloph deviates from the middle region of the entoloph and divides the mesosinus in two. Similar to the anterosinus, the mesosinus has a small cingulum at the exit. The metaloph is straight and connected to the central region of the hypocone. The posteroloph is long and well-developed. Its labial end adjoins the posterior side of the metacone and closes the posterosinus or occupies an isolated position (so that the posterosinus is open). As the tooth is worn, all the folds remain open for a long time and the posterosinus gradually becomes shorter.

Plate 8



M^2 differs from M^1 in its longer labial folds and the undulating metaloph. The labial end of the posteroloph is not connected to the metacone, the posterosinus is open, and its exit is relatively narrow.

M^3 and M_1 are absent from the material.

M_2 is relatively low-crowned. The occlusal surface is rectangular in shape. The anterolophid has two well-developed arms, the labial arm is longer and more massive than the lingual arm. All folds are deep and wide. The anterosinusid and protosinusid are closed. The metalophid curves anteriorly and is connected to the anterolophid in the central region. The ectolophid is oblique and connects the posterolingual region of the protoconid with the labial side of the entoconid. The mesolophid is absent; however, a small expansion is observed in approximately the middle of the lingual side of the ectolophid. The mesosinusid is deep, long, and curved anteriorly. The external fold is deeper and wider than any of internal folds and is positioned almost perpendicularly to the longitudinal tooth axis. The hypoconid is relatively low and connected to the labial side of the entoconid where it fuses with the ectolophid. The arm of the hypoconid is relatively long. The posterolophid is long and narrow, and its lingual end is connected to the posterior side of the entoconid and closes the posterosinusid. The point of fusion between the posterolophid and the entoconid is substantially lower than the apex of this cusp; it is likely that the occlusal surfaces of these elements are united at a relatively late stage of wear.

M_3 is similar in structure to M_2. Its anterosinusid and protosinusid are also closed, the oblique ectolophid has a projection in place of the mesolophid, and the posterosinusid is closed. However, it differs in the square outline of the crown and the short posterior cingulum and posterosinusid.

Measurements in mm. Length × width: M^1, 4.1×3.5 (PIN, no. 4516/28), 4.3×4.0 (collection DK); M_2, 3.6×3.2 (PIN, no. 4516/199); M_3, 3.5×3.4 (collection DK).

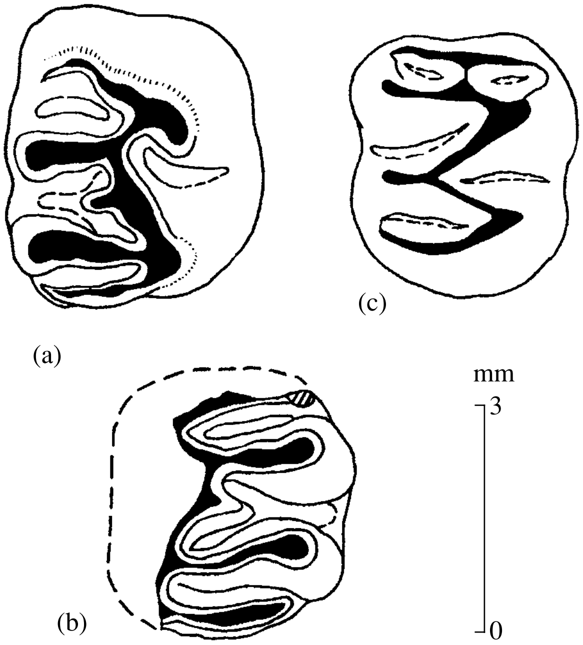


Fig. 41. *Tachyoryctoides* sp.: (a) specimen PIN, no. 4516/28, right M^1; (b) specimen PIN, no. 4516/200, fragmentary left M^2, and (c) specimen PIN, no. 4516/199, right M_2; Altynshokysu locality, Aral Formation, Bone Bed 4.

Comparison. The form in question differs from *T. obrutschewi, T. intermedius, T. pachygnathus,* and *T. glikmani* in its considerably smaller measurements.

Remarks. The differences between the form in question and *Eumysodon spurius* were discussed above. The specimens representing this small member of *Tachyoryctoides* were described by Bendukidze (1993) from the Akespe, Altynshokysu, and Zherlepes localities. Assignment of this form to a certain species requires additional data on the variation of measurements and dental structure in *T. glikmani* and *Aralomys gigas.*

Material. Five isolated teeth from Bone Bed 4 of the Altynshokysu locality: M^1 (PIN, no. 4516/28), a

Explanation of Plate 8

All specimens come from the Aral Formation.

Fig. 1. *Tachyoryctoides glikmani* (Vorontzov, 1963), holotype PIN, no. 1971/1, left dentary fragment with M_1 and M_2: (1a) labial and (1b) occlusal views, ×4; (1c) M_1 and M_2, occlusal view, ×8; Zherlepes locality.

Figs. 2 and 3. *Tachyoryctoides* sp.: (2) specimen PIN, no. 4516/28, right M^1; and (3) specimen PIN, no. 4516/199, right M_2, ×8; Altynshokysu locality, Bone Bed 4.

Figs. 4 and 5. *Aralomys gigas* Argyropulo, 1939: (4) holotype PIN, no. 210/263, right dentary fragment with M_1–M_3: (4a) labial and (4b) occlusal views, ×4; (4c) M_1–M_3, occlusal view, ×8; and (5) specimen PIN, no. 210/772, right M_1, ×8; Akespe locality.

Figs. 6–10. *Eumysodon spurius* Argyropulo, 1939: (6) holotype PIN, no. 210/264, left dentary fragment with M_1–M_3: (6a) labial and (6b) occlusal views, ×5; (6c) M_1–M_3, occlusal view, ×10; (7) specimen PIN, no. 210/264a (holotype of *Eumysodon orlovi* Argyropulo, 1939), left dentary fragment with M_2 and M_3, occlusal view: (7a) general appearance, ×5; (7b) M_2 and M_3, ×10; (8) specimen PIN, no. 210/264e, worn left M_2; (9) specimen PIN, no. 210/264d, left M_3, ×10; and (10) specimen PIN, no. 210/264b, right dentary fragment with an incisor and heavily worn M_2 and M_3, ×5; Akespe.

Figs. 11 and 12. *Yindirtemys birgeri* Bendukidze, 1993: (11) specimen PIN, no. 4516/4, fragmentary right maxilla with P^4–M^1; and (12) specimen PIN, no. 4516/201, left M_2, ×8; Altynshokysu, Bone Bed 4.

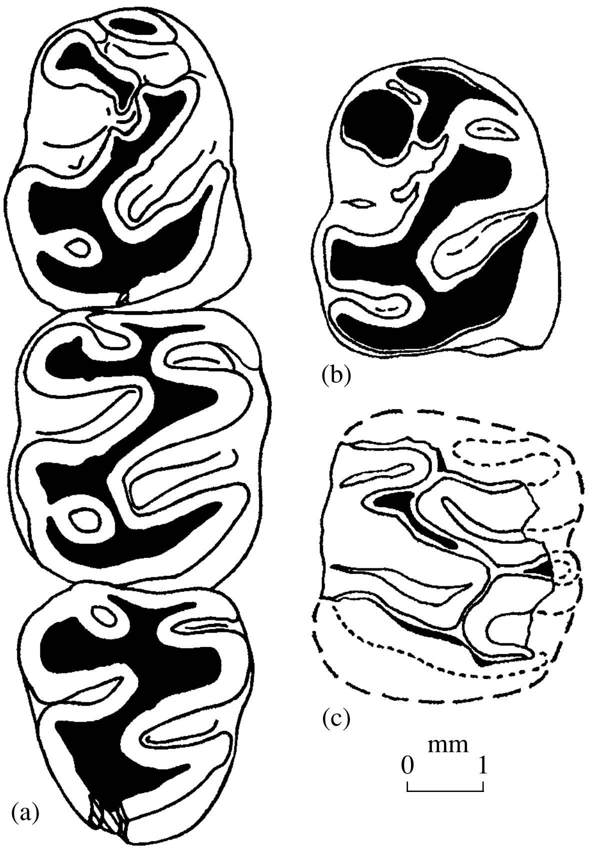


Fig. 42. *Aralomys gigas* Argyropulo, 1939: (a) holotype PIN, no. 210/263, right M_1–M_3; (b) specimen PIN, no. 210/772, right M_1; Akespe locality, Aral Formation; and (c) specimen PIN, no. 4516/523, fragmentary left M_2; Altynshokysu locality, Aral Formation, Bone Bed 4.

fragment of M^2 (PIN, no. 4516/200), and M_2 (PIN, no. 4516/199), stored at the PIN; and M^1 and M_3, stored at the DK.

Genus *Aralomys* Argyropulo, 1939

Aralomys gigas Argyropulo, 1939

Plate 8, figs. 4 and 5

Aralomys gigas: Argyropulo, 1939a, p. 113, text-fig. a; Gromov, 1962, p. 157, text-fig. 147; Vorontzov, 1982, p. 196, text-fig. 158b; Bendukidze, 1993, p. 75, pl. XXII, figs. 7 and 8.

Aralomys sp.: Bendukidze, 1993, p. 77, pl. XXIII, figs. 1–5.

Holotype. PIN, no. 210/263, right dentary fragment with M_1–M_3; Kazakhstan, North Aral Region, Akespe locality; Lower Miocene, Aral Formation.

Description (Fig. 42). The lower jaw is massive; the masseteric fossa is large and deep, and its anterior border is in line with the center of M_2. The lower molars are low-crowned and have short lingual folds.

M_1 is elongated. The anteroconid expands slightly transversely and is slightly displaced labially with reference to the longitudinal tooth axis. The labial arm of the anterior cingulid is relatively long, while the lingual arm is short (terminating short of reaching the metaconid: specimen PIN, no. 210/772) or absent (holotype). The anteroconid and metaconid are connected at the base by a short anterolophulid (PIN, no. 210/772) or are completely isolated (holotype). The metaconid is massive at the base and has a posterolabially extended posterior projection, which comes into contact with the anterior arm of the protoconid to form metalophid I. The anterosinusid is very shallow and posterolabially extended. The protosinusid is substantially larger than the anterosinusid and extends mainly transversely. The protoconid extends posterolingually and is fused with the ectolophid, which is stout, obliquely positioned, and connected to the labial side of the entoconid. The external fold is deep, extends to the middle of the occlusal surface, and is bordered externally by the labial projection of the hypoconid, which is connected to the base of the labial wall of the protoconid. The mesolophid is poorly pronounced and resembles a small expansion (holotype) or a small process of the ectolophid (PIN, no. 210/772), which extends into the mesosinusid (its lingual region is substantially lower that the labial region, and this lowering is extremely abrupt). The mesosinusid is deep, long, and open. The entoconid is massive and transversely positioned; at late stages of wear, its occlusal surface is rectangular in outline. The arm of the hypoconid is very short and connects the labial side of the entoconid to the lingual region of the hypoconid. The posterolophid is wide and stout but relatively short. The posterosinusid is relatively small and closed (holotype) or has a narrow exit (PIN, no. 210/772).

M_2 is rectangular. The anterolophid has two arms, the labial arm is substantially longer than the lingual arm. The anterosinusid is small and has a narrow exit. The protosinusid is large and open. The anterolophulid is short and connected to metalophid I, which is long and curved anteriorly. The metaconid is slightly displaced anteriorly in relation to the protoconid. The external fold is very deep and open; the ectolophid is strongly displaced lingually, but it is inclined posterolingually to a substantially lesser extent than that of M_1. The mesosinusid curves anteriorly. The hypoconid extends posterolingually. The arm of the hypoconid is located near its lingual region. The posterolophid is short. The posterosinusid is wide but very short; in a worn tooth, it is closed (holotype).

M_3 (holotype) is longitudinally short, and its talonid is reduced. The anterolophid has two arms. The anterosinusid is small and closed. The protosinusid is open. The anterolophulid is short and connected to the middle of metalophid I. The metaconid and protoconid are opposed to each other, and metalophid I is straight. The ectolophid is slightly oblique, while the ectosinusid is almost transverse. The entoconid and hypoconid are positioned close to each other. The posterosinusid is indiscernible.

Measurements in mm. Holotype: length of M_1–M_3, 11.0; teeth (length × width): M_1, 4.1 × 3.1; M_2, 4.0 × 3.4; and M_3, 3.5 × 3.2.

M_1 (PIN, no. 210/772) at the occlusal surface, 4.0 × 2.7; at the base, 4.4 × 3.2.

Comparison. *A. gigas* differs from *A. kokonorensis* (Li et Qiu, 1980) in its considerably smaller measurements and the presence of a rudimentary mesolophid on M_1.

Remarks. Argyropulo (1939a) assigned no. 210/7 to the holotype of *Aralomys gigas*. However, it was subsequently replaced by no. 210/263, because Gromova (1959) gave this number to another specimen.

The species considered is not compared with *A. padre* Tyutkova, 2000 from the Early Miocene Ayaguz locality (eastern Kazakhstan), because this small rodent (dimensions of M_1 are 1.65 × 1.1 mm, see Tyutkova, 2000) has a substantially simplified structure of the occlusal surface and should be assigned to a separate genus.

Occurrence. North Aral Region; Lower Miocene, Aral Formation.

Material. In addition to the holotype, isolated M_1 (PIN, no. 210/772) from the Akespe locality and M_2 fragment (PIN, no. 4516/523) from Bone Bed 4 of the Altynshokysu locality.

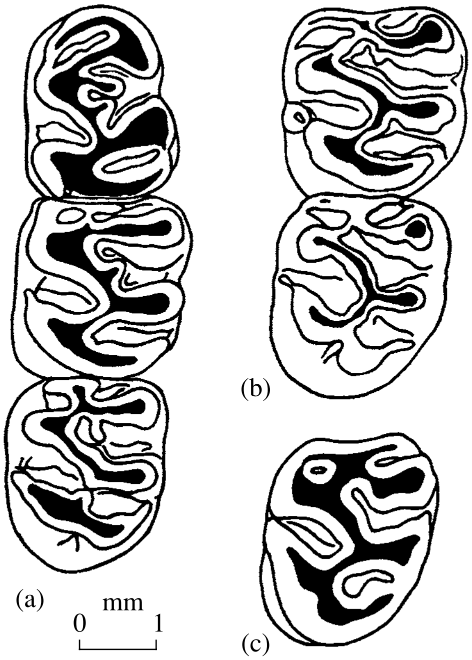


Fig. 43. *Eumysodon spurius* Argyropulo, 1939: (a) holotype PIN, no. 210/264, left M_1–M_3; (b) specimen PIN, no. 210/264a (holotype of *Eumysodon orlovi* Argyropulo, 1939), left M_2 and M_3; and (c) specimen PIN, no. 210/264d, left M_3.

Genus *Eumysodon* Argyropulo, 1939

Eumysodon spurius Argyropulo, 1939

Plate 8, figs. 6–10

Eumysodon spurius: Argyropulo, 1939a, p. 112, text-fig. b; Gromov, 1962, p. 158, text-fig. 144; Vorontzov, 1982, p. 195, text-fig. 157b.

Eumysodon orlovi: Argyropulo, 1939a, p. 113, text-figs. c and d; Gromov, 1962, p. 158, text-figs. 145 and 146; Vorontzov, 1982, p. 195, text-fig. 157a.

Holotype. PIN, no. 210/264, left dentary fragment with M_1–M_3; Kazakhstan, North Aral Region, Akespe locality; Lower Miocene, Aral Formation.

Description (Fig. 43). The horizontal ramus of the lower jaw is high and massive; anteriorly, the masseteric area reaches the line of the talonid of M_2. The incisor is stout and rounded triangular in cross section. The molars are low-crowned and lophodont.

M_1 is extended, and its anterior border is rounded. The anteroconid is indiscernible in the composition of the arched crest of the anterolophid, which borders the anterolabial corner of the occlusal surface. The ends of the anterolophid are connected to the anterior sides of the protoconid and metaconid and close a relatively large anterior fold that consists of the protosinusid and the anterosinusid. The metaconid is substantially displaced anteriorly with reference to the protoconid. The metaconid is massive and triangular at the base. The base of the protoconid is crescentic. Metalophid I is long, wide, straight, and positioned at an angle of approximately 45° to the longitudinal tooth axis. The posterior arm of the protoconid deviates from the middle of the lingual side of the cusp. The arm is long, free, and lingually oriented; it terminates at the base of the posterior wall of the metaconid. The ectolophid extends posterolingually. The mesolophid is short, directed anterolingually, and adjoins the posterior arm of the protoconid. The external fold is deep and closely approaches the center of the occlusal surface. The mesosinusid is deep and open. The entoconid is anterolingually extended. The arm of the hypoconid is short and connected to the central region of the hypoconid. The posterolophid is long, wide, and stout. The posterosinusid is long; at the base, it is closed lingually.

M_2 is subsquare in outline. The anterolophid has two arms, and the labial arm is somewhat longer than the lingual arm. The anterosinusid and protosinusid are shallow, have narrow exits, and close to form fossettes at the early stages of wear. The anterolophulid is absent, and metalophid I is connected directly to the anterolophid at one (Fig. 43b) or two points (Fig. 43a). The metaconid is slightly displaced anteriorly relative to the protoconid. The external fold is deep and reaches the center of the occlusal surface. The ectolophid is strongly inclined and, in some specimens, positioned subtransversely (Fig. 43b); it has a short mesolophid or a fine projection in the middle region. The entoconid is transversely extended. The arm of the hypoconid is relatively long. In an unworn tooth, a small supplementary cuspule (ectostylid) is observed anterolabial to the

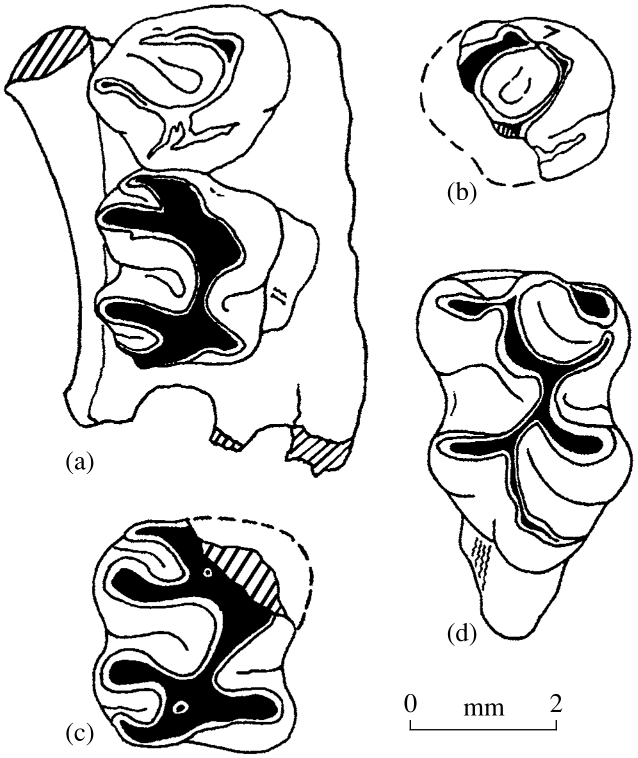


Fig. 44. *Yindirtemys birgeri* Bendukidze, 1993: (a) specimen PIN, no. 4516/4, fragmentary right maxilla with P^4–M^1; (b) specimen PIN, no. 4516/65, fragmentary right P^4; (c) specimen PIN, no. 4516/21, fragmentary right M^2; (d) specimen PIN, no. 4516/201, left M_2; Altynshokysu locality, Aral Formation, Bone Bed 4.

hypoconid; as the tooth is worn, it fuses with the appropriate projection of the cusp. The mesosinusid is straight. The posterolophid is long and wide. The posterosinusid is open; however, it has a basal cingulid at the base; therefore, this fold closes in a heavily worn tooth (when the mesosinusid and ectosinusid also close; see Pl. 8, fig. 8).

M_3 is similar in structure to M_2 but differs in its narrower and posteriorly rounded talonid. The arm of the hypoconid is shorter, the ectolophid curves anteriorly, and the mesolophid is absent. The metaconid occasionally has a specific spur in the area where it connects to the metalophid (Fig. 43a). The posterolabial side of the crown has a small but distinct fold that marks the boundary between the hypoconid and the posterolophid, resembling the hyposynusid of ctenodactylids.

In a heavily worn molar, all folds become closed (Pl. 8, figs. 8, 9; Fig. 43c). In an extremely heavily worn molar, some structural elements disappear and the occlusal surface becomes smooth or even concave (Pl. 8, fig. 10).

Measurements in mm. Holotype: length of M_1–M_3, 7.2; teeth (length × width): M_1, 2.5 × 1.8; M_2, 2.4 × 2.1; and M_3, 2.4 × 1.95. Specimen PIN, no. 210/264a: length of M_2–M_3, 5.2; teeth: M_2, 2.6 × 2.3; M_3, 2.7 × 2.15; specimen PIN, no. 210/264e, M_2, 2.3 × 2.1. Specimen PIN, no. 210/264d, M_3, 2.7 × 2.1. Specimen PIN, no. 210/264b: length of M_2–M_3 at the base, 5.2.

Comparison. The sole species of the genus.

Remarks. *Eumysodon* differs from *Tachyoryctoides* and *Aralomys* in the absence of the anterolophulid and the presence of the free posterior arm of the protoconid of M_1, the shape of the posterolophid of M_3, and the less posteriorly inclined external fold of the lower molars. It differs from *Ayakozomys* Tyutkova, 2000 in the lower and less lophodont crowns, the presence of the posterior arm of the protoconid and mesolophid on M_1, and nonreduced M_3.

The differences between *E. orlovi* and *E. spurius* are insignificant and fit into the intraspecific variation; therefore, *E. orlovi* is considered a junior synonym for *E. spurius.*

Argyropulo (1939a) assigned no. 210/3 to the holotype of *Eumysodon spurius*; no. 210/4 to the holotype of *E. orlovi*; no. 210/5 to the dentary fragment with very heavily worn teeth, which was referred to *E. orlovi*; and no. 210/6 to the specimen determined as M^2 of *E. orlovi*. However, Gromova (1959) gave the same numbers to other specimens; therefore, the numbers of the specimens Argyropulo had examined were replaced by nos. 210/264, 264a, 264b, and 264c, respectively. Subsequently, specimen no. 210/264c was lost. Judging from the figures (Argyropulo, 1939a, text-fig. c; Gromov, 1962, text-fig. 145), this was M_2 rather than M^2. Two unnumbered lower jaw fragments of *E. spurius* received nos. 210/264d (with M_3) and 264e (with M_2).

Material. In addition to the holotype, the PIN collection contains four fragmentary dentaries from the type locality: with M_2 and M_3 (holotype of *Eumysodon orlovi*, no. 210/264a), with M_3 (no. 210/264d), with M_2 (no. 210/264e), and with an incisor and worn M_2 and M_3 (no. 210/264b).

Family Ctenodactylidae Zittel, 1893

Subfamily Tataromyinae Lavocat, 1961

Genus *Yindirtemys* Bohlin, 1946

Yindirtemys birgeri Bendukidze, 1993

Plate 8, figs. 11 and 12

Yindirtemys birgeri: Bendukidze, 1993, p. 64, pl. XXI, figs. 2–4.

Holotype. IP, no. 15/28, upper jaw fragment with two complete rows of cheek teeth; Kazakhstan, North Aral Region, Altynshokysu locality; Lower Miocene, Aral Formation.

Description (Fig. 44). P^4 is round in outline and double-rooted; the lingual root is stout, while the labial root is relatively small. The paracone is displaced posteriorly relative to the protocone. The deep oval centrofossa is located in the center of the crown; it has a narrow exit in the anterolabial corner of the occlusal surface or is completely closed, depending on the presence of a complete or incomplete protoloph (anterior transverse crest). The anterior cingulum is undeveloped. Labially, the centrofossa is bordered by the paracone; posteriorly and lingually, it is limited by a narrow and posteriorly curved crest of the metaloph, which connects the protocone and the paracone. The tooth has a short talon that is substantially narrower than the tooth's anterior lobe from which it is separated by shallow lateral folds. A narrow posterolingually oriented posteroloph is located on the talon and is connected to the central region of the metaloph by two small ridges.

M^1 is subrectangular in outline and three-rooted. It is longer but somewhat narrower than P^4. The anterocone is clearly differentiated. The labial arm of the anteroloph is present. The anterosinus is very small and narrow. The paracone is displaced anteriorly with reference to the protocone. The protoloph is stout and the anterocone is connected to the middle of the protoloph. The lingual region of the mesosinus slightly curves posteriorly. The metacone is displaced anteriorly relative to the hypocone. The metaloph is wide. The entoloph connects the protocone to the center of the metaloph. The entosinus is posterolabially directed. The posteroloph is short. The posterosinus is weakly developed and small.

M^2 is substantially larger than M^1 and is similar to the latter in structure. It differs in its deeper and longer folds, especially the anterosinus and posterosinus. The posterior part of the tooth has a small round fossette bordered by the metaloph, posteroloph, and metacone antecrochet; the antecrochet divides the posterosinus into two parts.

M^3, P_4, M_1, and M_3 are absent from the material.

M_2 is elongate. The basal anterior cingulid is weak. The protoconid and metaconid are opposed to each other. Metalophid I slightly curves anteriorly. The posterior arm of the protoconid reaches the posterior region of the metaconid, forms metalophid II, and closes the trigonid basin. The crests of the talonid cusps are crescentic in shape. The short ectolophid is connected to the arms of the hypoconid and entoconid, which form the anteriorly curved hypolophid. The hypoconulid is large, and its arm is long. The sinusid is very large and slightly forked. The mesosinusid is wide and relatively short. The posterosinusid is long and crescentic in shape. Its labial end is directed anteriorly. The hyposinusid is shallow and oriented anterolingually.

Measurements in mm. Length × width: P^4, 2.25×2.7; M^1, 2.7×2.5; M^2, 3.3×2.9; and M_2, 4.25×3.0.

Comparison. *Y. birgeri* differs from *Y. deflexus* (Teilhard de Chardin, 1926), *Y. gobiensis* (Kowalski, 1974), *Y. suni* (Li et Qiu, 1980), and *Y. sajakensis* Bendukidze, 1993 in its substantially smaller measurements; it differs from *Y. grangeri* (Bohlin, 1946) (= *Y. woodi* Bohlin, 1946) and *Y. xiningensis* Wang, 1997 in its larger measurements, posteriorly curved mesosinuses of the upper molars, and better pronounced crescentic shape of the talonid crests of the lower molars; it differs from *Y. ambiguus* Wang, 1997 in the less anteriorly inclined transverse lophs of the upper molars; and it differs from *Y. aralensis* Bendukidze, 1994 in its large measurements and open mesosinuses.

Remarks. Bendukidze (1993) described two species of the genus *Yindirtemys* from the Aral Formation, i.e., large *Y. sajakensis* and medium-sized *Y. birgeri*. Subsequently, this researcher reduced *Y. birgeri* to a junior synonym for *Y. sajakensis* (Bendukidze, 1994) and regarded it as the subspecies *Y. sajakensis birgeri* (Bendukidze, 1997). In fact, these species substantially differ in size (see Bohlin, 1946; Kowalski, 1974; Wang, 1991, 1997) and stoutness of cusps (which are clearly more massive in *Y. sajakensis*); therefore, it is unreasonable to take them for synonyms. Wang (1997) considers *Y. sajakensis* to be a junior synonym for *Y. deflexus*, since the variation in dental measurements of the first fits into the variation range of the second and because the stoutness of the cusps, inclination of the lophs, development of the metacone antecrochet and spurs, and structure of the trigonid basin are similar in these species. In my opinion, the transverse lophs of the upper molars of *Y. sajakensis* are inclined and curved to a lesser extent than those of *Y. deflexus*; in addition, certain dental measurements (e.g., the length of M_1–M_2 and the width of M^2, M^3, and P_4) fall beyond the lower limits of variation in *Y. deflexus* (see Bendukidze, 1993, pp. 61, 63; Wang, 1997, pl. 9, 10). Therefore, I consider *Y. sajakensis* and *Y. birgeri* to be separate species that originated from the Oligocene *Y. deflexus* and *Y. ambiguus*, respectively.

Occurrence. North Aral Region; Lower Miocene, Aral Formation.

Material. Fragmentary right maxilla with P^4–M^1 (PIN, no. 4516/4); isolated P^4 (PIN, no. 4516/65), M^2 (PIN, no. 4516/21), and M_2 (PIN, no. 4516/201) from Bone Bed 4 of the Altynshokysu locality.

CHAPTER 5. AGE OF THE ARAL FAUNA AND CORRELATION WITH THE MAMMAL BIOCHRONOLOGICAL UNITS OF EUROPE AND CENTRAL ASIA

Review of Ideas Concerning the Age of the Aral Faunal Assemblage

The Aral Mammal Fauna was originally dated to the Late Oligocene (Orlov, 1939; Borissiak, 1943; Borissiak and Beliajeva, 1948; Beliajeva, 1964; Beliajeva and Trofimov, 1967; *Zoogeography…*, 1974; Russell and Zhai, 1987; etc.), Early Miocene–Aquitanian (Vyalov, 1945), or Burdigalian (Yanshin, 1953). These conclusions were based mainly on the taxonomic composition of large mammals. The data on small mammals suggest that the Aral Fauna should be dated as the Early Aquitanian and correlated with European zones MN1–MN2 (Gabunia, 1981, 1986; Agadjanian, 1986;

Bendukidze, 1993; Lopatin, 1996, 1997, 1998, 1999a, 1999b, 2000a, 2001, 2002a).

The following arguments in favor of a Late Oligocene age of the Aral Fauna were adduced: (1) the presence of a giant rhinoceros that is closely related to the Oligocene genera *Indricotherium* and *Baluchitherium* (Orlov, 1939); (2) the discovery of the aquatic rhinoceros (Amynodontidae), determined as the Eocene–Oligocene genus *Gigantamynodon* (Bayshashov, 1994a, 1994b); (3) the absence of proboscideans (Yanshin, 1953); (4) the presence of primitive Oligocene ruminants determined as *?Lophiomeryx* sp., *?Miomeryx* sp., and *?Prodremotherium* sp. (Orlov, 1939; Lucas *et al.*, 1998); (5) the presence of an insectivore that is closely related to *Palaeoscaptor acridens* (Orlov, 1939; Borissiak, 1943; Borissiak and Beliajeva, 1948; Bendukidze, 2000) and characteristic of the Oligocene Shand-Gol Fauna from Mongolia (Matthew and Granger, 1924; Mellett, 1968); (6) the primitive appearance of insectivores, lagomorphs, and rodents from the Aral Fauna (i.e., the presence of many genera and species of Oligocene origin), which closely resemble those of the Oligocene Shand-Gol Fauna from Mongolia (Argyropulo, 1940) and the Late Oligocene Taben Buluk Fauna from China (Lucas *et al.*, 1998; Bendukidze, 2000).

To date, none of these arguments stand up.

(1) The giant rhinoceros from the Akespe locality proved to be more specialized than Oligocene indricotheres and was referred to a separate genus and species, *Aralotherium prohorovi* Borissiak, 1939 (Borissiak, 1939). Subsequently, Gromova (1959) showed that it should be assigned to the genus *Paraceratherium*. This genus includes *Baluchitherium* and *Dzungariotherium* as synonyms and is known from the Upper Oligocene and Lower Miocene of Serbia, Romania, Kazakhstan, Mongolia, China, and Pakistan (Reshetov, 1994; Lucas, 1994; McKenna and Bell, 1997).

(2) A revision of the rhinocerotoid that was referred by Bayshashov (1994b) to the family Amynodontidae and established as the species *Gigantamynodon akespensis* has shown that, in reality, it belongs to the genus *Aceratherium* (or *Protaceratherium*) of the family Rhinocerotidae (Lucas and Emry, 1996).

(3) Proboscideans first appeared in Europe at the beginning of Zone MN4 or at the end of MN3 (Burdigalian), 17.5–18.5 Ma (see Kowalski and Kubiak, 1993; Bulot and Ginsburg, 1993; Michaux and Aguilar, 1995; Rögl, 1999; Made, 1999). In central Asia, the earliest proboscideans occurred at a level correlated with MN3 (Zhangjiaping Fauna, China), about 18.5–19 Ma (Qiu and Qiu, 1995; Flynn, 2000; Lindsay, 2001; Wang and Qiu, 2002). The first proboscideans from southern Asia (*Proboscidean Datum*, PD) are dated within the range from 18.3 Ma (Barry *et al.*, 1985) to 20.5 Ma (Downing *et al.*, 1993). Thus, the absence of proboscideans in the Aral Faunal Assemblage indicates only a pre-Burdigalian (rather than Oligocene) age.

(4) The preliminary identification of ruminants from the Akespe locality (*?Lophiomeryx* sp., *?Miomeryx* sp., and *?Prodremotherium* sp.), which was performed by Flerov (Orlov, 1939), was not corroborated by subsequent studies (Trofimov, 1962; Flerov, 1962). Among the specimens collected later, *Lophiomeryx turgaicus* Flerov, 1940 (Musakulova, 1971), *Prodremotherium* sp. (Musakulova, 1971; Bendukidze, 1977), *Amphitragulus* sp. (Flerov, 1962; Bendukidze, 1977; Vislobokova, 1990), *A. boulangeri* Pomel, 1853, and *Micromeryx flourensianus* Lartet, 1851 (Kozhamkulova and Orlovskaya, 1971; Vislobokova, 1983, 1990; Russell and Zhai, 1987; Tleuberdina *et al.*, 1989) were identified in the Aral Formation. Descriptions of these specimens have not been published (moreover, there is no exact stratigraphic assignment for the specimens determined as *Amphitragulus boulangeri* and *Micromeryx*), and only *Amphitragulus* sp. was figured (Flerov, 1962, text-fig. 481). Therefore, there is a need to corroborate these identifications (except for that of *Amphitragulus* sp.). In the case of *Lophiomeryx*, one specialized species of this genus (*Lophiomeryx* sp. from the Shawa Formation of the Dzungarian Basin) was discovered in the Lower Miocene of China (Qiu, 1965). Some researchers (Qiu and Qiu, 1995) believe that it may belong to a new, evolutionarily advanced genus.

The specimens tentatively identified by Flerov are thought to be lost (Trofimov, 1962). However, many ruminant limb bones that were collected in 1939 in Akespe are presently stored at the PIN. According to Vislobokova (1997, p. 222), all specimens from Akespe that were determined as *?Lophiomeryx* sp., *?Miomeryx* sp., and *?Prodremotherium* sp. in fact belong to *Amphitragulus*, while a small bovid that was earlier referred to as the Oligocene genus *Palaeohypsodonthus* (Lavrov *et al.*, 1985) belongs to the more advanced genus *Sinopalaeoceros*. *Amphitragulus* is characteristic of the Late Oligocene (MP28–MP30) and Early Miocene (MN1–MN5) of Eurasia (Vislobokova *et al.*, 1996). *Sinopalaeoceros* is known from the Early Miocene of China (Chen, 1988; Qiu and Qiu, 1995; Vislobokova, 1997).

(5) The data on the presence of *Palaeoscaptor acridens* in the Aral Formation are in error. The specimens identified as this species in actuality belong to the genus *Amphechinus* (Lopatin, 1999a), which is widespread in both the Oligocene and Miocene of Eurasia.

(6) The taxonomic composition of small mammals from the Aral Fauna is analyzed in subsequent sections of this chapter. However, it should be noted here that the assignment of some taxa in the open nomenclature (Bendukidze, 1993) to Oligocene central Asian species (*Amphechinus* cf. *rectus, Desmatolagus* aff. *gobiensis, D.* aff. *robustus, Sinolagomys* aff. *gracilis, S.* aff. *kansuensis, Parasminthus* aff. *tangingoli, Eucricetodon* cf. *caducus, Tachyoryctoides* aff. *obrutschewi*) provided a basis for dating the Aral Fauna to the Late Oligocene (Lucas *et al.*, 1998). This conclusion was also favored

by some erroneous and dubious identifications, such as *Palaeoscaptor acridens*, *Amphechinus minimus*, *Gobisorex kingae* (Bendukidze, 1993), *Propalaeocastor habilis*, and *P. kazachstanicus* (Tyutkova, 1994). In general, the species composition of small mammals from the Aral Fauna considerably differs from that of Oligocene central Asian (Ulantatalian and Tabenbulukian) faunas. The major indicator of the Early Miocene age of the Aral Fauna is the presence of the lagomorph *Sinolagomys pachygnathus* (Lopatin, 1998). It should also be emphasized that the Aral Formation yielded no rodents of the families Tsaganomyidae and Cylindrodontidae, which are characteristic of the Oligocene of Mongolia, China, and Kazakhstan, widespread to the west as far as Georgia (Benara Fauna: Gabunia, 1964; Chochieva *et al.*, 2001), and known from the terminal Oligocene Lanzhou Fauna, China (Qiu and Gu, 1988; Qiu and Qiu, 1995; Wang and Qiu, 2000b).

In my opinion, the Aral Fauna should be dated to the Aquitanian (early half of the Early Miocene), a conclusion that agrees with the currently accepted concept (Gabunia, 1986; Agadjanian, 1986; Bruijn *et al.*, 1992; Bendukidze, 1993). Nevertheless, comprehensive analysis of the taxonomic composition of small mammals from the Aral Assemblage is required to adequately substantiate this point of view.

Analysis of the Taxonomic Composition of the Aral Small Mammal Assemblage

To date, about 40 small mammal species of 30 genera and 14 families have been registered in the Aral Fauna. Table 1 shows a complete list of these taxa accompanied by their synonyms and localities.

The majority of small mammal genera from the Aral Faunal Assemblage are characteristic of the Oligocene. However, the majority of species differ from typical Oligocene forms in degree of evolutionary advantage. A similar state of affairs characterizes the Aquitanian of Europe and the early half of the Early Miocene of China (Qiu and Qiu, 1995).

Insectivora. Insectivore specimens are substantially less abundant than the Rodentia and Lagomorpha. Nevertheless, insectivores from the Aral Fauna are rather diverse and represented by three families, the Erinaceidae, Talpidae, and Soricidae. The Erinaceidae include shrew-hedgehogs (Galericinae), short-faced hedgehogs (Brachyericinae), and true hedgehogs (Erinaceinae).

The Aral short-faced hedgehog *Exallerix efialtes* displays a number of advanced characters as compared to *E. hsandagolensis* from the Lower Oligocene of Mongolia (McKenna and Holton, 1967), since its P_4 is significantly reduced, M_1 is enlarged and has a shearing paralophid, and the masseteric crest of the lower jaw is very stout (Lopatin, 1996). It is similar in these characteristics to *E. gaolanshanensis* from the Upper Oligocene of Lanzhou (Gansu, China), which is considered to be more specialized, since it has lost P_3 and enamel sculpturing on the labial side of its teeth (Qiu and Gu, 1988). *E. efialtes* supposedly retained P_3, and its P_4 is reduced to the same extent as that of *E. gaolanshanensis* or even greater, while M_1 is more specialized (Lopatin, 1999a; Lopatin and Zazhigin, 2003).

The Aral Formation yielded at least three species of true hedgehogs from the genus *Amphechinus*. *A. akespensis* belongs to the phylogenetic lineage of *A. rectus*; however, it differs in its narrower molars and the small metaconid of P_4. *A. microdus* displays a greater reduction of M_3 than the Oligocene *A. minimus* from central Asia, which is similar in size. The Erinaceinae from Akespe that were previously referred to the Oligocene *Palaeoscaptor acridens* in actuality belong to *Amphechinus* sp.

The Talpidae are scarce in the Oligocene and Early Miocene central Asian assemblages: only isolated specimens assigned to this group have been registered (Bohlin, 1942; Lopatin, 2002c). However, they are rather common in European localities of this age. The Aral Fauna is similar in this respect to the European fauna of the Aquitanian Age.

The genus *Desmanella* (Uropsilinae) was widespread in Europe and western Asia from Mammal Zone MP28 (Late Oligocene) to MN13 (Late Miocene); in the Balearic Islands, it survived up to the middle of the Pliocene (MN16). Regarding the structure and measurements of its teeth, *D. compacta* sp. nov. is similar to the earliest *Desmanella* sp. from the Upper Oligocene and Lower Miocene of Germany (Hoek Ostende, 1989; Ziegler, 1990, 1998).

The true Talpidae (Talpinae) are represented by three genera, *Pseudoparatalpa*, *Myxomygale*, and *Hugueneya*. *Pseudoparatalpa* was endemic to Asia and occurred in the Early Oligocene of Kazakhstan (Lopatin, 1999a). The genus *Myxomygale* dwelt from the Early Oligocene (MP23) to the Early Miocene (MN3). *Hugueneya* occurred from the terminal Oligocene (MP30) to the Early Miocene (MN2) of Europe (Ziegler, 1990). *M. asiaprima* sp. nov. is more closely related to the Oligocene species *M. antiqua* than to the Miocene *M. minor*, *M. hutchisoni*, and *M. engesseri*.

Shrews (Soricidae) are represented by two subfamilies, the Heterosoricidae and Crocidosoricinae. *Gobisorex akhmetievi* sp. nov. (Heterosoricinae) differs from the Oligocene *G. kingae* (Mongolia, Shand-Gol) in the structural details of its lower molar and the depth of the horizontal mandibular ramus and is likely a more specialized form. *Atasorex edax* gen. et sp. nov. is a primitive heterosoricine that resembles the Oligocene genera *Quercysorex*, *Gobisorex*, and *Domnina*. *Aralosorex kalini* (Crocidosoricinae) is considered to be closely related to the European *Carposorex* Crochet, 1975 from MN2–MN4 (Lopatin, 2004).

In the insectivore association from the Aral Fauna, the prevalence of crocidosoricine shrews among small

Table 1. List of small mammal taxa from the Aral Faunal Assemblage

Taxon	Species	Synonyms	Localities, (1, 2, 4) Bone Bed of Altynshokysu, (B) Altynshokysu and others after Bendukidze (1993)
Insectivora			
Erinaceidae			
Galericinae:	*Galerix* sp.	*Lantanotherium* sp.: Bendukidze (1993)	Altynshokysu 2, (B); Akotau
Brachyericinae:	*Exallerix efialtes* Lopatin, 1996	–	Altynshokysu 4
Erinaceinae:	*Amphechinus akespensis* Lopatin, 1999	–	Akespe
	A. microdus Lopatin, 1999	*A. minimus* Bohlin, 1942: Bendukidze (1993)	Altynshokysu 1, 2, 4; Akespe, Akotau
	Amphechinus sp.	*Palaeoscaptor acridens* Matthew et Granger, 1924: Borissiak and Beliajeva, 1948;	Akespe, Altynshokysu 2, Zhilansai
		A. cf. *rectus* (Matthew et Granger, 1924): Bendukidze, 1993	
Talpidae			
Uropsilinae:	*Desmanella compacta* sp. nov.	*Asthenoscapter* sp.: Bendukidze, 1993	Altynshokysu 2, (B)
Talpinae:	*Pseudoparatalpa lavrovi* (Bendukidze, 1993)	*Mygalea lavrovi*: Bendukidze, 1993	Altynshokysu 4, (B); Sayaken
	Myxomygale asiaprima sp. nov.	–	Altynshokysu 1
	Hugueneya sp.	*Proscapanus* sp.: Bendukidze, 1993	Altynshokysu 4, (B)
Soricidae			
Heterosoricinae:	*Gobisorex akhmetievi* sp. nov.	*Gobisorex kingae* Sulimski, 1970: Bendukidze, 1993;	Altynshokysu 4, (B)
		Gobisorex sp.: Lopatin, 1999	
	Atasorex edax gen. et sp. nov.	*Gobisorex* aff. *kingae* Sulimski, 1970: Bendukidze, 1993	Altynshokysu 1, 2, 4
		Heterosoricinae gen. et sp. indet: Lopatin, 1999	
Crocidosoricinae:	*Aralosorex kalini* Lopatin, 2004	–	Altynshokysu 2
Lagomorpha			
Desmatolagidae:	*Desmatolagus simplex* (Argyropulo, 1940)	*D.* aff. *shargaltensis* Bohlin, 1937: Bendukidze, 1993	Akespe; Altynshokysu 2, 4, (B); Akotau, Sayaken
	D. periaralicus Lopatin, 1998	*D.* aff. *gobiensis* Matthew et Granger, 1923: Bendukidze, 1993	Altynshokysu 1, 2, (B)
	D. veletus Lopatin, 1998	*Amphilagus* aff. *robustus* (Matthew et Granger, 1923): Bendukidze, 1993	Altynshokysu 4, (B)

Table 1. (Contd.)

Taxon	Species	Synonyms	Localities, (1, 2, 4) Bone Bed of Altynshokysu, (B) Altynshokysu and others after Bendukidze (1993)
Ochotonidae			
Sinolagomyinae:	*Sinolagomys pachygnathus* Li et Qiu, 1980	*S.* aff. *gracilis* Bohlin, 1942; *S.* aff. *kansuensis* Bohlin, 1937: Bendukidze, 1993;	Altynshokysu 2, 4; Akespe, Sayaken, Zhilansai, Zherlepes
		Sinolagomys sp.: Bendukidze, 1977	
Rodentia			
Aplodontidae			
Prosciurinae:	*Prosciurus daxnerae* Lopatin, 2000	–	Altynshokysu 2
Ansomyinae:	*Ansomys crucifer* Lopatin, 1997	–	Altynshokysu 4
Sciuridae			
Sciurinae:	*Palaeosciurus* sp.	*Sciurus* sp.: Bendukidze, 1977	Zhilansai (B)
Castoridae			
Castorinae:	*Steneofiber kumbulakensis* (Lytschev, 1970)	*Propalaeocastor kumbulakensis*: Lytschev, 1970;	Kumbulak; Altynshokysu 1, 4, (B); Akotau, Sayaken
		Propalaeocastor sp.: Bendukidze, 1977;	
		Capacikala sajakensis Bendukidze, 1993: Bendukidze, 1993	
	S. schokensis (Bendukidze, 1993)	*Capatanka schokensis*; *C.* aff. *schokensis*; *Palaeocastor* sp.: Bendukidze, 1993	Altynshokysu 4, (B); Akotau, Kumbulak, Zhilansai
Castoroidinae:	*Asiacastor* sp.	*Asiacastor* aff. *orientalis*: Bendukidze, 1993;	Altynshokysu 4, (B); Akotau
		Anchitheriomys aff. *orientalis*: Bendukidze, 1997;	
		Capacikala aff. *sciuroides* (Matthew, 1907): Bendukidze, 1993;	
		C. antecedens (Lytschev, 1987): Bendukidze, 1997	
Eomyidae			
Eomyinae:	*Eomyodon bolligeri* Lopatin, 2000	–	Altynshokysu 1, 2
	Pseudotheridomys yanshini Lopatin, 2000	–	Altynshokysu 2, 4
Zapodidae			
Sicistinae:	*Plesiosminthus tereskentensis* Lopatin, 1999	–	Altynshokysu 1
	Parasminthus debruijni Lopatin, 1999	*P.* aff. *tangingoli* Bohlin, 1946: Bendukidze, 1993	Altynshokysu 2, 4
	Bohlinosminthus cubitalus Lopatin, 1999	–	Altynshokysu 2

Table 1. (Contd.)

Taxon	Species	Synonyms	Localities, (1, 2, 4) Bone Bed of Altynshokysu, (B) Altynshokysu and others after Bendukidze (1993)
Cricetidae			
Eucricetodontinae:	*Eucricetodon occasionalis* Lopatin, 1996	*E.* aff. *caducus* (Shevyreva, 1967): Bendukidze, 1993; Bendukidze, 1997	Altynshokysu 1, 2, 4; Akespe, Akotau
		E. caducus: Bendukidze, 1997	
	E. sajakensis Bendukidze, 1993	*Leidymys sajakensis*: Bendukidze, 1997	Sayaken, Altynshokysu (B), Akotau
Cricetinae:	*Eumyarion tremulus* Lopatin, 1996	*Eucricetodon* aff. *youngi* Li et Qiu, 1980: Bendukidze, 1993;	Altynshokysu 1, 2, 4; Akespe
		Leidymys youngi: Bendukidze, 1997	
	Eumyarion sp.	–	Altynshokysu 1
Cricetodontinae:	*Aralocricetodon schokensis* Bendukidze, 1993	*Eumyarion schokensis*: Bendukidze, 1997	Altynshokysu 1, 2, (B)
Spalacidae:	*Argyromys aralensis* Argyropulo, 1939	*A. woodi* (Argyropulo, 1939);	Akespe
		Protalactaga borissiaki Argyropulo, 1939	
Tachyoryctoididae:	*Tachyoryctoides glikmani* (Vorontzov, 1963)	*Aralomys glikmani*: Vorontzov, 1963;	Zherlepes, Akespe, Altynshokysu (B), Akotau, Sayaken (B)
		T. aff. *obrutshewi* Bohlin, 1937: Bendukidze, 1993;	
		T. obrutshevi: Bendukidze, 1997	
	Tachyoryctoides sp.	*Tachyoryctoides spurius* (Argyropulo, 1939): Bendukidze, 1993	Altynshokysu 4, (B); Akespe, Zherlepes (B)
	Aralomys gigas Argyropulo, 1939	*Aralomys* sp.: Bendukidze, 1993;	Akespe; Altynshokysu 4, (B); Akotau, Sayaken, Kumbulak, Kuzhasai
		A. aff. *kokonorensis* (Li et Qiu, 1980): Bendukidze, 1997	
	Eumysodon spurius Argyropulo, 1939	*E. orlovi* Argyropulo, 1939	Akespe
Ctenodactylidae			
Tataromyinae:	*Yindirtemys sajakensis* Bendukidze, 1993	*Tataromys* aff. *deflexus* Teilhard de Chardin, 1926: Bendukidze, 1977	Sayaken, Akotau, Altynshokysu (B)
	Y. birgeri Bendukidze, 1993	*Y. sajakensis birgeri*: Bendukidze, 1997	Sayaken, Akotau, Altynshokysu 4, (B)
	Y. aralensis Bendukidze, 1994	*Tataromys* sp.: Bendukidze, 1977;	Zhilansai, Kuzhasai (B)
		“*Tataromys*” cf. *sigmodon* Matthew et Granger, 1923: Bendukidze, 1993	

forms and the presence of fossorial Talpidae (*Hugueneya* sp.), which is atypical of Oligocene assemblages from central Asia, are of special interest. However, such an association of the Talpidae (genera *Desmanella, Myxomygale,* and *Hugueneya*) occurred in Europe in the terminal Oligocene (MP30) and the basal Miocene (MN1–MN2) (Ziegler, 1990).

It is evident that insectivores from the Aral Assemblage are successive relative to the Oligocene Asian species (*Exallerix efialtes* is a descendant of *E. hsandagolensis; Amphechinus akespensis* evolved from *A. rectus; A. microdus,* from *A. minimus, Amphechinus* sp., from *A. kansuensis; Pseudoparatalpa lavrovi,* from *P. shevyrevae*; and *Gobisorex akhmetievi,* from *G. kingae*).

Lagomorpha. Contrary to the opinion of some researchers (Gabunia, 1986; Bendukidze, 1993), lagomorphs from the Aral Formation do not show evolutionary steadiness. The Desmatolagidae from the Aral Fauna are actually rather similar to the Oligocene species of the genus *Desmatolagus* (see Matthew and Granger, 1923; Bohlin, 1942; Huang, 1987; Erbajeva and Sen, 1998). However, the Aral species demonstrate obvious differences associated with their evolutionary advantage. In particular, *D. veletus* is larger than *D. robustus,* which is characterized by similar measurements and dental structure, and the anteroexternal fold of its P_3 and folds between the hypoconulid and talonid of P_4–M_2 contain cement. *D. periaralicus* is similar to *D. gobiensis,* though it differs in the deeper hypostriae of its upper cheek teeth and almost completely reduced hypoconulids. *D. simplex* is most advanced with regard to lingual hypsodonty. At the same time, it is similar to the Late Oligocene *D. shargaltensis* in the structure of the upper and lower cheek teeth and measurements but differs from this species in the substantially reduced external roots of P^4–M^2 and partially fused roots of P_4 and M_1. The evolutionary significance of these characters has been noticed in a number of studies (Teilhard de Chardin, 1926; Tobien, 1978).

The *Sinolagomys* specimens from the Aral Formation that Bendukidze (1993) determined as *S.* aff. *gracilis* and *S.* aff. *kansuensis* in actuality belong to *S. pachygnathus.* This species was first described from the Xiejia locality (Qinghai, China), which is correlated with Zone MN2 (Li and Qiu, 1980; Qiu and Qiu, 1995; Qiu *et al.*, 1999). This species is considered a descendant of the Oligocene *S. kansuensis.* In this lineage, the trigonids of P_4–M_2 are substantially wider than the talonids, as opposed to those of the other group of species, including *S. major, S. gracilis,* and *S. ulungurensis. S. pachygnathus* differs from *S. kansuensis* in the completely reduced roots of its upper cheek teeth and, hence, represents a more advanced stage of the development of hypsodonty in the family Ochotonidae.

S. pachygnathus was widespread in the Early Miocene of central Asia and Kazakhstan (Erbajeva, 1994a, 1994b). The presence of *S. pachygnathus* in the Aral Faunal Assemblage is one of the most important indicators of its Early Miocene age. The association of *Desmatolagus* and *Sinolagomys pachygnathus* is atypical of the later half of the Early Miocene of Kazakhstan (Erbajeva, 1994a) and China (Qiu and Qiu, 1995); therefore, we can infer that the Aral Fauna should be dated as the beginning of the Miocene.

Regarding the number of specimens, lagomorphs are the second most abundant small mammals of the Aral Fauna, while rodents occupy first place. Apparently, they were the most abundant small herbivores in the Aralian; the same is true of the Oligocene of central Asia. However, in contrast to Oligocene assemblages, the lagomorph association of the Aral Fauna was dominated by relatively highly specialized sinolagomyines (which had hypsodont teeth and were better adapted to feeding on coarse plants) rather than primitive desmatolagids.

Rodentia. Rodents are represented by nine families: Aplodontidae, Sciuridae, Castoridae, Eomyidae, Zapodidae, Cricetidae, Spalacidae, Tachyoryctoididae, and Ctenodactylidae.

Prosciurus daxnerae, a primitive member of the Aplodontidae, is characterized by the strongly narrowed trigonid of M_1, which clearly distinguishes this form from other species of this genus. As compared to the Oligocene central Asian *P. arboraptus,* it displays certain advanced Prosciurinae characters, in particular, the rudimentary crests of the metastylid and mesostylid (Lopatin, 2000a). *Ansomys crucifer* is intermediate between the Late Oligocene *A. shantungensis* and the Early Miocene *A. orientalis* (China, Sihong Fauna; MN4) with reference to the structure of elements of the occlusal surface of P_4 (Lopatin, 1997).

The family Castoridae is represented by three species: *Steneofiber kumbulakensis, S. schokensis,* and *Asiacastor* sp. The genus *Asiacastor* is characteristic of the Miocene of Kazakhstan (Lytschev, 1987) but has not been registered in the Oligocene.

Eomyodon bolligeri and *Pseudotheridomys yanshini* are the first representatives of the Eomyidae in the Aral Formation. They are probably related to *Eomyodon dangheensis* and *Pseudotheridomys* sp., respectively, which occur in the Upper Oligocene of China (Wang and Emry, 1991; Wang, 2002). In the extent of morphological advantage of teeth, *E. bolligeri* is closely similar to *E. volkeri* (MP28–MP29) and *E. mayoi* (MP30–MN1). The dental structure of *P. yanshini* (low crowns and closed labial folds of the upper molars) is comparable to that of the European *P. schaubi* (MP30–MN1) and *P. bernensis* (MN1).

The Zapodidae are represented by the genera *Plesiosminthus, Parasminthus,* and *Bohlinosminthus.* Judging from its dental structure, *Parasminthus debruijni* is related to the Oligocene *P. tangingoli,* while *Bohlinosminthus cubitalus* is most likely a direct descendant of *B. parvulus* (Lopatin, 1999b). *Plesiosminthus tereskentensis* is the first species of *Plesiosminthus* sensu stricto (neither *Parasminthus* nor *Heterosminthus,* see Lopatin, 2001) described from Asia

Table 2. Correlation of Bone Beds in the Altynshokysu locality with other localities of the Aral Fauna

Bone Bed	Localities
Altynshokysu 6	–
Altynshokysu 5	Akotau, Sayaken, Kuzhasai, Zhilansai
Altynshokysu 4	Akespe, Kumbulak
Altynshokysu 3	–
Altynshokysu 2	–
Altynshokysu 1	–

(Lopatin, 1999b). To date, *Plesiosminthus* sp. has also been registered in the Upper Oligocene of Mongolia and China (Höck *et al.*, 1999; Wu *et al.*, 2001). *P. tereskentensis* is especially similar in size and dental structure to the Oligocene European *P. promyarion* and is obviously related to the lineage of *P. promyarion* (MP29–MP30)—*P. admyarion* (MP30)—*P. myarion* (MN1–MN2).

The Cricetidae are represented in the Aral Fauna by the subfamilies Eucricetodontinae, Cricetinae, and Cricetodontinae. *Eucricetodon occasionalis* apparently belongs to the Asian *E. caducus* lineage. In the evolutionary stage of dental structure, it is comparable to the European *E. hesperius* (MN1). *E. sajakensis* (absent from the material examined in the present study) is comparable to the European *E. haslashensis* (MN2) (Bendukidze, 1993, p. 113). *Eumyarion tremulus* is especially closely related to the Early Miocene *E. carbonicus* (Turkey; MN1); however, it differs in the reduced posterior arm of the hypoconid of the lower molars, which is also characteristic of later members of this genus, i.e., the Miocene species.

Argyromys aralensis is the earliest known member of the family Spalacidae, which is more primitive than *Heramys eviensis* from MN4 of Greece (Klein Hofmeijer and Bruijn, 1985) and *Debruijnia arpati* from MN3 of Turkey (Ünay, 1996, 1999).

Tachyoryctoides, *Aralomys*, and *Eumysodon* are considered to be members of the separate family Tachyoryctoididae of the superfamily Spalacoidea. The genus *Tachyoryctoides* is known from the Lower Oligocene–Lower Miocene of Asia (Qiu and Qiu, 1995); thus, its presence in the Aral Formation does not conflict with its Early Miocene age. *Aralomys* is more specialized, since its M_3 is clearly reduced and the mesolophid of M_1 is rudimentary. In the extent to which the mesolophid is reduced, *A. gigas* is more primitive than *A. kokonorensis* from the Xiejia locality (ca. MN2). A more advanced genus, *Ayakozomys*, is known in the Lower Miocene (ca. MN3) of eastern Kazakhstan (Tyutkova, 2000).

The Ctenodactylidae are represented by three species of the genus *Yindirtemys*. This genus is characteristic of both the Late Oligocene and the early half of the Early Miocene of Asia.

In general, the Aral Fauna is similar to Oligocene assemblages from central Asia. Zapodids dominate the association of small rodents and tachyoryctoidids and ctenodactylids dominate large forms, while aplodontids, sciurids, and eomyids are scarce. It is worth noting that tsaganomyids and cylindrodontids are absent from the fossorial taxa. Beavers occupy the leading position among them. An important point that indicates the onset of a new stage in the historical development of Asian small mammals is the high diversity of cricetids, which is atypical of the Oligocene.

On Different Ages of Localities of the Aral Assemblage

Mammals occur, at least, at six levels of the Aral Formation. On the basis of the somewhat different composition of small mammals, Bendukidze (1989) assumed that the known localities differ in age (Sayaken, Kuzhasai, and Zhilansai are younger than Akespe) and compared them with different bone beds of Altynshokysu. Subsequently, two small mammal subassemblages were recognized within the Aral Assemblage (Bendukidze, 1993; Lopatin, 1996). However, it is difficult to determine the extent to which the differences in the taxonomic composition of small mammals from individual localities and bone beds depend on the incompleteness of collections and on true faunal changes. The study of extensive materials from the Altynshokysu locality has revealed certain differences in the composition of small mammals from bone beds 1, 2, and 4. In particular, in Bone Bed 1, lagomorphs are represented by *Desmatolagus periaralicus* only; Bone Bed 2 yielded *D. periaralicus, D. simplex*, and *Sinolagomys pachygnathus*; and Bone Bed 4 yielded *D. simplex*, *D. veletus*, and *S. pachygnathus* (this association is also characteristic of Akespe). Zapodids are represented by *Plesiosminthus tereskentensis* in Bone Bed 1, *Parasminthus debruijni* and *Bohlinosminthus cubitalus* in Bone Bed 2, and *P. debruijni* in Bone Bed 4. The cricetids *Eumyarion tremulus* and *Aralocricetodon schokensis* occur in bone beds 1 and 2, *Eucricetodon occasionalis* is characteristic of the three beds, and *E. sajakensis* is only known from Bone Bed 5 of Altynshokysu and from Sayaken (Bendukidze, 1993). Bone beds 1 and 2 of Altynshokysu are most likely older than the assemblage from the Akespe locality; Bone Bed 4 correlates with Akespe and Kumbulak; and Bone Bed 5 correlates with Sayaken, Kuzhasai, and Zhilansai (Table 2).

Mammal remains from the Zhilansai and Kuzhasai localities occurred in a member composed of interbedding grayish yellow, fine-grained, micaceous quartz sands and grayish green clays that yielded shark teeth and rare shells of *Nodularia akbaurensis* Mad. and *Lentidium kuzhasaicum* (Merkl.) (Bendukidze, 1977). This member was initially referred to as the upper part of the Baygubek Formation (Merklin, 1974; Gabunia, 1986); according to a recent conception, it was subsequently assigned to the Aral Formation (Popov *et al.*, 1993b).

Bendukidze (1993) indicated that, in the Zhilansai locality, mammals occurred in the Kintykche Subformation of the Aral Formation. This researcher noticed that "the strata of the Aral Regional Stage (including the Kintykche Subformation) in Zhilansai are wedged between the Kotsakhurian *Oncophora* Beds and relatively thick (23 m) underlying marine sediments of the Baygubek type" (Bendukidze, 1993, p. 5). In actuality, apparently, these strata belong to the Aral Formation, whereas the Kintykche Beds are represented by an overlying member composed of fine-grained and strongly micaceous sands, which spread directly under the Bishtyubya Formation characterized by a specific molluskan assemblage, including typical Miocene elements (Popov *et al.*, 1993b), and a younger mammal fauna, including mastodonts and muntjacs (Gabunia, 1986).

Large mammals from the Kuzhasai and Zhilansai localities (Bendukidze, 1977) share the following taxa with the Akespe Assemblage: Felidae gen.?, *Paraceratherium* sp., Rhinocerotidae gen.?, and *Amphitragulus* sp. (= *Amphitragulus* cf. *boulangery*, see Kozhamkulova and Orlovskaya, 1971). The first small mammals from these localities were identified as *Sinolagomys* sp., *Sciurus* sp., *Palaeocastor* sp., *Steneofiber* sp., *Propalaeocastor* sp., *Aralomys gigas*, and *Tataromys* sp. (Kozhamkulova and Orlovskaya, 1971; Bendukidze, 1977). To date, the list of small mammals from Kuzhasai and Zhilansai has been revised (see Table 1). These localities contain mammals of the Aral Fauna (rather than the Kintykche Fauna, as followed from the stratigraphic description proposed by Bendukidze) and should not be considered separately.

Correlation with European Biochronological Units

First and foremost, one should recognize the boundary between which units of the European mammal biochronological chart corresponds to the Oligocene–Miocene boundary. The Oligocene–Miocene boundary is traditionally placed between zones MP30 (= MN0) and MN1 (see Mein, 1975, 1979, 1990, 1999; Gabunia, 1981; Fahlbusch, 1989; McKenna and Bell, 1997; Steininger, 1999), which means that the roof of MP30 is the bottom of MN1. At the same time, because of certain contradictory faunal data and uncertainty in the stratotype area of the Aquitanian Stage (see Hugueney and Ringead, 1990), some researchers have proposed placing the Paleogene–Neogene boundary inside Zone MN1 (Steininger *et al.*, 1982), inside Subzone MN2a (Steininger *et al.*, 1990), or at the MN2a/MN2b boundary (Bernor, 1984; Tobien, 1987; Lucas *et al.*, 1998; Kordikova, 1998). At one time, it was widely accepted that the MN2a/MN2b boundary is the boundary between the Paleogene and Neogene; therefore, the correlation of the Aral Faunal Assemblage with MN1 did not conflict with its Late Oligocene age (Lucas *et al.*, 1998).

At present, the boundary in question is placed either at the MP30/MN1 boundary (McKenna and Bell, 1997; Steininger, 1999; Mein, 1999) or even lower, i.e., inside Zone MP30 (Hoek Ostende, 2001a). In view of the magnetostratigraphic data, this boundary is considered to coincide with the end of MP30; however, it is placed approximately 0.5 Ma earlier than the onset of MN1 (see Lindsay, 2001).

On the basis of magnetostratigraphic and geochronological data, the base of MN1 (23.8 Ma) is correlated with the base of Magnetozone C6Cn2n (Berggren *et al.*, 1995; Steininger *et al.*, 1996; Steininger, 1999), C6Cn3n (Sen, 1997), or C6Cn1n (Kempf *et al.*, 1997; Mödden, 1997). According to Lindsay (2001), the upper boundary of MP30 coincides with the lower boundary of chron C6Cn2n (23.8 Ma), whereas the lower boundary of MN1 falls in the middle of chron C6Br (ca. 23.3 Ma).

Comte (2000) proposed to transfer the Coderet Fauna (reference level for Zone MP30) to the basal Miocene. At the same time, MP30 (including the Küttigen Fauna as a new presumable reference level) is retained in the terminal Oligocene, while the Coderet Fauna and correlated faunas compose the new MN0 Zone, which bridges the time hiatus of about 0.5 Ma between MP30 and MN1.

Comte gave the following substantiation of this. In the stratotype section of the Paleogene–Neogene boundary (Carrosio-Lemme, northern Italy), an increase in the content of oxygen isotope ^{18}O is observed between the base (65 m) and a level of 15 m (the Oligocene–Miocene boundary is placed at a level of 35 m). This phenomenon is accounted for by a drop in temperature that was named the Mi-1 Event (Miller *et al.*, 1991). In the upper strata of the section, δ^{18}O decreases. The onset of the Mi-1 Event (bottom of Zone Mi-1) is determined by the greatest drop in temperature (23.8 Ma), which marks the Paleogene–Neogene boundary (the beginning of this decrease in temperature is dated as 24.0 Ma). At the beginning of the Miocene, in Zone Mi-1, δ^{18}O gradually decreased; this marked an increase in temperature.

The isotope analysis of charophyte gyrogonites from the Oligocene–Miocene localities of Switzerland revealed the greatest drop in temperature and a decrease in faunal diversity at the level of Rickenbach (MP29, 24.4 Ma); an increase in temperature and growth of diversity occurred at the level of La Milloque (MP29) and Küttigen (MP30); and, then, a new drop in temperature and decrease in mammal diversity took place near the Oligocene–Miocene boundary (Dieupentale and Brochene Fluh 53 localities, MP30, 23.9 Ma). The younger faunas from Coderet, Venelles, and Thezels fall into the basal part of Zone Mi-1 and, hence, into the basal Miocene. It has been proposed to transfer these faunas from MP30 to the new MN0 Zone, where the Baudry 2 Fauna (dated ca. 23.4 Ma and usually considered equivalent to the fauna from Paulhiac, the reference level for MN1) is also placed.

Table 3. Chronological distribution of small mammal genera known from the Aral Fauna in the Late Oligocene and Early–Middle Miocene of Europe and Asia Minor: (+) registered, (–) not registered, (*) not registered but occurrence is supposed on the basis of its presence in the underlying and overlying beds, (?) identified only tentatively, (< +) first appearance, (+ >) last appearance, and (–+) absent from Europe but known in Turkey

Genus	MP						MN					
	25	26	27	28	29	30	1	2	3	4	5	6
Galerix (=*Tetracus*)	+	+	–	–	–	–+	–+	–+	+	+	+	+
Amphechinus	+	+	+	+	+	+	+	+	*	+	*	+
Desmanella	–	?	–	+	+	+	+	+	+	+	+	+
Myxomygale	+	*	+	+	+	+	+	+	+ >	–	–	–
Hugueneya	–	–	–	–	–	< +	+	+ >	–	–	–	–
Palaeosciurus	*	*	*	+	*	+	+	+	+	+ >	–	–
Steneofiber	*	*	*	+	+	+	+	+	+	+	+	+
Eomyodon	–	–	–	< +	+	+	+ >	–	–	–	–	–
Pseudotheridomys	–	–	–	< +	+	+	+	+	+	+ >	–	–
Plesiosminthus	–	< +	+	+	+	+	+	+ >	–	–	–	–
Eucricetodon	+	+	+	+	+	+	+	+	+ >	–	–	–
Eumyarion	–	–	–	–	–	–	< +	+	+	+	+	+

Although the above reasoning appears to be well-grounded, the existence of separate MN0 (Comte, 2000) requires additional verification, since the mammals found in the parastratotype section of the Aquitanian in the Cap de Nautes Formation (which has been reliably dated to the Oligocene on the basis of marine organisms) suggest that this formation correlates with MP30 (Hugueney *et al.*, 1987; Hugueney and Ringeade, 1990). Therefore, I here follow the traditional biochronological chart (where the Oligocene–Miocene boundary is placed between MP30 and MN1) that was adopted by the International Stratigraphic Commission in 1995 (Steininger *et al.*, 1994).

Below, the age and biochronological position of the Aral Fauna are substantiated using the composition of small mammals. The temporal distribution of insectivore, lagomorph, and rodent genera and the level of morphological advantage of species from certain phylogenetic lineages are analyzed. On this basis, the concurrent range of these taxa is determined and taken as the most probable age of the Aral Fauna.

The Aral Fauna shares the following genera with European and East Mediterranean (Turkish) assemblages of Oligocene and Early Miocene small mammals: *Galerix, Amphechinus, Desmanella, Myxomygale, Hugueneya, Eomyodon, Pseudotheridomys, Plesiosminthus, Palaeosciurus, Steneofiber, Eucricetodon,* and *Eumyarion*. *Desmatolagus* (Lopez and Thaler, 1974; Remy *et al.*, 1987) and *Parasminthus* (Fejfar, 1987) from Europe were described on the basis of extremely poorly preserved specimens and, consequently, these identifications are questionable. Table 3 shows the distribution of the above genera in the Late Oligocene and the Early–Middle Miocene of Europe and Turkey (Hugueney, 1972, 1997, 1999a, 1999b; Doukas, 1986; Ziegler and Fahlbusch, 1986; Alvarez Sierra *et al.*, 1987; Brunet and Vianey-Liaud, 1987; Engesser, 1987, 1990, 1999; Engesser and Mayo, 1987; Fahlbusch and Heissig, 1987; Remy *et al.*, 1987; Carroll, 1988; Hoek Ostende, 1989, 2001d, 2001e; Ziegler, 1989, 1990, 1998, 1999; Hugueney and Ringead, 1990; Mein, 1990; Bruijn and Saraç, 1991; Xu, 1994; Werner, 1994; Crochet, 1995; Gould, 1995; Engesser and Mödden, 1997; Bruijn, 1999; Daxner-Höck, 1999). The analysis of Table 3 suggests that the concurrent range of the above genera includes Biozones MN1–MN2.

Only some rodent species from the Aral Formation can be compared to European species. *Pseudotheridomys yanshini* is comparable to *P. schaubi* and *P. bernensis* (MP30–MN1) in the crown height and the structure of the occlusal surface. *E. bolligeri* is similar in evolutionary level to *E. volkeri* (MP28–MP29) and *E. mayoi* (MP30–MN1). *Eucricetodon occasionalis* is comparable to *E. hesperius* (MN1); however, it is more primitive than *E. aquitanicus* (MN2b). *E. sajakensis* correlates with the European *E. haslashensis* (MN1–MN2). *Eumyarion tremulus* is similar to *E. carbonicus* from the Lower Miocene of Turkey (MN1). The concurrent range of the European species involved in comparison fits into Zone MN1.

Thus, based on the composition of small mammals, the Aral Faunal Assemblage is correlated with Zone MN1 of the European scale, namely, the beginning of the Agenian Land Mammal Age (Early Aquitanian).

Table 4. Chronological distribution of small mammal genera known from the Aral Fauna (shown in column NMU1) in Central Asia and Kazakhstan: (+) registered, (–) not registered, (*) not registered but occurrence is supposed on the basis of the presence in the underlying and overlying beds, and (?) identified only tentatively

Genus	Oligocene		Miocene, NMU					
	Ulantatalian	Tabenbulukian	1	2	3a	3b	4	5
Galerix	–	–	+	–	–	–	?	–
Exallerix	+	+	+	–	–	–	–	–
Amphechinus	+	+	+	+	*	+	+	*
Desmanella	+	*	+	–	–	–	–	–
Myxomygale	+	*	+	–	–	–	–	–
Hugueneya	–	–	+	–	–	–	–	–
Gobisorex	+	*	+	–	–	–	–	–
Desmatolagus	+	+	+	–	–	–	–	–
Sinolagomys	+	+	+	+	+	+	+	–
Prosciurus	+	*	+	–	–	–	–	–
Ansomys	–	+	+	–	–	–	+	+
Palaeosciurus	–	–	+	–	–	–	–	–
Steneofiber	+	*	+	*	*	*	*	*
Asiacastor	–	–	+	–	–	+	+	*
Eomyodon	–	+	+	–	–	–	–	–
Pseudotheridomys	–	+	+	*	*	*	*	*
Plesiosminthus	–	+	+	–	–	–	–	–
Parasminthus	+	+	+	+	–	–	–	–
Bohlinosminthus	+	+	+	–	–	–	–	–
Eucricetodon	+	+	+	+	–	–	–	–
Eumyarion	–	–	+	*	*	*	*	*
Tachyoryctoides	+	+	+	–	?	?	?	?
Aralomys	–	–	+	+	–	–	–	–
Yindirtemys	–	+	+	+	–	–	–	–

Correlation with Central Asian Biochronological Units

The correlation with the Asian biochronological units is performed with the use of schemes proposed for the Paleogene of central Asia (Russell and Zhai, 1987) and the Neogene of China (Qiu and Qiu, 1995; Qiu *et al.*, 1999), where individual levels were recognized and correlated with the European scale.

Almost all the genera registered in the Aral Fauna were also found in Oligocene and Lower Miocene localities of Asia. Table 4 shows the stratigraphic distribution of Oligocene and Miocene insectivores, lagomorphs, and rodents from Asia (Bendukidze, 1993; Lopatin, 1994a, 1996, 1997, 1998, 1999a, 1999b, 2000a; Erbajeva, 1994b; Lindsay, 1994; Martin, 1994; Qiu, 1994; Wang, 1994, 1997; Xu, 1994; Gould, 1995; Qiu and Qiu, 1995; Qiu *et al.*, 1999; Zazhigin and Lopatin, 2000a; Wang and Qiu, 2000a, 2000b; Kordikova and Bruijn, 2001). The analysis of Table 4 shows that the concurrent range of the majority of these genera includes falls into the Early Miocene (beginning of the Xiejian Land Mammal Age). However, some genera (*Exallerix*, *Gobisorex*, and *Prosciurus*) have not been recorded in the Miocene; at the same time, a number of genera (*Asiacastor, Eumyarion,* and *Aralomys*) are absent from the Oligocene.

The analysis of the evolutionary level of species from the Aral Formation shows that they are more advanced than the currently known Oligocene species of the same genera; however, they are relatively more primitive than the younger Miocene species. The presence of *Sinolagomys pachygnathus* directly indicates the Early Miocene age of the Aral Assemblage.

The Aral Fauna can confidently be assigned to the Xiejian Land Mammal Age of the Chinese scale. According to the mammalian biochronological zonation of the Neogene of China (Qiu *et al.*, 1999), this interval includes three type local faunas from the Suosuoquan, Xiejia, and Zhangjiaping localities, which are correlated with European zones MN1, MN2a, and MN2b, respectively. The Zhangjiaping Fauna contains proboscideans and is obviously younger than the Aral Fauna. The age of the Suosuoquan Fauna is commonly substantially underestimated; in my opinion, it should be assigned to the later half of the Early Miocene (Lopatin, 2002a; see also Chapter 6 of this study). The Xiejia locality yielded *Sinolagomys pachygnathus, Eucricetodon youngi, Parasminthus huangshuensis, Yindirtemys suni, Aralomys kokonorensis, Sinopalaeoceros xiejiaensis,* and *Diceratherium* sp. (Li and Qiu, 1980; Chen, 1988; Qiu and Qiu, 1995). The Aral Fauna is probably somewhat older than the Xiejian Fauna, since it includes species that are more primitive, such as *Tachyoryctoides glikmani, Aralomys gigas, Eucricetodon occasionalis,* and *Parasminthus debruijni*.

The Gaolanshan (= Lanzhou) Fauna and the faunas of approximately the same age from the vicinity of Lanzhou in Gansu Province are currently correctly assigned to the Late Oligocene (Wang and Qiu, 2000a, 2000b), although they were previously assumed to belong to the Early Miocene (Qiu and Qiu, 1995; Qiu *et al.*, 1999). This dating was supported by the presence of *Yindirtemys suni*, which is characteristic of Xiejia, and the higher specialization of *Exallerix gaolanshanensis* compared to *E. hsandagoliensis* from Shand-Gol (Qiu and Qiu, 1995). The presence of *Yindirtemys grangeri, Tataromys,* and, especially, *Tsaganomys*, which are characteristic of the Oligocene, strongly suggests the Late Oligocene age for the Gaolanshan Fauna (Lopatin, 2002a). The Aral Fauna, which lacks the typical Oligocene ctenodactylid and tsaganomyid species, is obviously younger than this fauna.

Mammals have not been found in the basal Lower Miocene of Mongolia. I believe that the so-called Biozone D, which was recognized in the Paleogene–Neogene strata of Mongolia (Daxner-Höck *et al.*, 1997; Höck *et al.*, 1999) and dated as the Oligocene–Miocene boundary (MP30/MN1), contains a mixture of two faunas (a Late Oligocene fauna from the Shand-Gol Formation and a fauna from the later half of the Early Miocene of the Loo Formation). This mixture may have appeared as a result of either redeposition or inexact stratigraphic assignment of the specimens collected there (see Chapter 6). Comparisons between small mammal species from the Aral Fauna and the Oligocene species of the same genera strongly suggest that the Aral Fauna is younger.

Thus, comparison of the Aral Fauna with Chinese mammal biochronological units has shown that it belongs to the beginning of the Xiejian Land Mammal Age (beginning of the Early Miocene) and is somewhat older than the Xiejia Local Fauna (ca. MN2) and younger than the Late Oligocene Lanzhou Fauna. Apparently, the Aral Fauna forms a special stage in the development of the Neogene fauna of Asian mammals. The geographical range of the Aral Fauna remains an open question. To date, mammals of this age are only known in western and central Kazakhstan (Biryukov *et al.*, 1962, 1968; Tleuberdina and Rayushkina, 1993). Nevertheless, the Aral Fauna should be regarded as a separate unit that occupies the most basal position in the unified Asian biochronological scale elaborated for the Neogene on the basis of mammals (Lopatin, 2002a).

CHAPTER 6. MAMMALIAN BIOCHRONOLOGY IN THE EARLY MIOCENE OF INNER ASIA

By analogy with the chart of biochronological units elaborated on the basis of mammals for the Neogene of Europe (MN zones), a chart for the Neogene of China was created in the past decade (Qiu and Qiu, 1995; Qiu *et al.*, 1999). Its Miocene part includes 11 faunal units (NMU, Neogene Mammal Faunal Units) combined in three faunal assemblages (NMSU, Neogene Mammal Faunal Superunits): *Aprotodon*–Tataromyidae NMSU (NMU1–NMU3, ca. MN1–MN2b, Early Miocene); *Platybelodon*–*Alloptox* NMSU (NMU4–NMU7, ca. MN4–NMU7+8, terminal Early Miocene and Middle Miocene); and *Hipparion*–Siphneidae NMSU (NMU8–NMU11, ca. MN9–MN13, Late Miocene). The Early Miocene part of this scheme is insufficiently supported by evidence; in particular, the following points are questionable: (1) the assignment of the Suosuoquan Local Fauna to NMU1 (ca. MN1); (2) the correlation of the Gaolanshan (= Lanzhou) Fauna with the Xiejia Fauna, which is the type fauna for NMU2 (ca. MN2a); (3) correlation of the Zhangjiaping Fauna, which is the type of NMU3, with MN2b; and (4) the absence of a special NMU that correlates with MN3.

The data accumulated during the last few years on Miocene mammals from Kazakhstan and Mongolia suggest that the central Asian and Kazakhstan faunas have much in common. This enables us to elaborate a unified Neogene mammalian biochronological scale for the whole of inner Asia. The following five NMU are proposed for the Early Miocene: NMU1 (ca. MN1), NMU2 (ca. MN2–MN3a), NMU3a (ca. MN3a/MN3b), NMU3b (ca. MN3b), and NMU4 (ca. MN4). NMU5 (ca. MN5) is a boundary unit that corresponds to the end of the Early Miocene and the beginning of the Middle Miocene. Table 5 shows the sequence of the biochronological units discussed and their brief characteristics based on the stepwise nature of the faunal evolution of Asian mammals. Below, they are described in more detail and the questions of their dating are discussed. Figure 45 shows correlations between Asian and European biochronological units.

NMU1 (Aralian, or the Earliest Xiejian)

Local faunas. Altynshokysu, Akespe, and correlated localities in western Kazakhstan (North Aral Region), Aral Faunal Assemblage (Bendukidze, 1993; Lopatin, 1996, 1997, 1998, 1999a, 1999b, 2000a, 2002a).

Characteristics. The majority of mammalian genera of Oligocene origin are represented by advanced species. Such typical Oligocene taxa as Didymoconidae,

Table 5. Mammal biochronological units in the Early Miocene of Inner Asia and their characteristics

NMU	Local Faunas	First appearance datum (FAD)	Last appearance datum (LAD)	Typical species of evolutionary lineages
NMU4, Early Shanwangian	Sihong, Wuertu, Ulan-Tologoi, Kushuk, Bishtyubya, Mynsualmas, Akzhar, and Zaisan	*Lantanotherium, Postexallerix, Mioechinus, Plesiosorex, Alloptox, Parapetaurista, Shuanggouia, Eutamias, Plesiosciurus, Youngofiber, Microdyromys, Diatomys, Eozapus, Xenosminthus, Protalactaga, Megacricetodon, Primus, Neocometes*	*Parapetaurista, Shuanggouia, Xenosminthus*	*Postexallerix securis, Bellatona kazakhstanica, Sayimys minor, Ansomys orientalis, Eozapus prosimilis, Protalactaga major, P. sheverevae, P. aenigmatica, Heterosminthus mongoliensis, H. honestus, H. nanus*
		Anchitherium, Lagomeryx, Palaeomeryx, Platybelodon, Dorcatherium, Semigenetta, Dionysopithecus, Stephanocemas, Eotragus, Gobiocerus, Hypsodontus		
NMU3b, Late Xiejian	Suosuoquan, Ayaguz	*Synexallerix, Amphilagus, Bellatona*, Distylomyinae (*Prodistylomys, Distylomys*), *Ayakozomys, Democricetodon, Cricetodon, Gomphotherium*	*Prodistylomys*	*Synexallerix junggarensis, S. otus, Amphechinus bohlini, Sinolagomys ulungurensis, Bellatona kazakhstanica, Distylomys qianlishanensis, Sayimys obliquidens, Heterosminthus firmus*
NMU3a, Middle Xiejian	Zhangjiaping	Ctenodactylinae (*Sayimys*)		*Sinolagomys pachygnathus*
		Proboscidea	*Paraceratherium* (= *Dzungariotherium*), *Aprotodon, Hyaenodon*	*Paraceratherium orgosense*
NMU2, Early Xiejian	Xiejia	*Atlantoxerus*	Tataromyinae (*Yindirtemys*), *Parasminthus, Aralomys*	*Sinolagomys pachygnathus, Yindirtemys suni, Y. xiningensis, Parasminthus huangshuensis, Eucricetodon youngi, Aralomys kokonorensis*
		Diceratherium		
NMU1, Earliest Xiejian or Aralian	Akespe, Altynshokysu, Kumbulak, Akotau, Sayaken, Kuzhasai, Zhilansai, Zherlepes	*Atasorex, Aralosorex, Asiacastor, Eumyarion, Aralocricetodon, Argyromys, Aralomys, Eumysodon*	*Exallerix, Pseudoparatalpa, Gobisorex, Atasorex, Aralosorex, Desmatolagus, Prosciurus, Bohlinosminthus, Eomyodon, Argyromys, Tachyoryctoides, Eumysodon*	*Exallerix efialtes, Amphechinus akespensis, A. microdus, Desmatolagus periaralicus, D. simplex, D. veletus, Sinolagomys pachygnathus, Yindirtemys sajakensis, Y. birgeri, Prosciurus daxnerae, Ansomys crucifer, Steneofiber kumbulakensis, S. schokensis, Parasminthus debruijni, Bohlinosminthus cubitalus, Eucricetodon occasionalis, Tachyoryctoides glikmani, Aralomys gigas*
		Sinopalaeoceros		*Paraceratherium prohorovi, Aceratherium aralense, Aprotodon borissiaki*
Tabenbulukian, Biozone C1	Gaolanshan, Xiagou, Taben-Buluk, Shargaltein, Shine-Us, Yagan-Tologoi	*Tshotgoria, Mongoloscapter, Bohlinotona, Yindirtemys, Ansomys, Pseudotheridomys, Plesiosminthus, Litodonomys, Heterosminthus*	Didymoconidae, Tupaiodontinae, Tsaganomyidae, *Bohlinotona, Tataromys, Litodonomys*	*Exallerix gaolanshanensis, Amphechinus rectus, A. kansuensis, A. minimus, A. gigas, Desmatolagus shargaltensis, Sinolagomys kansuensis, S. major, S. gracilis, Tataromys plicidens, T. sigmodon, T. parvus, Yindirtemys grangeri, Y. deflexus, Y. ambiguus, Y. gobiensis, Ansomys shantungensis, Parasminthus asiaecentralis, P. tangingoli, Bohlinosminthus parvulus, Tachyoryctoides obrutchewi, T. pachygnathus, T. intermedius*
		Paraceratherium (= *Dzungariotherium*), *Dremotherium*		

Ma	Epoch	Age	Europe		Asia	
			Land Mammal Age	MN	Land Mammal Age	NMU
17	Early Miocene	Burdigalian	Orleanian	MN4	Shanwangian	NMU4
18						
19				MN3b	Xiejian	NMU3b
20				MN3a		NMU3a NMU2
21		Aquitanian	Agenian	MN2		
22						
23				MN1		NMU1
24	Oligo-cene	Chat-tian	Occitanian	MP30 (MN0)	Tabenbulukian	Gaolanshan

Fig. 45. Correlation of the Early Miocene mammal biochronological units of Asia and Europe.

Tupaiodontinae, *Bohlinotona*, Tsaganomyidae, Cricetopinae, *Selenomys*, and *Tataromys* are absent.

Association: *Exallerix efialtes, Amphechinus akespensis, A. microdus, Gobisorex akhmetievi, Desmatolagus simplex, D. veletus, Sinolagomys pachygnathus, Yindirtemys sajakensis, Y. birgeri, Prosciurus daxnerae, Ansomys crucifer, Steneofiber kumbulakensis, S. schokensis, Parasminthus debruijni, Bohlinosminthus cubitalus, Eucricetodon occasionalis, Eumyarion tremulus, Tachyoryctoides glikmani, Aralomys gigas, Paraceratherium prohorovi, Aceraterium aralense,* and *Aprotodon borissiaki.*

First Appearance Datum (FAD): *Atasorex, Aralosorex, Asiacastor, Eumyarion, Aralocricetodon, Argyromys, Aralomys, Eumysodon, Sinolagomys pachygnathus*, and *Sinopalaeoceros*.

Last Appearance Datum (LAD): *Exallerix, Pseudoparatalpa, Gobisorex, Atasorex, Aralosorex, Desmatolagus, Prosciurus, Eomyodon, Bohlinosminthus, Argyromys, Tachyoryctoides*, and *Eumysodon*.

Discussion. Substantiation of the age and biochronological correlation of the Aral Fauna was given in the preceding chapter. Bendukidze (1997) proposed to establish special Land Mammal Ages in the Oligocene and Early Miocene of Kazakhstan, namely, the Agispeyan Age for the faunas from Akespe and Bone Bed 1 of Altynshokysu and the Sajakenian Age for the faunas from the Sayaken, Akotau, Kuzhasai, and Zhilansai localities and the upper bone beds of Altynshokysu. In my opinion, these names are unnecessary, since the Aral Faunal Assemblage belongs to an integrated biochron that should be taken as the earliest phase of the Xiejian Asian Land Mammal Age. Because the early, middle, and late phases of the Xiejian Age are clearly distinguished in China (NMU2, NMU3a, and NMU3b), the Aral level can be designated as the **Earliest Xiejian** or **Aralian**.

The Suosuoquan Fauna, which is considered to be the type fauna for NMU1 (Qiu *et al.*, 1999), is in fact much younger, since it includes a number of typical Miocene taxa, such as *Sinolagomys ulungurensis, Cricetodon, Atlantoxerus*, and *Prodistylomys*. This suggests that it should be assigned to NMU3b. The short-faced hedgehog *"Metexallerix" junggarensis* Bi, 1999, which was considered to be more primitive than *M. gaolanshanensis* Qiu et Gu, 1988 from Lanzhou (Bi, 1999; Qiu *et al.*, 1999), in actuality belongs to a separate genus of the Brachyericinae, *Synexallerix*, which is characteristic of NMU3b (Lopatin and Zazhigin, 2003) (see below).

The Suosuoquan Fauna comes from the lower strata of the Suosuoquan Formation in the Ulungur River Valley in Xinjiang. It was originally dated as the beginning of the Miocene (Ye *et al.*, 2000). It consists of 13 mammal species, 11 of which are small mammals. They include the hedgehogs *Synexallerix junggarensis, Amphechinus bohlini*, and *A.* cf. *minimus* (Bi, 1999, 2000; Lopatin and Zazhigin, 2003) and zapodid and tachyoryctoidid rodents that are more advanced than the Late Oligocene species of the same families from Taben Buluk. *Sinolagomys ulungurensis* is more similar to Miocene members of this genus than to *Sinolagomys* from Taben Buluk (Tong, 1989). In addition, the fauna includes *Cricetodon*, which was recorded in Turkey beginning with MN1 (Bruijn *et al.*, 1993).

NMU2 (Early Xiejian)

Local faunas. Xiejia locality, lower part of the Xiejia Formation; Qinghai Province, northern China (Li and Qiu, 1980; Qiu and Qiu, 1995; Wang, 1997).

Characteristics. The association includes advanced species of the Oligocene rodent genera.

Association: *Sinolagomys pachygnathus, Parasminthus huangshuensis, Eucricetodon youngi, Yindirtemys suni, Y. xiningensis,* and *Aralomys kokonorensis.*

FAD: *Atlantoxerus* and *Diceratherium*.

LAD: Tataromyinae (*Yindirtemys*), *Parasminthus*, and *Aralomys*.

Discussion. The Xiejia Fauna is the sole Early Miocene local fauna of China that is older than the appearance of proboscideans (Proboscidean Datum, PD). The Early Miocene age of this fauna was initially supported by the relatively high morphological advantage of its taxa; the presence of separate small mammal species from such Oligocene genera as *Sinolagomys, Parasminthus, Yindirtemys*, and *Tachyoryctoides*; and the high evolutionary level of the dental structure in *Eucricetodon youngi*, resembling that of *E. aquitanicus* and *E. infralactorensis* from the Early Miocene (MN1–MN3) of Europe (Li and Qiu, 1980; Li *et al.*, 1984). Subsequently, the position of the Xiejia Fauna in the NMU scale of China was supported by comparative faunal analysis (Qiu and Qiu, 1995).

Apparently, the mammal fauna from the Askazansor locality (Askazansor 1, upper strata of the Askazansor Formation) in southern Kazakhstan belongs to the same NMU. This fauna lacks proboscideans but includes *Diaceratherium, Protaceratherium, Plesiaceratherium, Xenohyus*, and *Brachyodus* and is dated as MN2–MN3 (Kordikova, 2001). Made (1999) dated the penetration in Eurasia of the African genus *Brachyodus* belonging to anthracothere suiforms (Brachyodus Event) as 21 Ma; this falls into the terminal Aquitanian and Zone MN2.

The Gaolanshan Fauna from the Lanzhou Basin (Gansu), which was assigned to NMU1 (Qiu and Qiu, 1995) or NMU2 (Qiu *et al.*, 1999), contains typical Oligocene genera, such as *Tsaganomys* and *Tataromys* (Qiu and Gu, 1988), and, hence, should be dated as Late Oligocene. This fauna comes from the lower member of the Xianshuihe Formation, which is composed of yellow sandstones at the base and overlying red siltstone (Wang and Qiu, 2000a). According to magnetostratigraphic data, these yellow sandstones fit into chrons C8r and C8n; this corresponds to 27–26 Ma, i.e., the upper part of European Zone MP26 and the MP26/MP27 hiatus (Flynn *et al.*, 1999; Lindsay, 2001). The Gaolanshan Fauna and the Xiagou, Shangxigou, and Quijachuan faunas of the same age come from red siltstones; the Xiagou and Shangxigou faunas are confined to the middle strata, while the Quijachuan Fauna is in the lower strata. The small mammal association from the three localities consists of the Didymoconidae *Didymoconus* berkeyi; the hedgehogs *Amphechinus* cf. *rectus, A.* cf. *minimus,* and *Amphechinus* sp.; the soricid Soricidae gen. indet.; the lagomorphs *Desmatolagus* cf. *gobiensis, Sinolagomys kansuensis, S.* cf. *major,* and *Ordolagus* sp.; and the rodents *Parasminthus asiaecentralis, P. tangingoli, Parasminthus* sp., *Bohlinosminthus parvulus, Sinosminthus* sp., *Heterosminthus lanzhouensis, Litodonomys huangheesis, Tataromys plicidens, Yindirtemys grangeri, Y. xiningensis, Y. ambiguus*, Tataromyinae indet., *Eucricetodon* sp., *?Tachyoryctoides* sp., and *Tsaganomys altaicus* (Wang and Qiu, 2000a, 2000b). In the Xiagou and Shangxigou faunas combined in the Xiagou Local Fauna, 11 species are also known in the Late Oligocene Taben Buluk Fauna and only one (*Y. xiningensis*) is known from the Early Miocene of the Xiejia locality (Wang, 1997). Thus, the local fauna from Xiagou is regarded as a close analogue of the Taben Buluk Fauna and should be dated to the Late Oligocene (Wang and Qiu, 2000b). The Quijachuan Fauna contains taxa characteristic of Shand-Gol and, hence, is somewhat older than the Xiagou Fauna. The Gaolanshan Fauna contains *Exallerix gaolanshanensis* (see Lopatin and Zazhigin, 2003), *Tataromys sigmodon, Yindirtemys grangeri, Y. suni, Tsaganomys* cf. *altaicus*, and *Aprotodon* sp. and should also be placed in the Oligocene on the basis of both stratigraphic and biochronological characteristics.

NMU3a (Middle Xiejian)

Local faunas: Zhangjiaping, lower part of the middle member of the Xianshuihe Formation (yellow sand); Lanzhou Basin, Gansu, northern China; Jiaozigou, Linxia Basin, Gansu (Qiu and Qiu, 1995; Wang, 1997; Qiu *et al.*, 1999).

Characteristics. The first appearance of proboscideans (PD), which co-occur with the last giant rhinoceroses (*Paraceratherium* [= *Dzungariotherium*] *orgosense*); the first appearance of the Ctenodactylinae (*Sayimys*); and the last appearance of *Hyaenodon, Aprotodon*, and *Sinolagomys pachygnathus.*

Discussion. The correlation of the local fauna from Zhangjiaping with the end of MN2 (Qiu *et al.*, 1999) is based on the assumption that proboscideans appeared almost simultaneously in China and Pakistan about 20.5–21 Ma (for data on Pakistan, see Downing *et al.*, 1993).

However, according to recent magnetostratigraphic data (Flynn *et al.*, 1999; Flynn, 2000; Lindsay, 2001), the lower strata of the middle member of the Xianshuihe Formation (white sandstone) correlate with chrons C5En, C5Dr, and C5Dn and the beginning of C5Cr (the roof of MN3a and the bottom of MN4). PD in central Asia coincides with chron C5En and, hence, should be dated as, at most, 18.5–19 Ma. Thus, NMU3a is tentatively correlated with MN3a/MN3b.

NMU3b (Late Xiejian)

Local faunas: Suosuoquan in northern China (Wang, 1997; Qiu *et al.*, 1999), Ayaguz in eastern Kazakhstan (Zazhigin and Lopatin, 2000a).

Characteristics. FAD: Distylomyidae, *Democricetodon*, *Cricetodon*, and *Ayakozomys*; the lagomorph association, including *Amphilagus*, *Sinolagomys ulungurensis*, and *Bellatona kazakhstanica*; and the rodent association, including *Democricetodon*, *Heterosminthus*, *Sayimys*, Distylomyidae, and Tachyoryctoididae (*Ayakozomys*). Proboscideans are represented by the genus *Gomphotherium*.

Discussion. The age of the Suosuoquan Fauna was substantiated above.

Daxner-Höck *et al.* (1997) and Höck *et al.* (1999) established Biozone D in the Paleogene–Neogene sediments of central Mongolia and dated it to the Oligocene–Miocene boundary, MP30/MN1. Devyatkin *et al.* (2002, text-fig. 3) correlated Biozone D with Late Oligocene zones MP29–MP30. The combined list of small mammals from the Biozone D (Höck *et al.*, 1999; Daxner-Höck, 2001) includes *Tsaganomys* sp., *Cyclomylus* sp., *Prodistylomys* sp., *Distylomys* sp., *Democricetodon* sp., *Heterosminthus firmus, Parasminthus asiaecentralis, Plesiosminthus* sp., Eomyidae indet., Aplodontidae indet., *Tachyoryctoides kokonorensis*, *Tachyoryctoides* sp., Petauristidae indet., and Sciuridae indet. The researchers noted that this association came from the clay and sand of the Loo Formation. In my opinion, the typical Oligocene taxa of this association (*Tsaganomys*, *Cyclomylus*, and *Parasminthus*) come from sediments of the Shand-Gol Formation (possibly redeposited). The presence of *Democricetodon* and *Heterosminthus firmus* correlates this level with the Ayaguz Fauna and, consequently, with NMU3b. The identification of "*Tachyoryctoides kokonorensis,*" which is characteristic of the Xiejia Fauna, may be in error: this is based on my preliminary study of specimens collected by N.S. Shevyreva in Ayaguz and localities of the Akzhar and Zaisan formations of the Zaisan Depression and specimens collected by V.S. Zazhigin in Ulan-Tologoi. This study shows that a large tachyoryctoidid that resembles this species is characteristic of NMU3b and NMU4 (see also Kordikova and Bruijn, 2001, pl. 3, figs. 8–10). The form discovered in Ayaguz was recently given the name *Ayakozomys sergiopolis* (Tyutkova, 2000).

The following taxa were identified in the Kintykche Beds of the Baygubek Formation of the Northern Ustyurt Plateau (western Kazakhstan): Mustelidae gen.?, Ursidae gen.?, *Zygolophodon* aff. *gromovae*, Rhinocerotidae gen.?, and *Stephanocemas aralensis* (Bendukidze, 1977). Because of the presence of primitive proboscideans and the stratigraphical position of this locality, the Kintykche Fauna is tentatively correlated with MN3 and NMU3.

NMU4 (Early Shanwangian)

Local faunas: Wuertu, Duitinggou, and Tiejianggou in northern China; Sihong in southern China (Qiu and Qiu, 1995; Wang, 1997, 2003; Qiu *et al.*, 1999); Ulan-Tologoi in Mongolia (Zazhigin and Lopatin, 2000a, 2000b) (= Biozone D1: Höck *et al.*, 1999; Daxner-Höck, 2001); Kushuk, Bishtyubya, and Mynsualmas in western Kazakhstan (Dmitrieva *et al.*, 2003); Akzhar and Zaisan faunas in eastern Kazakhstan (Zazhigin and Lopatin, 2000a, 2000b; Lopatin and Zazhigin, 2000); and Aktau 1 in southeastern Kazakhstan (Kordikova, 2000; Kordikova and Bruijn, 2001).

Characteristics. FAD: *Anchitherium, Megacricetodon, Lantanotherium, Postexallerix, Mioechinus, Plesiosorex, Youngofiber, Semigenetta, Dionysopithecus, Lagomeryx, Palaeomeryx, Platybelodon, Dorcatherium, Stephanocemas, Eotragus, Gobiocerus, Hypsodontus*, etc. (the first extensive faunal exchange in the Neogene); presence of the mastodont *Gomphotherium*. The rodent association consists of *Democricetodon* (= *Karydomys*), *Megacricetodon* (= *Aktaumys*), *Primus, Neocometes, Diatomys, Sayimys*, Distylomyidae, *Heterosminthus, Protalactaga, Eozapus, Xenosminthus, Litodonomys, Ansomys, Youngofiber, Parapetaurista, Shuanggouia, Eutamias, Plesiosciurus, Microdyromys*, and Tachyoryctoididae; and the lagomorph association includes *Amphilagus, Sinolagomys, Bellatona*, and *Alloptox*.

Discussion. The Bishtyubya locality is situated at the foot of the steep northeastern slope of the Ustyurt Plateau. There, in 1992, I found the lagomorph *Sinolagomys* cf. *pachygnathus*. The rodent *Atlantoxerus* sp. (Sciuridae) has also been described from this locality (Bendukidze, 1993). In addition, the Bishtyubya Fauna contains the large mammals Ursidae gen., Mustelidae gen., *Gomphotherium* (*Serridentinus*) *inopinatus, Dicerorhinus* sp., *Lagomeryx* sp., and *Stephanocemas aralensis*. This association is characteristic of the later half of the Early Miocene, the Burdigalian (Lavrov *et al.*, 1985; Gabunia, 1986; Tleuberdina *et al.*, 1993).

The Bishtyubya Faunal Assemblage is usually correlated with MN3 (Gabunia, 1981) or MN4 (Agadjanian, 1986). It is confined to the Bishtyubya Formation (*Oncophora* Beds), which contains *Rzehakia dubiosa* and is dated as Kotsakhurian (Gabunia, 1986) and, hence, the middle of the Burdigalian (Popov *et al.*, 1993b). It appears quite correct to correlate this assemblage with MN4. The Bishtyubya Assemblage is comparable to the Kushuk Fauna and the Miocene Aktau Fauna in Kazakhstan (Tleuberdina *et al.*, 1993), the Sihong Fauna (NMU4) in China, and the Ulan-Tologoi Fauna in Mongolia.

The Mynsualmas locality is situated in the Mynsualmas stow of the northwestern Ustyurt Plateau. In 1992, a PIN expedition collected various vertebrates there: fishes *Araloselachus agespensis, Esox* sp., *Rutilus* cf. *frisii kutum*, Cyprinidae indet., and *Channa* cf. *tverdislovi*; the turtles *?Melanochelys* sp. and Trionychidae indet.; the birds *Urmiornis brodcorbi, Grus* sp., and Accipitridae indet. (Karhu, 1994, 1997); and the mammals Ochotonidae indet., Sciuridae indet., *?Hyaenodon* sp., *?Pseudaelurus* sp., Proboscidea indet., Rhinocerotoidea indet., Suiformes indet., and *Eotragus artenensis* (Dmitrieva *et al.*, 1995, 2003). The find of the archaic bovid *Eotragus artenensis*, which is characteristic of the Middle Burdigalian of Europe (Zone MN4), is especially significant from the biostratigraphic point of view.

CHAPTER 7. ZOOGEOGRAPHICAL RELATIONSHIPS AND ENVIRONMENT OF MAMMALS FROM THE ARAL FAUNAL ASSEMBLAGE

The Aral Assemblage of small mammals is specific in the co-occurrence of many genera characteristic of the Late Oligocene and Early Miocene of Europe (the insectivores *Desmanella, Myxomygale*, and *Hugueneya* and the rodents *Palaeosciurus, Eomyodon, Pseudotheridomys*, and *Eumyarion*) and a number of forms closely related to Oligocene central Asian species (the insectivores *Exallerix efialtes, Amphechinus akespensis, A. microdus*, and *Gobisorex akhmetievi*; the lagomorphs *Desmatolagus veletus, D. periaralicus, D. simplex*, and *Sinolagomys pachygnathus*; and the rodents *Ansomys crucifer, Prosciurus daxnerae, Eomyodon bolligeri, Pseudotheridomys yanshini, Parasminthus debruijni, Bohlinosminthus cubitalus, Eucricetodon occasionalis, Tachyoryctoides glikmani, Yindirtemys sajakensis*, and *Y. birgeri*). This suggests the presence of a zoogeographical link between Europe and Asia at the Oligocene–Miocene boundary. Western Kazakhstan, which was then the northeastern marine area of the Eastern Paratethys and adjacent seaside plain, probably provided the land bridge where mammal fauna of central Asian origin mixed with migrants from Europe.

According to recent data (see Popov *et al.*, 1993b, 2001, 2002), the northern regions of Europe and Asia came in contact at the end of the Eocene (terminal Beloglinian Time), when the Turgai Strait connecting the Eastern Paratethys with the marine basin of Western Siberia disappeared as a result of extensive regression. Apparently, the penetration of certain central Asian elements into the European mammal fauna occurred during this regression at the Eocene–Oligocene boundary. Over the whole of the Oligocene, western Europe was isolated from Asia by a strait connecting the Paratethys with the basin of northwestern Europe (in Pshekhian Time) and by extensive lowlands, which were from time to time filled by seawater (including the area of the Turgai Strait). In the Late Oligocene, the Eurasian Zoogeographical Region was formed, combining the clearly differentiated (because of the above reasons) West European, North Asian, and South Asian subregions (*Zoogeography*…, 1974). The North Asian Subregion included the Balkan–Caucasian, Kazakhstan, and Central Asian provinces. It was assumed that, since the Mediterranean area of Europe was then represented by an archipelago, faunal exchange was insignificant up to the later half of the Miocene (*Zoogeography*…, 1974). However, the presence of many European genera of small mammals in the Aral Fauna suggests that, as early as the very beginning of the Miocene, the West European Subregion was connected to the western area of the North Asian Subregion by distinct zoogeographical links. Apparently, it was in the Aralian that the prerequisites developed for the formation of an integrated European–Siberian Zoogeographical Subregion, which was characteristic of subsequent Miocene stages of evolution of mammal fauna in Eurasia (Vislobokova, 1994).

Thus, many European genera of small mammals penetrated into central Asia and Kazakhstan as early as the later half of the Early Miocene and the beginning of the Middle Miocene. In particular, typical Europe rodents, such as *Keramidomys, Leptodontomys, Eumyarion, Megacricetodon, Democricetodon, Spanocricetodon*, and *Primus*, are known in northern China (Qiu, 1994; Lindsay, 1994; Qiu and Qiu, 1995); the lagomorph *Amphilagus*, which is characteristic of the Late Oligocene and Early–Middle Miocene of Europe, has been discovered in eastern Kazakhstan and Mongolia (Erbajeva, 1988, 1994a, 1994b). The same is true for large mammals (Vislobokova, 1994). Apparently, species of European origin migrated to central Asia through western Kazakhstan along the northern coast of the Paratethys. This was possible at the Oligocene–Miocene boundary because of the emergence of extensive dry land in an area previously occupied by sea and depressions with a lagoon-lacustrine regime (Popov *et al.*, 1993b, text-figs. 16, 19, 20).

It is commonly accepted that, in the Late Oligocene and the beginning of the Early Miocene, the extensive lowlands of the Turgai Depression and North Aral Region (along the northern and southern slopes of the Kazakh Plateau) were characterized by excessive moistening, abundant lakes, some swamping, and the development of hydrophilous flora and forest fauna (*Zoogeography*…, 1974). These conditions were rather similar to the situation in Europe at that time. It is likely that the migration of European small mammals was associated with the favorable environment in this area.

It is of interest to consider from the zoogeographical point of view the history of mammalian development in western Kazakhstan throughout the Early Miocene. The composition of the Bishtyubya Mammal Assemblage suggests that, in the Kotsakhurian, the climate increased in aridity compared to the Aralian. At that time, western Kazakhstan most likely belonged to the European–Siberian Zoogeographical Subregion, since, in the Burdigalian, Europe, Siberia, northern China, and western, central (Kushuk), and eastern (Aktau and Zaisan) Kazakhstan were rather similar in terms of composition of mammal faunas (Tleuberdina *et al.*, 1993; Vislobokova, 1994).

The study of vertebrates from the Mynsualmas locality suggests that they dwelt under relatively dry and warm conditions. The presence of *Eotragus artenensis*, which is characteristic of the Burdigalian of Europe, is evidence of faunal links between western

Kazakhstan and Europe at that time (Dmitrieva *et al.*, 1995, 2003).

This area and Europe displayed even closer faunal relationships in the Middle Miocene (Gabunia, 1986).

The hypothesis of the presence of faunal links between Asia and North America at the Oligocene–Miocene boundary (Bendukidze, 1993; Vislobokova, 1996) is mainly based on the erroneous assumption that the Aral Fauna included Early Miocene North American genera of the family Castoridae, *Capatanka* and *Capacikala* (Bendukidze, 1993). The beavers registered in the Aral Fauna in actual fact belong to the Eurasian genus *Steneofiber.* Other small mammal genera marked in both the Aral Fauna and North America were found in Asia beginning with the Lower Oligocene (*Prosciurus*) or appeared in North America in the Miocene (*Amphechinus* and *Pseudotheridomys*). This agrees well with the traditional point of view that faunal links between Asia and North America were broken after the Early Oligocene and were renewed only in the Early Miocene after the Aralian (*Zoogeography*…, 1974; Kalandadze and Rautian, 1992).

The mammals of the Aral Fauna are usually subdivided into two ecological assemblages, the assemblage of streamside, paralimnetic stations, and moderately humid forests and the assemblage of dry open and semiopen landscapes and thin forests (Flerov and Yanovskaya, 1971; *Zoogeography*…, 1974; Bendukidze, 1993; Lopatin, 1996). It is usually noted that the Aral Fauna is dominated by inhabitants of open and semiopen landscapes (Flerov and Yanovskaya, 1971; *Zoogeography*…, 1974).

According to palynological analysis data, deciduous forests dominated by the Fagaceae and Juglandaceae and enriched with certain subtropical elements (Palmae, *Liquidambar,* and *Magnolia*) were widespread in the Aralian. Conifers dominated by various species of *Picea* and *Tsuga* were abundant. The xerophytization and expansion of open landscapes is evident from the presence of steppe and meadow vegetation composed of the Chenopodiaceae, *Sparganium, Artemisia,* and Compositae (Panova, 1979; Akhmetiev, 1994a). Rayushkina (1977) proposed that the tall-grass steppes and lacustrine–marsh phytocenoses were characteristic of that time.

Small mammals are of special interest for paleoecological analysis. This is primarily associated with a much greater dependence of rodents, insectivores, and lagomorphs on specific conditions of local biotopes than other vertebrates (Gromov, 1962; Lavrov, 1979). In addition, it is known that rodents compose about 90% of the individuals of living vertebrate communities (Maleeva, 1983). This proportion appears to have been retained since the end of the Paleogene (Shevyreva, 1983). It is particularly remarkable that fossil small mammals are frequently represented by extensive materials. This allows for successive application of quantitative methods of analysis.

Paleoecological analysis includes the discovery of taxonomic diversity, restoration of the mode of life of each species, and recognition of biocenotic groups as well as quantitative estimation of the abundance of particular species (Maleeva, 1983). I restrict my discussion to the three first points, since quantitative analysis of the assemblage is impossible because mammals from different size classes had different probabilities of ending up in samples in different bone beds (specimens were collected in each bone bed using somewhat different techniques). In particular, specimens from Bone Bed 1 of the Altynshokysu locality were obtained by washing, while, in Bone Bed 2, both washing and dissolution of lumachelle samples were used. Therefore, in the material from these beds, small and very small animals prevail. In Bone Bed 4, specimens were obtained by excavation and collected on the exposed surface; hence, they were mainly larger in size.

In regard to number of species, rodents occupy the leading position in the Aral Fauna (approximately 60%). The proportions of insectivores and lagomorphs are 30 and 10%, respectively.

The mode of life of extinct animals is reconstructed on the basis of cranial, dental, and postcranial morphological characteristics, which are considered using the actualistic approach, i.e., the adaptive significance of particular characters is interpreted by analogy with living (but not necessarily closely related) taxa. As regards small mammals from the Aral Fauna, the following paleoecological conclusions can be drawn.

Erinaceidae. The structure of the dentition and lower jaw of *Exallerix efialtes* suggest a predatory mode of life (Lopatin, 1996, 1999; Lopatin and Zazhigin, 2003). This animal probably consumed both vertebrates and invertebrates and was not strictly limited ecologically.

The hedgehogs of the genus *Amphechinus* lack characteristics that are typical for living hedgehogs adapted to open landscapes (Gureev, 1979); therefore, they most likely inhabited the forest and shrub biotopes (Bendukidze, 1979, 1993).

Galerix belongs to microphagous insectivores with a wide adaptive range (Gureev, 1979).

Talpidae. *Desmanella* belongs to the subfamily Uropsilinae, the extant members of which are cursorial terrestrial moles inhabiting forest biotopes and resembling shrews in appearance and mode of life (Gureev, 1979). Members of the genus *Myxomygale* are usually considered to be lowly specialized fossorial animals confined to humid streamside and paralimnetic habitats (Gureev, 1979; Bendukidze, 1993).

The structure of the humerus in the mole *Hugueneya* suggests that it was a relatively highly specialized fossorial mammal that was apparently adapted for digging to almost the same extent as living members of the tribe Scalopini. Extant members of this tribe inhabit open sites of the forest zone, plains, and mountain slopes (Gureev, 1979).

Heterosoricinae. Shrews of the subfamily Heterosoricinae are commonly considered to inhabit humid floodplain forests (Gureev, 1979). However, *Gobisorex akhmetievi* and *Atasorex edax* are similar in the structure of teeth and lower jaw to the extremely lowly specialized genera of this group, such as *Domnina* and *Quercysorex*. Apparently, they were not strictly limited ecologically and inhabited forest and shrub thickets as well as open landscapes.

Crocidosoricinae. In Europe, the subfamily Crocidosoricinae is usually associated with faunas from humid forests (Ziegler, 1989). Judging from its dimensions and dental morphology, *Aralosorex* was adapted to feeding on small insects and other invertebrates.

The wide diversity of insectivores in the Aral Fauna suggests that invertebrates (insects, worms, and terrestrial mollusks) were abundant in appropriate biotopes of the Aralian; apparently, the vegetation was rather variable, the soils were soft, and the climate was relatively warm and humid.

Lagomorpha. *Sinolagomys pachygnathus*, judging from its hypsodont teeth, fed on relatively coarse herblike plants. Similarly to extant pikas, it most likely inhabited open landscapes. The less specialized genus *Desmatolagus* had brachyodont (*D. veletus*) or partially hypsodont (*D. simplex* and *D. periaralicus*) teeth. It is of interest that, in *D. simplex* and *D. periaralicus*, the upper incisors have a deep groove that forms a triangular notch in the cutting edge. Among living lagomorphs, only pikas have such a deep groove, which is used for the fixation of plant stalks in the mouth, a structure that is especially important when they accumulate food reserves (Gureev, 1964). It appears reasonable that the same function was performed by this structure in Miocene desmatolagids. This suggests that, in the Aralian, there were periods (seasons) when the growth of grass vegetation was inhibited. The incisors of *D. veletus* lack a deep notch and the cheek teeth are low-crowned. This species probably consumed relatively sappy food (shrub leaves, soft meadow plants, etc.) and was confined to forest and shrub biotopes.

Aplodontidae. By analogy with the Oligocene central Asian *Prosciurus arboraptus*, one may propose that the Aralian *P. daxnerae* inhabited forests or, at least, was associated with shrub thickets (Shevyreva, 1976). Following the technique proposed by Shevyreva (1976) for determination of dependence between the ratio of P^3 to P^4 and the food consumed by extant and extinct Sciuromorpha (and, hence, their mode of life), *Ansomys* should be regarded as a forest arboreal or semiarboreal form.

Castoridae. Extant beavers are adapted to a semiaquatic mode of life and feeding on relatively coarse plants. The low-crowed teeth with wide folds lacking cement and the small dimensions of the Aral beavers from the genus *Steneofiber* indicate that they predominantly fed on soft nearshore plants (Lytschev, 1970; Bendukidze, 1993) and probably led a fossorial (burrowing) mode of life in riverside and paralimnetic habitats. *Asiacastor* has high-crowned cheek teeth with narrow folds. This suggests that it fed on relatively coarse plants (possibly, subterranean plant organs) and inhabited open interfluves.

Eomyidae. Members of the extinct family Eomyidae are usually considered to be ecological analogues of extant cricetid rodents (Wang and Emry, 1991). They were supposedly seed-eaters and dwelt in closed habitats. New data provide evidence that at least some Eomyidae were similar in mode of life to living small flying squirrels from the family Pteromyidae, since an imprint of soft tissues that was preserved together with the skeletal elements of *Eomys quercyi* (Oligocene of Germany) displayed a flying membrane on each side of the body (Storch *et al.*, 1996). Thus, the presence of the Eomyidae suggests noticeable development of woodlands.

Zapodidae. Extant birch mice occur in forest, forest–steppe, and steppe zones and inhabit mountains of Eurasia up to the alpine zone inclusive (Sokolov, 1977; Gromov and Erbajeva, 1995). Judging from the dental structure, *Plesiosminthus*, *Parasminthus*, and *Bohlinosminthus* most likely fed on seeds, berries, sappy overground and subterranean plant organs, and insects and other small invertebrates. In the Aralian, these genera could inhabit forests, shrub thickets, and open sites.

Cricetidae. Shevyreva (1967) believed that small hamsters of the genus *Eucricetodon* were the ecological analogue of extant mice. They inhabited moderately humid and dry forests of interfluves and meadows. The dental structure of these rodents (low crowns and opposite positions of cusps) suggests that they fed mainly on seeds and fruits, with a minor admixture of insects, and never consumed cellulose. The relatively higher tooth crowns of hamsters of the genus *Eumyarion* is evidence that their diet included meadow herblike plants; apparently, they occupied more open sites of forests and plains.

Spalacidae. Living spalacids occur in steppe and forest–steppe zones of Eurasia. They are specialized diggers leading a completely subterranean mode of life. *Argyromys* most likely consumed subterranean plant organs and preferred open biotopes.

Tachyoryctoididae. It is commonly supposed that *Aralomys* and *Tachyoryctoides* led a fossorial (burrowing) mode of life in open habitats with relatively dry land (Lavrov, 1959; Vorontzov, 1963, 1982; Mellett, 1968; Bendukidze, 1993) and were ecologically similar to living bamboo rats (Rhizomyidae). Bendukidze correctly reasoned that the relatively low-crowned teeth of these rodents are evidence that they inhabited humid biotopes (probably grassy savanna rather than typical arid landscapes).

Ctenodactylidae. Extant ctenodactylids are characteristic of arid and semiarid landscapes. Extinct members of this family had brachyodont teeth and most likely inhabited relatively humid biotopes.

Thus, the Aral Fauna includes small mammals adapted to relatively dry open and semiopen landscapes and species inhabiting humid woodlands. Large mammals display similar ecological differentiation (Flerov and Yanovskaya, 1971; *Zoogeography…*, 1974). The data on other vertebrates (freshwater fish, giant salamanders, crocodiles, and birds) suggest the presence of extensive freshwater bodies and a relatively humid and warm climate. Apparently, the seaside plain, which existed in the Aralian, had humid coastal (streamside, paralimnetic, floodplain, and lowland) forests that alternated with extensive semiopen (shrub thickets and thin forests) and open (grassy savanna) landscapes with relatively dense ground. The humid forest biotopes were inhabited by various insectivores (the hedgehogs *Galerix* and *Amphechinus*; the talpids *Desmanella*, *Myxomygale*, and *Hugueneya*; and the soricids *Gobisorex*, *Atasorex*, and *Aralosorex*); leaf-eating lagomorphs (*Desmatolagus veletus*); seed-eating rodents (*Prosciurus daxnerae, Ansomys crucifer, Eomyodon bolligeri, Pseudotheridomys yanshini*, and *Eucricetodon occasionalis*); and beavers (*Steneofiber kumbulakensis* and *S. schokensis*). Open and semiopen biotopes were dominated by fossorial rodents (*Argyromys aralensis*, *Tachyoryctoides glikmani*, *Aralomys gigas*, and *Asiacastor* sp.); animals capable of feeding on relatively coarse grassy plants (the lagomorphs *Sinolagomys pachygnathus* and *Desmatolagus* simplex and the rodent genera *Eumyarion*, *Aralocricetodon*, and *Yindirtemys*) and small seed-eating rodents (Zapodidae) were abundant. In general, the above assumption is in line with the earlier reconstruction of environments characteristic of the Aral Mammal Fauna (Flerov and Yanovskaya, 1971; Lavrov, 1979; Bendukidze, 1993). However, certain important details have been revised on the basis of new data on the significant diversity of small mammals from forest habitats, which support the conclusion that appropriate biotopes were widespread.

CONCLUSIONS

The present study provides the first complete characteristics of the taxonomic composition of small mammals from the Aral Fauna.

The Aral Faunal Assemblage is extremely rich in small mammals. Insectivores are represented by the erinaceids *Galerix* sp., *Exallerix efialtes* Lopatin, 1996, *Amphechinus akespensis* Lopatin, 1999, *A. microdus* Lopatin, 1999, and *Amphechinus* sp.; the talpids *Desmanella compacta* sp. nov., *Pseudoparatalpa lavrovi* (Bendukidze, 1993), *Myxomygale asiaprima* sp. nov., and *Hugueneya* sp.; and the soricids *Gobisorex akhmetievi* sp. nov., *Atasorex edax* gen. et sp. nov. and *Aralosorex kalini* Lopatin, 2004.

Lagomorphs are represented by *Desmatolagus simplex* (Argyropulo, 1940), *D. periaralicus* Lopatin, 1998, *D. veletus* Lopatin, 1998 (Desmatolagidae), and *Sinolagomys pachygnathus* Li et Qiu, 1980 (Ochotonidae).

Rodents are very diverse, including the aplodontids *Prosciurus daxnerae* Lopatin, 2000 and *Ansomys crucifer* Lopatin, 1997; the beavers *Steneofiber kumbulakensis* (Lytschev, 1970), *S. schokensis* (Bendukidze, 1993) and *Asiacastor* sp.; the eomyids *Eomyodon bolligeri* Lopatin, 2000 and *Pseudotheridomys yanshini* Lopatin, 2000; the zapodids *Plesiosminthus tereskentensis* Lopatin, 1999, *Parasminthus debruijni* Lopatin, 1999, and *Bohlinosminthus cubitalus* Lopatin, 1999; the cricetids *Eucricetodon occasionalis* Lopatin, 1996, *Eumyarion tremulus* Lopatin, 1996, *Eumyarion* sp., and *Aralocricetodon schokensis* Bendukidze, 1993; the archaic spalacid *Argyromys aralensis* (Argyropulo, 1939); the tachyoryctoidids *Tachyoryctoides glikmani* (Vorontzov, 1963), *Tachyoryctoides* sp., *Aralomys gigas* Argyropulo, 1939, and *Eumysodon spurius* Argyropulo, 1939; and the ctenodactylid *Yindirtemys birgeri* Bendukidze, 1993.

The taxonomic composition of the assemblage suggests that it should be dated as the beginning of the Miocene (Early Aquitanian) and correlated with European Mammal Zone MN1. The Aralian biochron is considered to be the reference level of NMU1, the basal unit of the biochronological scale of the Neogene of Inner Asia, which fits with the earliest phase of the Xiejian Asian Land Mammal Age (Earliest Xiejian or Aralian). The data on small mammals from the Aral Assemblage, which includes both European and central Asian genera, facilitate comparisons of Early Miocene biochronological units of China with the zones of the European scale.

A distinctive feature of the Aral Small Mammal Assemblage is the simultaneous presence of many genera characteristic of the Late Oligocene–Early Miocene of Europe and a number of taxa closely related to Oligocene central Asian species. Apparently, Europe and Asia came into close zoogeographical contact at the Oligocene and Miocene boundary. Mammals of European origin could migrate to central Asia through western Kazakhstan along the northern coast of the Eastern Paratethys.

Reconstruction of the mode of life and environments of small mammals from the Aral Fauna has shown that many insectivore and rodent species were probably confined to humid forest habitats; consequently, these biotopes were widespread in western Kazakhstan in the Aralian.

ACKNOWLEDGMENTS

I would like to recollect with words of gratitude the late Valerii Yur'evich Reshetov, Boris Aleksandrovich Trofimov, and Nina Semenovna Shevyreva (PIN), splendid Russian researchers who gave me invaluable support at the very beginning of my scientific activity, in particular, during the study of Early Miocene small mammals from the North Aral Region.

I am grateful to Prof. A.K. Agadjanian (PIN) and Prof. B.T. Yanin (Moscow State University) for discussions of the manuscript and valuable editorial remarks.

I am grateful to Prof. M.A. Akhmetiev (GIN) for advice concerning the stratigraphy of the studied area, to V.S. Zazhigin (GIN) and A.O. Averianov (Zoological Institute, Russian Academy of Sciences) for useful discussions of the morphological features of some small mammals, and to H. de Bruijn (IAUU), G. Daxner-Höck (NMW), T. Bolliger (PIUZ), and D. Kälin (NMB) for placing at my disposal their collections of small mammals from the Aral Fauna. I am also grateful to all my colleagues from the Paleontological Institute of the Russian Academy of Sciences who participated in field studies and identification of the fossils of various vertebrates that were collected in the North Aral Region and the Ustyurt Plateau: E.K. Sytchevskaya, M.A. Shishkin, V.B. Sukhanov, M.B. Efimov, A.A. Karhu, E.L. Dmitrieva, I.A. Vislobokova, and A.V. Lavrov.

This study was supported by the Russian Foundation for Basic Research, project nos. 01-05-65448, 02-04-48458, 03-04-06798, and 04-05-64805; by the Board of the President of the Russian Federation for Support of Leading Scientific Schools, project no. NSh-1840.2003.4; and by the grant of the President of the Russian Federation for Support of Young Scientists, project MK-726.2004.4.

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