ISSN 0031-0301, Paleontological Journal, 2006, Vol. 40, Suppl. 3, pp. S205–S405. © Pleiades Publishing, Inc., 2006.

Abstract—Early Paleogene insectivore mammal associations of Asia include true insectivores (superorder Insectivora: order Lipotyphla: suborders Erinaceomorpha and Soricomorpha; orders Didymoconida and Leptictida) and insectivore-like placentals (superorder Ferae: order Cimolesta: suborders Didelphodonta, Palaeoryctida, and Pantolesta). The associations from Mongolia are the most taxonomically diverse. The Late Paleocene association from the Zhigden Member of the Naran-Bulak Formation of the Tsagan-Khushu and Naran-Bulak localities includes the following soricomorph insectivores: the micropternodontid *Sarcodon pygmaeus* Matthew et Granger and *Hyracolestes ermineus* Matthew et Granger (Sarcodontinae), the geolabidid *Gobigeolabis verigranum* Lopatin, the nyctitheriid *Praolestes nanus* Matthew, Granger et Simpson, *P. maximus* Kondrashov, Lopatin et Lucas (Praolestinae subfam. nov.), *Jarveia erronea* Kondrashov, Lopatin et Lucas (Asionyctiinae). Moreover, the Zhigden association includes the didymoconid *Archaeoryctes euryalis* Lopatin (Ardynictinae), the palaeoryctid *Pinoryctes collector* gen. et sp. nov., and the pantolestid *Zhigdenia nemegetica* gen. et sp. nov. (Pantolestinae). The Early Eocene association from the Bumban Member of the Naran-Bulak Formation of the Tsagan-Khushu locality includes the micropternodontid *Prosarcodon maturus* Lopatin et Kondrashov (Sarcodontinae); the nyctitheriids *Bumbanius rarus* Russell et Dashzeveg (Praolestinae), *Oedolius perexiguus* Russell et Dashzeveg, *Edzenius lus* gen. et sp. nov. (Asionyctiinae), and *Eosoricodon terrigena* Lopatin (Eosoricodontinae); the plesiosoricid *Ordolestes ordinatus* gen. et sp. nov. (Butseliinae); and the cimolestids *Naranius infrequens* Russell et Dashzeveg, *Tsaganius ambiguus* Russell et Dashzeveg, and *Bagalestes trofimovi* gen. et sp. nov. (Cimolestidae). The Middle Eocene association from the Khaychin Formation of the Khaychin-Ula 2 and Khaychin-Ula 3 localities includes the erinaceomorphs *Eogalericius butleri* Lopatin and *Microgalericulus esuriens* gen. et sp. nov. (Erinaceidae, Galericinae), the soricomorphs *Metasarcodon reshetovi* Lopatin et Kondrashov (Micropternodontidae, Sarcodontinae), *Soricolestes soricavus* Lopatin (Soricidae, Soricolestinae), and *Asiapternodus mackennai* Lopatin (Apternodontidae, Asiapternodontinae subfam. nov.); the didymoconids *Ardynictis captor* Lopatin (Ardynictinae), *Khaichinula lupula* gen. et sp. nov. (Didymoconinae), *Kennatherium shirense* Mellett et Szalay, and *Erlikotherium edentatum* gen. et sp. nov. (Kennatheriinae subfam. nov.); and the palaeoryctid *Nuryctes gobiensis* Lopatin et Averianov (Palaeoryctidae). Late Paleocene insectivores from the Dzhilga 1a locality (Kazakhstan) comprise the nyctitheriids *Voltaia minuta* Nessov and *Jarveia minuscula* Nessov (Asionyctiinae). The faunal assemblage dated terminal Early Eocene from the Andarak 2 locality (Kyrgyzstan) includes the micropternodontid *Metasarcodon udovichenkoi* (Averianov), the erinaceid *Protogalericius averianovi* gen. et sp. nov. (Galericinae), and the palaeoryctids *Nuryctes alayensis* Lopatin et Averianov and Palaeoryctidae gen. et sp. indet. From the end of the Paleocene to the onset of the Middle Eocene, the taxonomic composition and ecological structure of insectivore communities of Central Asia gradually changed, insectivore-like placentals and primitive soricomorph groups were replaced by the Recent families of Lipotyphla. The morphological and evolutionary study of Early Paleogene Asian insectivores has provided important data on phylogenetic relationships of the Insectivora. The family Micropternodontidae is divided into the subfamilies Sarcodontinae and Micropternodontinae. The earliest insectivore family Geolabididae is recorded in the Paleogene of Asia. A new classification of the family Nyctitheriidae, dividing it into the subfamilies Nyctitheriinae, Amphidozotheriinae, Asionyctiinae, Eosoricodontinae, and Praolestinae subfam. nov., is proposed. Based on the morphological continuity between Eosoricodontinae (Nyctitheriidae) and Soricolestinae (Soricidae), the family Soricidae is proposed to originate from eosoricodontine nyctitheriids. The family Plesiosoricidae is divided into the subfamilies Butseliinae and Plesiosoricinae. A new subfamily, Asiapternodontinae subfam. nov., is established in the family Apternodontidae. The analysis of evolutionary transformations of the dental system suggests the continuity of molar types in the suborder Soricomorpha, which supports the validity of the infraorders Tenrecomorpha and Soricota (the latter includes the superfamilies Micropternodontoidea, Nesophontoidea, Soricoidea, Talpoidea, and Solenodontoidea). The subfamily Galericinae (Erinaceidae) is recorded in Asia at the Early–Middle Eocene boundary. The family Didymoconidae is divided into the subfamilies Ardynictinae, Didymoconinae, and Kennatheriinae subfam. nov. Some members of the subfamily Kennatheriinae display a clear edentate functional pattern, which is atypical for insectivores and is interpreted as an adaptation for feeding on colonial insects. The following scenario of insectivore evolution, describing the major stages of their history, is proposed: (1) in the first half of the Late Cretaceous, the first occurrence of Insectivora (probably in North America); (2) in the second half of the Late Cretaceous, the primary radiation of Insectivora, establishment of Leptictida, Didymoconida, and Lipotyphla; detachment of Erinaceomorpha and Soricomorpha; (3) at the Cretaceous–Paleocene boundary, the primary radiation of Soricomorpha and establishment of Tenrecomorpha (Africa) and Soricota (North America); (4) in the Paleocene, expansion of Soricota in the Northern Hemisphere, the primary radiation of Erinaceomorpha, and emergence of Erinaceidae (North America); (5) at the Paleocene–Eocene boundary, radiation of Soricota and Erinaceidae; (6) at the Early–Middle Eocene boundary, appearance of Soricidae, Talpidae, and Galericinae; (7) in the Middle Eocene–Oligocene, replacement of primitive groups by Recent families and related groups and the formation of the Recent subfamilial diversity of the families Soricidae, Talpidae, Erinaceidae, and Tenrecidae; (8) in the Miocene–Pliocene, disappearance of primitive groups of the Recent families, a decrease in the diversity of Erinaceomorpha, extensive radiation of Soricidae and the formation of the Recent generic diversity of insectivores.

DOI: 10.1134/S0031030106090012

Key words: Insectivores, lipotyphlans, soricomorphs, erinaceomorphs, didymoconids, insectivore-like placentals, cimolestids, palaeoryctids, pantolestids, Late Paleocene, Early Eocene, Middle Eocene, Asia, Mongolia, Kazakhstan, Kyrgyzstan.

INTRODUCTION

The superorder Insectivora comprises six Recent families of the order Lipotyphla (erinaceids, talpids, soricids, solenodontids, tenrecids, and chrysochlorids) and their extinct ancestors and relatives, the earliest of which are known from the end of the Cretaceous. Insectivores are the third most diverse group of living mammals (after rodents and chiropterans), represented by approximately 420 species and 60 genera. In addition, more than 250 extinct genera, more than 100 of which are known in the Paleogene, have been described. Summarizing available data, it is possible to assert that the Neogene–Quaternary history and the basic trends in the post-Paleogene evolution of the majority of insectivore groups are in general well understood. Paleogene insectivores are much more poorly investigated because of poor knowledge of Paleogene deposits compared to the Neogene–Quaternary strata and the infrequent occurrence and poor preservation of specimens. However, the basic problem is the essentially different taxonomic structure of this group in the Paleogene, which is complicated by the large number of extinct primitive lineages comprising remote relatives of Neogene and Recent insectivores.

The classification of insectivores was additionally complicated for a long time by the absence of a clear definition of the group and by the widely accepted idea of its primitiveness (see historical reviews: Butler, 1972; Symonds, 2005). Because of the long prevalence of the hypothesis of Huxley (1880) and Matthew (1909) concerning the origin of all placentals from insectivores, for almost 100 years any Early Paleogene or Cretaceous mammal of uncertain relationships with other orders was referred to Insectivora. As a result, Insectivora became a taxonomic wastebasket for early placentals. This situation began to change in the last quarter of the 20th century due to the development of a new concept of the order, i.e., the concept of Lipotyphla (see Butler, 1972). After this revision, more than 20 families were excluded from the insectivore order. Many of them were subsequently regarded as distinct orders (Leptictida, Pantolesta, Ptolemaiida, Didymoconida, and Palaeoryctida), while others were considered artificial composite groups (see Butler, 1972; Novacek, 1986; Simons and Bown, 1995; McKenna and Bell, 1997; Lopatin, 2001a; Averianov, 2003). Paleogene taxa resembling true insectivores, but showing remote relationships to them, were named *insectivore-like* placentals.

The taxonomic status of extant insectivores remains uncertain. They are traditionally regarded as a single order, which is divided into the suborders Erinaceomorpha and Soricomorpha (Gregory, 1910; Saban, 1954; Butler, 1956a). Erinaceomorpha is usually considered to include only the family Erinaceidae, or, less often, Erinaceidae and Talpidae (McKenna and Bell, 1997). Soricomorpha comprises the Soricidae, Talpidae, Solenodontidae, Tenrecidae, and Chrysochloridae. The families Tenrecidae and Chrysochloridae are often assigned to a separate suborder (named Zalambdodonta, Tenrecomorpha, or Tenrecoidea) or two suborders (Tenrecomorpha and Chrysochloridea); sometimes, only the Chrysochloridae are ranked suborder (Chrysochloromorpha), while the Tenrecidae are referred to Soricomorpha (see Butler, 1972; MacPhee and Novacek, 1993; Symonds, 2005). In the classification proposed by McKenna and Bell (1997), insectivores (Lipotyphla) are regarded as a taxon of superordinal rank (grandorder), including the orders Chrysochloridea, Erinaceomorpha, and Soricomorpha. In general, morphological data strongly suggest a monophyletic origin of Lipotyphla and their plesiomorphic position among Epitheria (Shoshani and McKenna, 1998; Asher, 1999).

Based on molecular genetic data, tenrecs and golden moles were recently assigned to the order Tenrecoidea (= Afrosoricida, = Zalambdodonta sensu Carroll, 1988; Kalandadze and Rautian, 1992), while other "insectivores in the narrow sense" were designated Eulipotyphla (Stanhope et al., 1998; Waddell et al., 1999, 2001; Malia et al., 2002; Springer et al., 2004). These two groups are considered to be unrelated, tenrecoids are united with proboscideans, sirenians, aardvarks, elephant shrews, and hyraxes in the superordinal rank group Afrotheria (Stanhope et al., 1998; Mouchaty et al., 2000; Liu et al., 2001; Madsen et al., 2001, 2002; Murphy et al., 2001; Scally et al., 2002; Corneli, 2003). Molecular genetic data on relationships of eulipotyphlans are contradictory. In some studies Erinaceomorpha are a sister group in relation to all other placentals, whereas Soricomorpha (including Soricidae, Talpidae, and Solenodontidae) are close to Chiroptera (Mouchaty et al., 2000; Arnason and Janke, 2002; Arnason et al., 2002). In some cases, the Talpidae are separated from the Soricidae; the first are placed close to Megachiroptera, while the second are close to Carnivora (Emerson et al., 1999, fig. 1). The other studies suggest a monophyletic origin of Eulipotyphla, either rejecting their division into Soricomorpha and Erinaceomorpha (Douady et al., 2002; Jow et al., 2002; Malia et al., 2002; Amrine-Madsen et al., 2003; Douady and Douzery, 2003; Springer et al., 2003; Waddell and Shelley, 2003; Roca et al., 2004) or supporting this division (Nikaido et al., 2001, 2003; Lin et al., 2002). The analysis of all available data (Liu et al., 2001; Grenyer and Purvis, 2003, fig. 1; Asher, 2005; Symonds, 2005, fig. 19) suggests that, based on the degree of phylogenetic affinity of families, the system of extant insectivores should be as follows: [[Chrysochloridae + Tenrecidae] [Erinaceidae [Solenodontidae [Soricidae + Talpidae]]]]. Consequently, the major insectivore groups are Tenrecoidea (Chrysochloridae and Tenrecidae), Erinaceomorpha (Erinaceidae), and Soricomorpha (Solenodontidae, Talpidae, and Soricidae).

There is no osteological evidence for the assignment of Tenrecoidea to Afrotheria (Asher, 1999, 2001;

Mason, 2003). The newest data on the musculature of the proboscis support the assignment of Tenrecoidea to Lipotyphla rather than to Afrotheria (Whidden, 2002). Geometrical morphometric analysis of the cranial structure in representatives of all extant and some extinct insectivore families agree with the concept of Lipotyphla (Gabriel and Polly, 2005). On the other hand, the structure of placenta suggests a probable affinity of tenrecs and elephant shrews (Mossman, 1987; Dantzer and Paulesu, 2002). Parallel computer analysis of all morphological and molecular genetic data supports the assignment of tenrecs and golden moles to Afrotheria (Asher et al., 2003; Asher, 2005). Symonds (2005) indicated profound differences in reproductive strategy between tenrecs and eulipotyphlans. A compromise idea was proposed by Pavlinov (2003); in his system, the orders Afrosoricida and Eulipotyphla are united in the cohort Insectivora (Pavlinov, 2003, p. 24) or Lipotyphla (ibid., p. 47) of the legion Epitheria.

Thus, the basic problem in the determination of the taxonomic structure of insectivores is the substantiation of the presence or absence of phylogenetic relationships between their basic groups (Erinaceomorpha, Soricomorpha, and Tenrecoidea), which requires the involvement of paleontological data.

The reduction of Lipotyphla by the removal of Tenrecoidea (= Afrosoricida) from their composition does not necessitate a change in the ordinal name, i.e., there is no need to replace the term Lipotyphla by Eulipotyphla (see also Archibald, 2003). The older name Insectivora is accepted here to designate a superordinal group of insectivoromorph mammals, including Lipotyphla and phylogenetically related groups.

When applied to extinct mammals, the term *insectivores* has three meanings:

(1) the ecological group of entomophages (insectivorous mammals);

(2) a grade comprising Lipotyphla and all insectivore-like groups of placentals (insectivorans, insectivoran-grade placentals: see Asher et al., 2002; Asher, 2005);

(3) a taxon including either true insectivores (Lipotyphla, or Insectivora sensu stricto) or, in addition, all closely related groups (Insectivora sensu lato), which can also be named insectivoramorphs.

The composition of the grade and taxon varies widely (insectivores, lipotyphlans, eulipotyphlans, soricomorphs, etc.). Therefore, one of two basic tasks in the study of Paleogene insectivores is to estimate the phylogenetic distances between extinct insectivore-like groups and true insectivores. The second task is to determine and provide support for phylogenetic relationships between extinct and extant groups of true insectivores, which would form the basis of a natural classification of this group (Lopatin, 2003e).

The resolution of these problems will be promoted by the study of Paleogene insectivores from promising and poorly investigated regions, such as Asia and Africa. During the past 20 years, the study of Paleogene Asian insectivores was intensified and gave preliminary results, showing that the origin and early development of many insectivore groups was connected with this period and this region (see Gabunia, 1987; Wang and Li, 1990; Tong and Wang, 1993; Lopatin, 2002c, 2003e, 2004a, 2004c, 2005a, 2005b, 2005c).

The basic purpose of this work is to study insectivores from the Paleocene and Lower–Middle Eocene of Mongolia, Kazakhstan, and Kyrgyzstan, to reconstruct the origin and establishment of the major taxonomic groups of insectivores, and to characterize the Early Paleogene stage in the evolution of insectivores in Asia, in particular, their diversity, phylogenetic relationships, adaptations, directions and rates of evolution.

For this purpose, the following tasks were accomplished:

(1) Analysis of all previously known material of Early Paleogene insectivores of Asia, including the study of their taxonomic position, phylogenetic relationships, stratigraphical and geographical ranges.

(2) Description of new specimens of Early Paleogene insectivores and insectivore-like placentals from Mongolia, Kazakhstan, and Kyrgyzstan, which added much to the knowledge of this stage in the evolution of insectivore mammal groups.

(3) Analysis of phylogenetic relationships of each insectivore group based on the evolutionary morphological approach.

(4) Comparison of the results obtained with available paleontological, morphological, and molecular genetic data and development of original concept for the classification of insectivores.

(5) Analysis of the vicissitudes of the development of insectivores in the Paleogene of Asia and relations between this process and faunal changes in other regions of the world; development of the evolutionary scenario of this group.

CHAPTER 1. MATERIAL, TECHNIQUE, AND TERMINOLOGY

1.1. Material and Localities

The material includes fossil remains of insectivores and insectivore-like mammals from a number of Paleocene and Eocene localities of Mongolia, Kazakhstan, and Kyrgyzstan (Fig. 1). The material includes more than 350 specimens housed in the Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia (PIN); Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia (ZIN); and Chernyshev Central Research Geological Museum of Karpinsky All-Russia Geological Research Institute, St. Petersburg, Russia (TsNIGR Museum). In addition, the rich collections of Late Paleogene and Neogene insectivores from several dozen localities of Mongolia

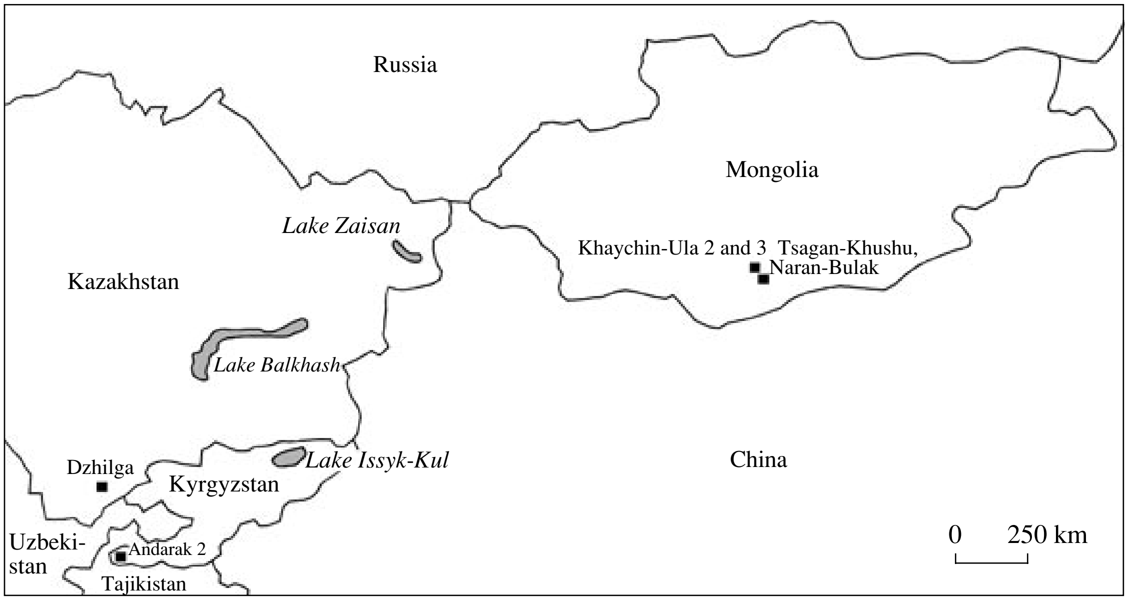


Fig. 1. Geographical position of the Early Paleogene localities investigated.

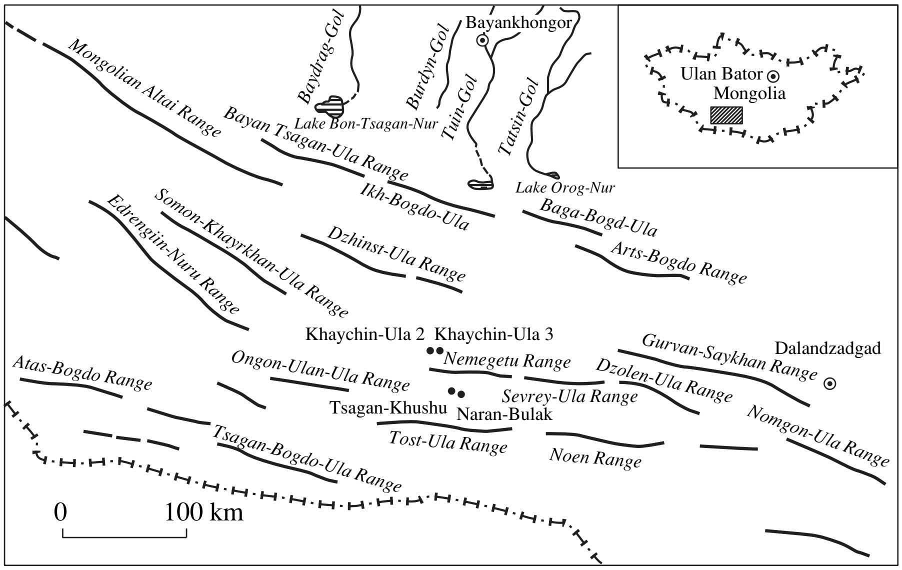


Fig. 2. Geographical position of the Early Paleogene localities investigated in the Nemegt Depression, Mongolia.

and Kazakhstan stored in PIN and the Geological Institute of the Russian Academy of Sciences, Moscow, Russia (GIN) and casts of the holotypes and original specimens from the American Museum of Natural History, New York, USA (AMNH), and Recent material housed in PIN and ZIN (a total of about 1000 specimens) were examined for comparison.

Mongolia. The Mongolian localities are in the Transaltai Gobi (Fig. 2), Nemegt Depression (Tsagan-Khushu and Naran-Bulak), and Bugin-Tsav Depression (Khaychin-Ula 2 and Khaychin-Ula 3). The stratigraphy of these localities was described in detail by Badamgarav and Reshetov (1985). Therefore, only brief geographical and stratigraphical characteristics of the material examined are given below.

Tsagan-Khushu locality is situated 6 km west of the Naran-Bulak Spring (approximately 43°28′ N, 100°23′ E). The material was collected in the Paleogene beds outcropping on the eastern slope of the Tsagan-Khushu cliff along a dry riverbed of the Tsagan-Sair. The material was collected by the South Gobi Party of the Joint Soviet–Mongolian Paleontological Expedition (YuGO SSMPE) headed by V.Yu. Reshetov (PIN) in 1980, 1983, 1985, and 1987. The specimens examined come from two members of the Naran-Bulak Formation, i.e., the Zhigden (Upper Paleocene) and Bumban (basal Eocene) members. The Naran Member (terminal Paleocene) separating these two has not yielded insectivores. During the last years, the Zhigden and Bumban faunas were studied intensively, they were assigned to the Gashatan and Bumbanian Asian land mammal ages, respectively.

In the Zhigden Member, the bone bed is restricted to the roof composed of poorly graded red aleurites. It has yielded the soricomorph insectivores *Sarcodon pygmaeus* Matthew et Granger, 1925, *Hyracolestes ermineus* Matthew et Granger, 1925 (Micropternodontidae), *Gobigeolabis verigranum* Lopatin, 2004 (Geolabididae), *Praolestes nanus* Matthew, Granger et Simpson, 1929, *P. maximus* Kondrashov, Lopatin et Lucas, 2004, and *Jarveia erronea* Kondrashov, Lopatin et Lucas, 2004 (Nyctitheriidae); the didymoconid *Archaeoryctes euryalis* Lopatin, 2001; the palaeoryctid *Pinoryctes collector* gen. et sp. nov.; and the pantolestid *Zhigdenia nemegetica* gen. et sp. nov. In addition, the Zhigden Mammal Assemblage includes the anagalid *Pseudictops lophiodon* Matthew, Granger et Simpson, 1929; the mixodonts *Eomylus zhigdenensis* Dashzeveg et Russell, 1988 and *Sinomylus* sp.; the rodentiaforms *Tribosphenomys minutus* Lopatin et Averianov, 2004 and *T. tertius* Lopatin et Averianov, 2004; the hapalodectid *Hapalodectes dux* Lopatin, 2001; and the notoungulate *Palaeostylops iturus* Matthew et Granger, 1925 (Dashzeveg, 1982; Badamgarav and Reshetov, 1985; Dashzeveg and Russell, 1988; Lopatin and Kondrashov, 2000; Lopatin, 2001a, 2001b, 2004d, 2004e; Lopatin et al., 2001; Lopatin and Kondrashov, 2003, 2004; Kondrashov and Lopatin, 2003; Kondrashov and Lucas, 2004a; Kondrashov et al., 2004a; Lopatin and Averianov, 2004a, 2004c).

In the Bumban Member, the bone beds are represented by gravel lenses in speckled clays at the base of the section. The Bumban Insectivore Mammal Association includes *Prosarcodon maturus* Lopatin et Kondrashov, 2004 (Micropternodontidae), *Bumbanius rarus* Russell et Dashzeveg, 1986, *Oedolius perexiguus* Russell et Dashzeveg, 1986, *Eosoricodon terrigena* Lopatin, 2005, *Edzenius lus* gen. et sp. nov. (Nyctitheriidae), and *Ordolestes ordinatus* gen. et sp. nov. (Plesiosoricidae, Butseliinae) and the cimolestids *Naranius infrequens* Russell et Dashzeveg, 1986, *Tsaganius ambiguus* Russell et Dashzeveg, 1986, and *Bagalestes trofimovi* gen. et sp. nov. (Lopatin and Kondrashov, 2004; Lopatin, 2005b). In addition, the Bumban Mammal Assemblage includes mixodonts, various rodents, the primate *Altanius orlovi* Dashzeveg et McKenna, 1977, creodonts, notoungulates, hyopsodont condylarths, dinocerats, perissodactyls, the earliest Asian artiodactyl *Tsaganohyus pecus* Kondrashov, Lopatin et Lucas, 2004 (Dashzeveg, 1977, 1979a, 1979b, 1990; Dashzeveg and McKenna, 1977; Badamgarav and Reshetov, 1985; Shevyreva, 1989; Dashzeveg et al., 1998; Kondrashov and Agadjanian, 1999; Kondrashov et al., 2001, 2004b; Hooker and Dashzeveg, 2003; Lavrov and Lopatin, 2003, 2004; Kondrashov, 2004; Kondrashov and Lucas, 2004b; Lucas and Kondrashov, 2004; Asher et al., 2005), and the earliest lagomorph (Lopatin and Averianov, 2005).

Naran-Bulak locality is situated 6 km east of the Tsagan-Khushu cliff (approximately 43°28′ N, 100°27′ E). The material was collected by YuGO SSMPE in 1980. The section of Paleogene beds in this locality is the same as in Tsagan-Sair. The bone bed in the Zhigden Member is present in reddish brown sabulous aleurites with carbonate nodules. The locality yielded the nyctitheriid *Praolestes maximus* (Kondrashov et al., 2004a). The same level of the Naran-Bulak locality also yielded the multituberculate *Prionessus lucifer* Matthew et Granger, 1925, the anagalid *Pseudictops lophiodon* Matthew, Granger et Simpson, 1929, mixodonts, pantodonts, dinocerats, notoungulates, and ernanodontids (Dashzeveg, 1982; Badamgarav and Reshetov, 1985).

Khaychin-Ula 2 locality is situated 8 km southeast of Khaychin-Ula Mountain (approximately 44° N, 100° E). The material was collected by YuGO SSMPE in 1970–1973, 1977, and 1978. The bone bed in the lower part of the Khaychin Formation, which has yielded insectivores, is in the light gray fine-grain sand and lenses of aleurites. The insectivore mammal association includes *Metasarcodon reshetovi* Lopatin et Kondrashov, 2004 (Micropternodontidae), *Asiapternodus mackennai* Lopatin, 2003 (Apternodontidae), *Soricolestes soricavus* Lopatin, 2002 (Soricidae), *Eogalericius butleri* Lopatin, 2004 (Erinaceidae), the didymoconid *Ardynictis captor* Lopatin, 2003, *Khaichinula lupula* gen. et sp. nov., *Kennatherium shirense* Mellett et Szalay, 1968 and *Erlikotherium edentatum* gen. et sp. nov., and the palaeoryctid *Nuryctes gobiensis* Lopatin et Averianov, 2004 (Lopatin, 2002c, 2003a, 2003b, 2003c, 2003e, 2004c; Lopatin and Averianov, 2004b; Lopatin and Kondrashov, 2004). In addition, the rich Khaychin Mammal Assemblage includes also Rodentia, Lagomorpha, Creodonta, Pantodonta, Dinocerata, Perissodactyla, Mesonychia, and Artiodactyla (Shevyreva, 1972, 1976; Shuvalov et al., 1974; Reshetov, 1975, 1979, 1993; Yanovskaya, 1975, 1980; Badamgarav and Reshetov, 1976, 1985; Dashzeveg, 1976, 1985; Russell and Zhai, 1987; Lavrov, 1996; Vislobokova, 2004a, 2004b; Lopatin and Averianov, 2006).

Khaychin-Ula 3 locality is situated 6 km east of the Khaychin-Ula 2 locality. The material was collected by YuGO SSMPE in 1973. The bone level in the lower part of the section of the Khaychin Formation is confined to interbeds of light gray fine-grain sand. It yielded a lower jaw fragment of the erinaceid *Microgalericulus esuriens* gen. et sp. nov. and a lower jaw fragment of the didymoconid *Khaichinula lupula* gen. et sp. nov. and remains of Lagomorpha, Rodentia, and Perissodactyla

(Badamgarav and Reshetov, 1985; Russell and Zhai, 1987; Lopatin and Averianov, 2006).

The Khaychin Fauna is dated Middle Eocene (Badamgarav and Reshetov, 1985; Russell and Zhai, 1987; Averianov and Godinot, 1998) or the end of the Middle Eocene–beginning of the Late Eocene (Beliajeva et al., 1974; Devyatkin, 1981, 1994; Devyatkin et al., 2002). I share the first point of view. The Khaychin Fauna belongs to the Irdinmanhan Asian Land Mammal Age, which is compared to the Middle–Late Bridgerian and Early–Middle Uintan of North America (Table 1). Thus, it should be dated the first half of the Middle Eocene.

Kazakhstan. *The Dzhilga 1a locality* (also named Zhilga or Zhylga) is in a sand quarry near the Zhylga railroad station in the Tashkentskie Chuli Area (Shimkent Region, southern Kazakhstan). The Late Paleocene mammal fauna from this locality includes the notoungulate *Kazachostylops occidentalis* Nessov, 1987, the ernanodontid *Asiabradypus incompositus* Nessov, 1987, the ischyromyid rodent *Asiaparamys schevyrevae* Nessov, 1987, the mixodont *Kazygurtia clivosa* Nessov, 1987, and the nyctitheriids *Voltaia minuta* Nessov, 1987 and *Jarveia minuscula* Nessov, 1987 (Nessov, 1987; Averianov et al., 1993; Averianov, 1995; McKenna and Bell, 1997; Averianov and Martin, 2001). The insectivore specimens collected by L.A. Nessov (St. Petersburg State University) in 1984 and 1985 and presently housed in the TsNIGR Museum are redescribed below.

Kyrgyzstan. *The Andarak 2 locality* is situated 3 km northeast of the village of Andarak (Lyailyakskii District, Osh Region, Fergana Depression, western Kyrgyzstan). The bone beds are confined to the lower part of the Alai Beds (Hecker et al., 1962), which was dated based on of the ichthyofaunal composition as the Late Ypresian, i.e., the end of the Early Eocene (Averianov and Udovichenko, 1993). The mammal assemblage is dominated by Irdinmanhan taxa (Reshetov et al., 1978; Reshetov, 1979; Reshetov and Trofimov, 1984; Averianov and Godinot, 1998).

The large mammal association from this locality includes the tapiroids *Teleolophus medius* Matthew et Granger, 1925 (= *Deperetella ferganica* Beliajeva, 1962), *Eoletes tianshanicus* Averianov et Godinot, 2005, the rhinocerotoid *Pataecops minutissimus* (Reshetov, 1979), the earliest amynodontid rhinoceros *Sharamynodon* (= *Andarakodon*) *kirghisensis* (Beliajeva, 1971), the chalicothere Eomoropidae indet., the mesonychid *Mesonyx* sp., the diacodexeid artiodactyls *Diacodexis* sp., *Eolantianius russelli* Averianov, 1996, and Diacodexeidae indet., the hyaenodontid creodonts *Isphanotherium ferganense* Lavrov et Averianov, 1998 and *Neoparapterodon* sp., and the anthracobunid *Pilgrimella* sp. (Reshetov et al., 1978; Reshetov, 1979; Averianov and Udovichenko, 1993; Averianov, 1996b; Averianov and Potapova, 1996; Averianov and Godinot, 1998, 2005; Lavrov and Averianov, 1998).

The small mammal assemblage includes the palaeoryctids *Nuryctes alayensis* Lopatin et Averianov, 2004 and Palaeoryctidae gen. et sp. indet., the insectivores *Metasarcodon udovichenkoi* (Averianov, 1994) and *Protogalericius averianovi* gen. et sp. nov., the mixodont *Anatolimys rozhdestvenskii* Shevyreva, 1994 (= *Anatolimylus rozhdestvenskii* Averianov, 1994), the strenulagid lagomorphs *Aktashmys montealbus* Averianov, 1994 (= *Valerilagus reshetovi* Shevyreva, 1995) and *Gobiolagus hekkeri* (Shevyreva, 1995), the ctenodactyloid rodents *Alaymys ctenodactylus* Averianov, 1993, *?Adolomys* sp. (Tamquammyidae), *Saykanomys* cf. *bohlini* (Dawson, 1964), *Petrokozlovia* cf. *notos* Shevyreva, 1972, *Advenimus* cf. *burkei* Dawson, 1964, *Khodzhentia vinogradovi* Averianov, 1996 (Chapattimyidae), and Ctenodactyloidea indet. (Averianov, 1991, 1993, 1994a, 1994b, 1996a, 1998; Shevyreva, 1994, 1995; Lopatin and Averianov, 2004b, 2006; Lopatin and Kondrashov, 2004; Averianov and Lopatin, 2005). The insectivores and insectivore-like mammals described below were collected by N.S. Shevyreva and V.Yu. Reshetov in 1975 and by A.O. Averianov in 1988 to 1995.

1.2. Technique

The material is mostly represented by jaw fragments and isolated teeth extracted by excavation of bone beds, disassembly of lenses, or total screen washing. The specimens stored in collections in a sandy-silt matrix, were prepared mechanically by hand (the matrix was softened by water) and impregnated with a solution of BF glue in alcohol. Some specimens were exposed to combined mechanical and chemical preparation, when the matrix containing calcium carbonate was treated with hydrochloric acid.

The specimens were prepared and subsequently examined under a stereoscopic microscope *Motic*, the measurements were performed using a stereoscopic microscope MBS-9 with an eyepiece micrometer. The measurements are given in mm, accurate to 0.05 mm. In Chapter 3 (Systematics), the measurements of each specimen are presented, or, in the case of a large number of specimens (more than 10), special tables show generalized data, including the number of specimens (*N*), variation ranges of parameters, and mean values (Δ).

Figures were produced by the author using the *Motic* microscope's drawing facilities and digital image processing software (Adobe Photoshop). Most of the photographs were produced in the photolaboratory of PIN, using ammonium chloride spray.

1.3. Classification, Morphological Description, Terminology, and Nomenclature

In the present work, the term *insectivore mammals* is used as a brief collective name of small placentals of appropriately similar appearance. It replaces the longer designation "insectivores and insectivore-like mam-

Table 1. Correlation of Early Paleogene Land Mammal Ages of North America (NALMA) and Asia (ALMA) (based on data from Clyde et al., 1994, 1997; Berggren et al., 1995; Prothero and Emry, 1996; Ting, 1998; Lindsay, 2001; Lucas, 2001)

Ma	Epoch		NALMA	ALMA
	Eocene	Middle	Duchesnean (40.0–37.0)	Sharamurunian
38				
39				
40			Uintan (47.5–40.0)	
41				Irdinmanhan
42				
43				
44				
45				
46				
47				
48			Bridgerian (50.3–47.5)	
49		Early		
50				Arshantan
51			Wasatchian (55.0/54.8–50.3)	Bumbanian
52				
53				
54				
55	Paleocene	Late	Clarkforkian (56.2–55.0/54.8)	Gashatan
56			Tiffanian (60.8/60.9–56.2)	Nongshanian
57				
58				
59				
60				
61		Early	Torrejonian (63.0/63.7–60.8/60.9)	Shanghuanian
62				
63			Puercan (65.0–63.0/63.7)	
64				

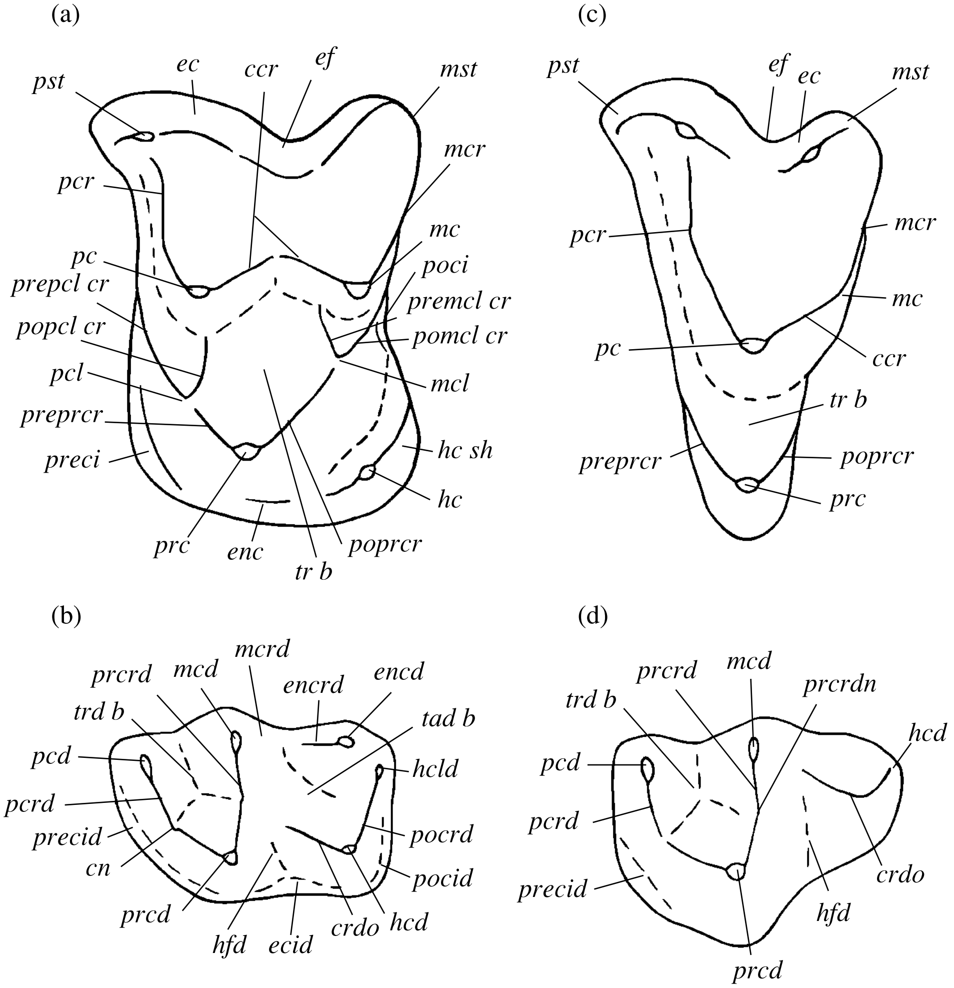


Fig. 3. Nomenclature of structural molar elements of insectivores: (a, b) dilambdomorph; (c, d) zalambdomorph; (a, c) left M^2; (b, d) left M_2. Designations: (*ccr*) centrocrista (= postprotocrista + premetacrista, = ectoloph), (*cn*) carnassial notch, (*crdo*) cristid oblique (= prehypocristid), (*ec*) ectocingulum, (*ecid*) ectocingulid, (*ef*) ectoflexus, (*enc*) entocingulum, (*encd*) entoconid, (*encrd*) entocristid, (*hc*) hypocone, (*hcd*) hypoconid, (*hcld*) hypoconulid, (*hc sh*) hypoconal shelf, (*hfd*) hypoflexid, (*mc*) metacone, (*mcd*) metaconid, (*mcl*) metaconule, (*mcr*) metacrista (= postmetacrista + metastylar crest), (*mcrd*) metacristid, (*mst*) metastyle, (*pc*) paracone, (*pcd*) paraconid, (*pcl*) paraconule, (*pcr*) paracrista (= parastylar crest + preparacrista), (*pcrd*) paracristid (= paraconid crest + preprotocristid, = paralophid), (*poci*) postcingulum, (*pocid*) postcingulid, (*pocrd*) postcristid (= posthypocristid + postentocristid, = hypolophid), (*pomcl cr*) postmetaconule crest, (*popcl cr*) postparaconule crest, (*poprcr*) postprotocrista, (*prc*) protocone, (*prcd*) protoconid, (*prcrd*) protocristid (= metalophid), (*prcrdn*) protocristid notch, (*preci*) precingulum, (*precid*) precingulid (= anterocingulid), (*premcl cr*) premetaconule crest, (*prepcl cr*) preparaconule crest, (*preprcr*) preprotocrista, (*pst*) parastyle, (*tad b*) talonid basin, (*tr b*) trigon basin, and (*trd b*) trigonid basin.

mals," which means insectivores (members of the superorder Insectivora) and extinct insectivore-like groups excluded from this superorder but more similar to it in skeletal structure than to any other placental groups.

This term is used not only due to both the current tradition and presumed ecological similarity of these groups as well as many contradictions in the treatment of phylogenetic relationships between some taxa of insectivores and insectivore-like mammals.

In the present study, a modified system of Insectivora based on the classification proposed by MacPhee and Novacek (Novacek, 1986; MacPhee and Novacek, 1993) is accepted. The Lipotyphla, Leptictida, and Didymoconida are regarded as orders of the superorder Insectivora (Lopatin, 2001a). The Cimolesta are regarded as an order of the superorder Ferae, while the Didelphodonta, Palaeoryctida, and Pantolesta are suborders of the Cimolesta (see McKenna and Bell, 1997; Averianov, 2003).

The present work gives descriptions of species and consistent diagnoses of superspecific taxa inclusive of superorders. The diagnoses of Recent groups are based mainly on dental and some cranial characters that are present in extinct material. Descriptions are based on the standard nomenclature of structural elements of the skeleton and teeth (Fig. 3), accepted by the majority of researchers dealing with particular insectivore groups

Table 2. Typology of the molar structure in insectivores

New terms			Analogues		
group of types	type	subtype	Gill, 1885	Butler, 1941, 1996; Gheerbrant, 1991	Hershkovitz, 1971
dilambdomorphy	protodilambdomorphy	–	dilambdodonty	predilambdodinty, trituberculate pattern	dilambdomorphic type, simple euthemorphic type
	eudilambdomorphy	entodilambdomorphy			
		ectodilambdomorphy		dilambdodonty	
	metadilambdomorphy	–			zalambdomorphic–dilambdomorphic type
zalambdomorphy	protozalambdomorphy		zalambdodonty	primitive zalambdodonty	
	euzalambdomorphy			true zalambdodonty	complex zalambdomorphic type
	parazalambdomorphy				

(Anderson, 1872; Butler, 1937, 1939, 1948, 1980; Reed, 1954; Van Valen, 1966, 1967; Szalay, 1969; Hutchison, 1974; Rich, 1981; Novacek, 1986; Russell and Dashzeveg, 1986; Asher et al., 2002; Lopatin and Kondrashov, 2004; etc.). The technique for tooth measurement follows Novacek (1976).

Because of a wide variety of interpretations, some terms of tooth morphology require explanatory notes. In dilambdomorph upper molars, the terms *paracrista* and *metacrista* designate integral (continuous) crests connecting the apices of labial cusps with respective styles (the paracrista connects the paracone to the parastyle, while the metacrista connects the metacone to the metastyle). These crests are often two-component, divided into a subhorizontal and subvertical portions (usual by notches or depressions at the base cusps). The paracrista is divided into the parastylar crest and preparacrista, and the metacrista is divided into the metastylar crest and postmetacrista. In the upper premolars having one labial cusp (paracone), the crest resembling the metacrista is refers to as the postcrista.

The centrocrista, which connects the paracone to the metacone, is always two-component; the paracone portion is named the postparacrista, while the metacone portion is named the premetacrista. In the case of advanced dilambdomorphy, the postparacrista and premetacrista are connected on the mesostyle rather than in the region of the notch; in this case, the centrocrista is called the ectoloph.

In regard to the crests of the lower molars, it is better to use the terms *paracristid, protocristid,* and *postcristid* rather than the paralophid, metalophid, and hypolophid, respectively. The term *lophid* means a flattened crest formed as a result of fusion between expanded cusps, whereas the crests discussed are typical *cristids*, i.e., formed by the edges of cusps. The paracristid and protocristid are always two-component; the paracristid is divided by the carnassial notch into the paraconid crest and the anterior crest of the protoconid (preprotocristid), the protocristid is divided by the median notch into the protoconid and metaconid portions. The postcristid is usually divided into two parts (named the posthypocristid and postentocristid) by the cuspule of the hypoconulid and adjacent notches; however, it remains continuous if the hypoconulid is reduced. The cristid oblique is also named the prehypocristid (see Butler, 1996).

The main cusp of zalambdomorph upper molars (zalambdocone after McDowell, 1958) is designated the paracone, according to the accepted homology (see Matthew, 1913; Butler, 1937, 1939, 1941, 1996; Hough, 1956, p. 534; Van Valen, 1966, 1967; Morgan and Ottenwalder, 1993; Asher et al., 2002; Asher and Sánchez-Villagra, 2005). Accordingly, transverse crests of zalambdomorph molars are named the preparacrista and postparacrista. In the primitive zalambdomorph teeth, the preservation of reduced metacone suggests to designate the parts of the posterior transverse crest as rudimentary centrocrista (located anterolingual to the metacone) and postmetacrista (located posterolabial to the metacone).

A new typology of the dental structure of insectivores was recently proposed (Lopatin, 2005c) based on the terminology of Hershkovitz (1971). Following Hershkovitz, the traditional terms *dilambdodonty* and *zalambdodonty* mean the presence of dilambdomorph and zalambdomorph molars, respectively. In doing so, the lower molars are correlated with the structure of the upper molars (Table 2) rather than characterized separately (using the terms *tuberculosectorial* or *tuberculate*, which are too general in the case of insectivores; see, e.g., Saban, 1958).

In the present study, the term *dilambdomorphy* comprises the group of structural types of initially tribosphenic molars with a well-developed paracone and metacone cusps on the upper teeth and a large, clearly differentiated talonid on the lower teeth. The dilambdomorphy corresponds to the dilambdodonty in the broad initial sense (sensu Gill, 1885; non Butler, 1941) and comprises the dilambdodonty in the narrow sense (sensu Butler, 1941, 1996), predilambdodonty, and, partially, the trituberculate, quadrituberculate, and sim-

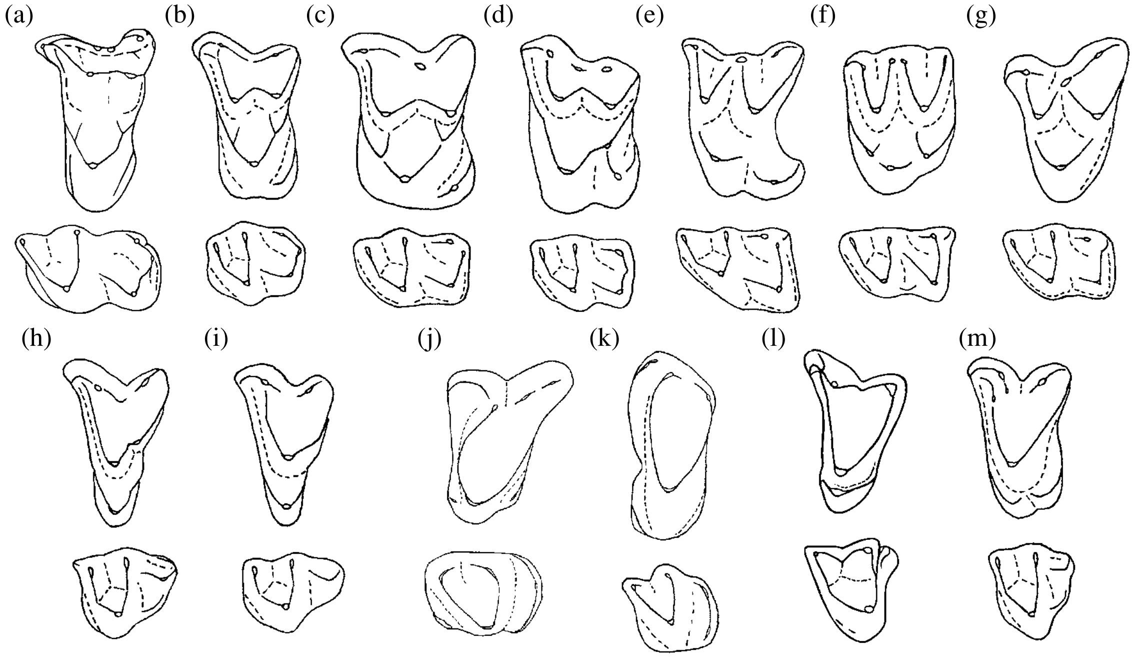


Fig. 4. The major types of molar structure in Lipotyphla: (a–g) dilambdomorph types: (a) protodilambdomorph type, *Batodo*n, Geolabididae, Late Cretaceous, Maastrichtian, North America; (b–f) eudilambdomorph type: (b–d) entodilambdomorph subtype: (b) *Centetodon*, Geolabididae, Early Eocene–Early Miocene, North America; (c) *Nyctitherium*, Nyctitheriidae, Early–Middle Eocene, North America; (d) *Plesiosorex*, Plesiosoricidae, Late Oligocene–Late Miocene of Europe, Early–Middle Miocene of North America; (e, f) ectodilambdomorph subtype: (e) *Myosorex*, Soricidae, Late Pliocene–Recent, Africa; (f) *Desmana*, Talpidae, Early Pliocene–Recent, Eurasia; (g) metadilambdomorph type, *Nesophontes*, Nesophontidae, Pleistocene–Holocene, Antilles; (h–m) zalambdomorph types: (h, i) protozalambdomorph type: (h) *Potamogale*, Tenrecidae, Recent, Africa; (i) *Protenrec*, Tenrecidae, Early Miocene, Africa; (j, k) euzalambdomorph type: (j) *Tenrec*, Tenrecidae, Recent, Madagascar; (k) *Setifer*, Tenrecidae, Recent, Madagascar; (l, m) parazalambdomorph type: (l) *Apternodus*, Apternodontidae, Middle Eocene–Early Oligocene, North America; (m) *Solenodon*, Solenodontidae, Pleistocene–Recent, Antilles. The teeth, left M^2 and M_2, are drawn out of scale, after Butler (1937, text-figs. 2, 5, 15, 25; 1972, text-figs. 2, 3), Schlaikjer, (1934, text-fig. 1), Clemens (1973, text-fig. 25b), and Storer (1991, text-fig. 10K), modified. Distribution of genera is given after McKenna and Bell (1997).

ple euthemorphic structural patterns (see Butler, 1941, 1996; Hershkovitz, 1971; Gheerbrant, 1991). The dilambdomorph group includes three distinct structural patterns: *protodilambdomorph, eudilambdomorph*, and *metadilambdomorph* (Figs. 4a–4g).

Protodilambdomorphy (or primitive dilambdomorphy) means the presence of the paracone and metacone (which are clearly detached, expanded only slightly transversely, and, consequently, do not form the characteristic W-shaped structure by their crests), large conules, massive protocone, rudimentary hypocone (initially, in the shape of a hypoconal shelf), and a well-developed and clearly differentiated talonid (Fig. 4a). The new term partially corresponds to the predilambdodonty, which means the absence of W-shaped pattern because of the clearly differentiated labial cusps and the presence of a rectilinear sublongitudinal centrocrista, which is longer than that of the initial tribosphenic molars of primitive placentals (Crochet, 1980; Gheerbrant and Russell, 1989; Gheerbrant, 1991). The protodilambdomorphy is characteristic of the most primitive members of Lipotyphla, i.e., Adapisoriculidae, Chambilestidae, and the earliest Geolabididae, Micropternodontidae, and Nyctitheriidae.

Eudilambdomorphy (advanced dilambdomorphy) is characterized by the presence of a well-developed hypocone and a more or less distinct W-shaped structure of the crests of the paracone and metacone. This structural type comprises a number of variants, involving more or less central positions of the paracone and the metacone, reduction or excessive development of particular elements of the tooth crown, i.e., the conules, styles, and hypocone (Figs. 4b–4f). Eudilambdomorphy means that well-developed crests of the paracrista, centrocrista (postparacrista and premetacrista), and metacrista form a W-shaped pattern on the labial cusps; note that the medial apex is not necessarily located on the mesostyle, its medial position is characteristic of the dilambdodonty in the narrow sense (see Butler, 1996; Figs. 4b–4d). Various variants of this structural molar type are observed in the majority of insectivores (except for the zalambdodont Tenrecidae, Chrysochloridae, Solenodontidae, and Apternodontidae; the metadilambdodont Nesophontidae; and the protodilambdodont early taxa). The eudilambdomorphy of the soricid–talpid structural pattern means the formation of a W-shaped centrocrista (or ectoloph), with the apices located on the parastyle, paracone, mesostyle, metacone, and metastyle; the lower molars acquire the characteristic high hypoconid, while the hypoconulid is displaced lingually and transformed into the entostylid, or disappears completely (Figs. 4e, 4f). This subtype, i.e., dilambdodonty in the narrow sense (sensu Butler, 1941, 1996), deserves a special name, which would eliminate the terminological ambiguity mentioned above. I suggest that this structural subtype is designated as *ectodilambdomorphy* (which reflects the external position of the central apex of the centrocrista, i.e., the presence of the so-called ectoloph). The eudilambdomorphy of a more primitive level (which comprises a number of variants, partially including the trituberculate pattern after Butler, 1941 and the predilambdodonty after Gheerbrant, 1991) is named *entodilambdomorphy* (Figs. 4b–4d, Table 2).

Metadilambdomorphy (nesophontoid dilambdomorphy) is established as a special type of dilambdomorph dental structure, which is characterized by the reduction of the paracone and disappearance of the hypocone and conules (Fig. 4g). Hershkovitz (1971) assigned molars of nesophontids to the "zalambdomorphic–dilambdomorphic" structural type. Most likely, this type developed independently based on the early eudilambdomorph type (by the reduction of certain elements); therefore, it deserves a special name.

Zalambdomorphy as a special group of structural types means that the trigon of the upper molars is formed by a large lingually located paracone, a paracrista that is V-shaped in projection, and styles; the metacone and protocone are considerably reduced or absent, the conules are absent (Butler, 1939, 1941; Hershkovitz, 1971). In this pattern, the lower molars are characterized by reduced talonids and excessively developed trigonids, including the formation of the oblique paracristid and a very high and broad transverse protocristid. Three structural types are recognized: *protozalambdomorph, euzalambdomorph*, and *parazalambdomorph* (Figs. 4h–4m).

The protozalambdomorphy (or primitive tenrecoid zalambdomorphy) means that the metacone is considerably reduced (however, its rudiment is preserved between a shortened centrocrista and postmetacrista), the paracone is displaced to the center, the protocone and talonid are reduced, and the hypocone is absent (Figs. 4h, 4i). This dental pattern is characteristic of the tenrecs *Potamogale* and *Protenrec* and Early Paleogene insectivore-like placentals of the family Palaeoryctidae (Matthew, 1913; Butler, 1941; Thewissen and Gingerich, 1989; Lopatin and Averianov, 2004b). This structural type was designated "primitive zalambdodont" by Butler (1941), "zalambdomorphic–dilambdomorphic" by Hershkovitz (1971), or "protodilambdodont" by Novacek (1976).

The euzalambdomorph (advanced tenrecoid zalambdomorph) structural type means complete loss of the metacone and protocone, the lingual displacement of the paracone to the position of the protocone, excessive development of the stylar shelf, and appearance of supplementary cingular elements (Figs. 4j, 4k). The talonid is extremely reduced and resembles a postcingulid. This structural pattern is characteristic of the majority of living tenrecs and golden moles.

The parazalambdomorph (solenodontoid zalambdomorph) structural type resembles the protozalambdomorph type, and differs in the complete absence of the metacone and the presence of the hypocone in the lingual lobe (the last is a facultative character). This structural pattern is characteristic of the extant Solenodontidae and Paleogene Apternodontidae (Figs. 4l, 4m). It is assumed that the parazalambdomorph structural type originate from the eudilambdomorph type, whereas the protozalambdomorph type (which gave rise to the euzalambdomorphy) developed from the protodilambdomorph type (Lopatin, 2005c).

The zalambdomorph structural type with the completely reduced metacone was designated "the true zalambdodont" (Butler, 1941) or "complex zalambdomorphic" type (Hershkovitz, 1971). In the classification proposed here, the structure of the lingual and labial lobes of the tooth are taken into account; the true zalambdomorph type comprises the euzalambdomorph and parazalambdomorph types as well as the most advanced variants of the protozalambdomorph type.

When describing the premolar shape, the degree of similarity to molars is frequently briefly characterized by such terms as *molarized, semimolarized, nonmolarized*, etc. These terms may have different meaning, depending on the general concept accepted by the researchers are structural dental features of the group examined (see Szalay, 1969; Krishtalka, 1976a).

Krishtalka provided explanations of the terms *premolariform*, *semimolariform*, and *submolariform* with reference to P^4 and P_4 of the Paleogene Lipotyphla (Krishtalka, 1976, p. 5; Scott, 2003). According to his definition, a premolariform P_4 is characterized by a large, dominating protoconid and an extremely shortened, usually unicuspid, talonid; a premolariform P^4 has two cusps, the paracone and protocone. In a semimolariform P_4, the talonid is substantially narrower than, but almost as long as that of molars, usually has two or three cusps; the paraconid is often better developed than in premolariform P_4, but is lower than the metaconid and located in the anterior part of the base of the protoconid. Semimolariform P^4 has a paracone, metacone, and protocone and is similar to M^1. According to Krishtalka, submolariform P_4 is similar in structure to M_1 but has a narrower talonid and smaller cusps of the trigonid.

In the present study, the types of premolar structure of dilambdodont insectivores and insectivore-like mammals are characterized using the terms *molari-*

Table 3. Typology of the premolar structure in dilambdodont insectivores

Structural type	Degree of molarization	Characteristics of cusp development (upper teeth / lower teeth)
molariform, submolariform	completely or almost completely molarized	paracone, metacone, protocone, hypocone (hypoconal shelf) / paraconid, protoconid, metaconid, talonid with basin and two or three cusps
semimolariform	semimolarized	paracone, protocone, metacone (or hypoconal shelf) / paraconid, protoconid, metaconid, talonid without basin and with one cusp
	partially molarized	paracone, protocone / paraconid, protoconid, reduced metaconid and (or) talonid
	slightly molarized	paracone, rudimentary protocone / protoconid, increased paraconid, and talonid
premolariform	nonmolarized	paracone, styles / protoconid, small paraconid and small unicuspid talonid
antemolariform	nonmolarized	low paracone / low protoconid

form, submolariform, semimolariform, premolariform, and *antemolariform* (Table 3).

In the case of molariform of submolariform structure (completely or almost completely molarized premolars), the upper premolars have a paracone, metacone, protocone, and hypocone (or a hypoconal shelf); the lower premolars have a paraconid, protoconid, metaconid, and a differentiated talonid with a basin and two or three cusps. A molariform premolar is hardly distinguished from molars, as is observed in a number of mammal groups. In the majority of insectivores, even quite molarized premolars usually differ from molars in dimensions and proportions (see above) and, therefore, are characterized as submolariform teeth. Examples are P^4 and P_4 of the Nyctitheriinae (Nyctitheriidae) and Didymoconinae (Didymoconidae).

In the case of semimolariform structure (semimolarized, partially molarized, slightly molarized premolars), the upper premolars have a paracone, protocone, and, usually, a metacone or hypocone; the lower premolars have a paraconid, protoconid, a more or less developed metaconid, and a trenchant or cingulid-like, unicuspid talonid without a basin. Examples are P^4 and P_4 of the Micropternodontidae and Geolabididae; P^4 of the Talpidae, Dimylidae, Erinaceidae, and Ardynictinae (Didymoconidae); and P_4 of the majority of Erinaceidae, Praolestinae, Eosoricodontinae (Nyctitheriidae), and Soricolestinae (Soricidae). The semimolariform pattern means a lower degree of a molarization than in submolariform teeth and all transitional levels of secondary premolarization (or demolarization after Sigé, 1976), excluding a completely premolariform pattern. Thus, distinctions in the degree of incomplete molarization or demolarizations of premolars are expressed by comparative characteristics, which are clearly determined only within particular groups. In general, the term *semimolarized* is applicable to the upper premolars possessing a metacone and a protocone and the lower premolars possessing a paraconid, a well-developed metaconid, and a nondifferentiated talonid. The *partially molariform* upper premolars are those having a well-developed protocone, but lacking the metacone, while the partially molariform lower premolars have a reduced metaconid and talonid. The *slightly molariform* upper premolars have a rudimentary protocone, the slightly molariform lower premolars have a general premolariform structure and enlarged paraconid and talonid regions.

The premolariform structure (nonmolarized or completely secondarily premolarized premolars also named simple premolars) of the upper premolars means that only the paracone and styles are present; the premolariform lower premolars have a protoconid, a more or less developed paraconid and a simple unicuspid talonid. Examples are P_4 of the Talpidae, Dimylidae, Asionyctiinae (Nyctitheriidae), and Ardynictinae (Didymoconidae) and P^2, P_2, P^3, and P_3 of many groups.

The antemolariform structure of the upper or lower premolars means that they are transformed into a small and low unicuspid tooth, usual with cingula (cingulids). Examples are P_4 of the majority of the Soricidae, Brachyericinae (Erinaceidae), and Dimylidae; P_2 and P_3 of the Plesiosoricidae; and the antemolars of the Soricidae, Talpidae, Dimylidae, and Erinaceinae.

The premolars of zalambdodont insectivores are typified based on the similarity to the molars; the molariform and submolariform types mean complete or almost complete similarity (this is characteristic of P^4 and P_4), the semimolariform type (P^3, P^4, and P_4) means partial similarity, and the premolariform type (P^3 and P_3) is greater similarity to the anterior premolars than to molars.

1.4. Biochronological Terminology, Characteristics of the Early Paleogene Stage of Small Mammal Evolution in Asia, Ecological Analysis

The Early Paleogene is considered here to include the Paleocene and the first half of the Eocene, the time of dominance of extinct orders and primitive extinct groups of extant orders among placentals of the Northern Hemisphere. This stage is opposed to the Late Paleogene (second half of the Eocene and the Oligocene), the time of modernization of the mammal fauna, when representatives of many extant families

Table 4. Composition of the small mammal fauna in the Paleocene–Early Eocene of Central Asia (Shevyreva, 1989; Dashzeveg et al., 1998; Meng et al., 1998, 2005; Ting, 1998; Wang et al., 1998; Guo et al., 2000; Lopatin, 2001a, 2004e, 2005b; McKenna and Meng, 2001; Huang and Zheng, 2002; Huang, 2003; Lopatin and Kondrashov, 2003, 2004; Huang et al., 2004; Kondrashov et al., 2004a; Lopatin and Averianov, 2005; original data)

ALMA	Phytophages	Entomophages
Bumbanian	MULTITUBERCULATA: Neoplagiulacidae: *Mesodmops*; MIXODONTIA: Eurymylidae: *Zagmys*, *Gomphos*, *Matutinia*; Rhombomylidae: *Rhombomylus*; Decipomyidae: *Decipomys*; LAGOMORPHA: Lagomorpha indet. RODENTIAFORMES: Alagomyidae: *Alagomys*; RODENTIA: Tamquammyidae (=Cocomyidae): *Cocomys*, *Adolomys* (=*Sharomys*), *Tsagankhushumys* (=*Tsagamys*), *Bumbanomys* (=*Kharomys*, *Ulanomys*); Chapattimyidae (=Yuomyidae): *Bandaomys*, *Advenimus*, *Esesempomys*; Ctenodactyloidea fam.: *Hannanomys*; Ischyromyidae: *Taishanomys*, ?*Acritoparamys*; Ivanantoniidae (=Orogomyidae): *Ivanantonia* (=*Orogomys*)	LIPOTYPHLA: Micropternodontidae: *Prosarcodon*, *Hsiangolestes*; Nyctitheriidae: *Bumbanius*, *Oedolius*, *Eosoricodon*, *Edzenius* gen. nov.; Plesiosoricidae: *Ordolestes* gen. nov.; Erinaceidae: *Changlelestes*; DIDYMOCONIDA: Didymoconidae: *Hunanictis*; CIMOLESTA: Cimolestidae: *Naranius*, *Tsaganius*, *Bagalestes* gen. nov.; Pantolestidae: Pantolestidae indet.
Gashatan	MULTITUBERCULATA: Taenilabididae: *Prionessus*, *Lambdopsalis*, *Sphenopsalis*; ANAGALIDA: Anagalidae: *Hsiuannania*, *Khashanogale*; Pseudictopidae: *Pseudictops*; MIXODONTIA: Eurymylidae: *Eurymelus*, *Eomylus* (=*Khaychina*), *Amar*, *Zagmys*, *Sinomylus*, *Palaeomylus*; Rhombomylidae: *Hanomys*; Mimotonidae: *Mimotona*; RODENTIAFORMES: *Tribosphenomys*; RODENTIA: Ischyromyidae: *Asiaparamys*	LIPOTYPHLA: Micropternodontidae: *Hyracolestes*, *Sarcodon*; Geolabididae: *Gobigeolabis*; Nyctitheriidae: *Praolestes*, *Jarveia*, *Bayanulanius*, *Voltaia*, *Asionyctia*; DIDYMOCONIDA: Didymoconidae: *Archaeoryctes*, *Wanolestes*; CIMOLESTA: Palaeoryctidae: *Pinoryctes* gen. nov.; Pantolestidae: *Zhigdenia* gen. nov.
Nongshanian	MULTITUBERCULATA: Multituberculata indet.; ANAGALIDA: Anagalidae: *Hsiuannania*, *Huaiyangale*; Pseudictopidae: *Haltictops*, *Allictops*, *Pseudictops*; MIXODONTIA: Eurymylidae: *Heomys*; Mimotonidae: *Mimotona*	LIPOTYPHLA: Micropternodontidae: *Hyracolestes*; DIDYMOCONIDA: Didymoconidae: *Archaeoryctes*
Shanghuanian	ANAGALIDA: Anagalidae: *Linnania*, *Huaiyangale*, *Diacronus*, *Eosigale*, *Qipania*, *Wanogale*, *Anaptogale*, *Chianshania*, *Stenanagale*; Astigalidae: *Astigale*, *Zhujegale*; Pseudictopidae: *Anictops*, *Paranictops*, *Cartictops*; MIXODONTIA: Eurymylidae: *Heomys*; Mimotonidae: *Mimotona*	LIPOTYPHLA: Micropternodontidae: *Carnilestes*, *Prosarcodon*; DIDYMOCONIDA: Didymoconidae: *Zeuctherium*

occupied important positions in the ecosystems, while primitive groups became extinct or relict (Lopatin, 2004a). This period comprises the Shanghuanian, Nongshanian, Gashatan, Bumbanian, Arshantan, and Irdinmanhan Asian land mammal ages. It is accepted that the Shanghuanian Age approximately corresponds to the Puercan and Torrejonian of the North American scheme, the Nongshanian, Gashatan, Bumbanian, and Arshantan are correlated with the Tiffanian, Clarkforkian, Wasatchian, and Early Bridgerian, respectively, while the Irdinmanhan fits the Middle–Late Bridgerian and most of the Uintan (Table 1) (Clyde et al., 1994, 1997; Berggren et al., 1995; Prothero and Emry, 1996; Ting, 1998; Lindsay, 2001; Lucas, 2001).

The Early Paleocene Asian fauna is mostly composed of endemic taxa (Ting, 1998; Wang et al., 1998). The small mammal fauna of the Shanghuanian Age substantially differs from North American and European faunas of approximately the same age. Small phytophages were represented in North America by numerous multituberculates, while, in Asia, the endemic anagalids and mixodonts dominated. Multituberculates became extinct in Asia at the end of the Cretaceous and appeared again in the Late Paleocene, in the Nongshanian Age, probably as immigrants from North America. In the Gashatan, three genera of Central Asian multituberculates were recorded; however, mixodonts and anagalids still dominated (Table 4). At the end of the Gashatan, anagalids abruptly decreased in diversity, while mixodonts became the dominant group of small phytophages. These animals apparently became abundant. The Zhigden Member of the Naran-Bulak Formation of the Tsagan-Khushu locality in Mongolia has yielded several hundred jaw fragments of two mixodont species, *Eomylus zhigdenensis* (= *Khaychina elongata*) and *Sinomylus* sp. (Dashzeveg and Russell, 1988; Lopatin and Kondrashov, 2000, 2003; Lopatin et al., 2001; Kondrashov and Lopatin, 2003).

The data on Paleocene rodents are restricted to several taxa. Several species of Ischyromyidae and one member of Alagomyidae are known from the Lower Clarkforkian of North America (Jepsen, 1937; Ivy, 1990; Dawson and Beard, 1996). In Asia, Late Paleocene rodents and (or) rodent-like mammals are known from three faunas: the Dzhilga locality in southern Kazakhstan has yielded isolated lower molars of the ischyromyid *Asiaparamys shevyrevae* (Nessov, 1987), the Bayan Ulan locality in China contains upper and lower jaws and bones of the postcranial skeleton of *Tribosphenomys minutus* (Meng et al., 1994b, 1998; Meng and Wyss, 2001), and the Zhigden Member of the Tsagan-Khushu locality in Mongolia contains jaw fragments of *Tribosphenomys secundus* and *T. tertius* (Lopatin and Averianov, 2004a, 2004c). Initially, *Tribosphenomys* was referred with some doubts to the family Alagomyidae, which also included the genus *Alagomys* from the Late Paleocene of North America and Early Eocene of Mongolia and China (Dashzeveg, 1990; Tong and Dawson, 1995; Dawson and Beard, 1996; Tong and Wang, 1998). However, it turned out that *Tribosphenomys* lacks Hunter–Schreger bands in the enamel microstructure of incisors, which are present in all rodents; therefore, it was excluded from the order Rodentia, but retained in the higher rank group Rodentiaformes (Meng and Wyss, 1994, 2001; Wyss and Meng, 1996). Thus, the earliest finds of Rodentiaformes in Asia are of approximately the same age as in North America. It is worth noting that, before the onset of the Eocene, rodents did not play a leading role in small phytophage communities of both continents.

Entomophages are the second basic component of terrestrial small mammal faunas. In the Paleocene of North America, primitive erinaceids (Litocherinae, Sespedectidae, and Erinaceidae incertae sedis), soricomorphs (Nyctitheriidae, and Apternodontidae), and small marsupials and insectivore-like placentals (Cimolestidae, Palaeoryctidae, Pantolestidae, and Apatotheria) were abundant. In the Paleocene of Asia, primitive soricomorphs dominated. The study of new material has shown a high diversity of Micropternodontidae and Nyctitheriidae and the presence of Geolabididae (Lopatin et al., 2001; Lopatin, 2004f; Kondrashov et al., 2004a; Lopatin and Kondrashov, 2004).

At the very beginning of the Eocene, the mammal fauna of the Northern Hemisphere underwent a great rearrangement, which was connected with the appearance and expansion of a number of new groups, including Perissodactyla, Artiodactyla, Hyaenodontidae, Hapalodectidae, Primates, and Chiroptera and a considerable adaptive radiation of Rodentia. The earliest reliable finds of the Hyaenodontidae, Hapalodectidae, and Primates come from the terminal Paleocene (Upper Gashatan) and those of Perissodactyla and Artiodactyla come from the basal Eocene (Lower Bumbanian) of China and Mongolia (Dashzeveg, 1988; Beard, 1998; Meng et al., 1998; Ting, 1998; Lopatin, 2001b; Lopatin et al., 2001; Kondrashov et al., 2004b). Since the Gashatan–Bumbanian boundary has recently been established based on magnetostratigraphic and isotope data within the interval of 55.7–54.97 Ma (Bowen et al., 2002), it is sometimes assumed that the groups discussed appeared in Asia somewhat earlier than in North America and Europe (the model of "East of Eden," see Beard, 1998, 2002; Beard and Dawson, 1999; Bowen et al., 2002; Ting et al., 2004).

These faunal changes correlated with a global climatic warming and humidification and a great eustatic regression of the sea level about 55.5 Ma (Kennet and Stott, 1991; Koch et al., 1992, 1995; Zachos et al., 1993; Bowen et al., 2004). These events supposedly allowed mammals from low latitudes (where Paleocene mammal faunas are poorly known) to penetrate into higher latitudes of the Northern Hemisphere (McKenna, 1975b, 1980, 1983; Krause and Maas, 1990; Storch, 1990; Hooker, 1998, 2000; Eberle and McKenna, 2002) and provided migrations between Asia and North America (through Bering Land) and between North America and Europe (through the North Atlantic Bridge). One of possible reasons for these events was the collision of Indian subcontinent and Asia at the Paleocene–Eocene boundary (Krause and Maas, 1990; Clyde and Khan, 2000). However, extant mammal orders are recorded in India after this collision (Clyde et al., 2003). After the formation of the northern Atlantic in the Early Eocene, about 53.5 Ma (Kalandadze and Rautian, 1992; Hooker, 2000; Radionova and Khokhlova, 2000), intercontinental faunal exchanges between North America and Eurasia could have occurred only through Bering Land.

In the Bumbanian, the composition of the Asian small mammal community changed considerably. Multituberculates were represented by one genus, anagalids became extinct, and, despite the high diversity of mixodonts, the leading position among small phytophages was for the first time occupied by rodents (Table 4). The first Lagomorpha appeared. In the Early Eocene, erinaceid insectivores penetrated into Asia. Primitive soricomorph groups, such as micropternodontids and nyctitheriids continued to develop (Russell and Dashzeveg, 1986; Kondrashov et al., 2001; Lopatin and Kondrashov, 2004).

In the Eocene, faunal exchanges between Asia and North America occurred repeatedly, which allows the intercontinental correlation of biochronological units based on mammals (Russell and Zhai, 1987; Stucky, 1992).

The Arshantan Asian Land Mammal Age is usually assigned to the Middle Eocene. However, it is presently compared to the Early Bridgerian (more precisely, it is considered to be younger than the Late Wasatchian and older than the Middle Bridgerian, see Lucas, 2001), which is assigned to the end of the Early Eocene, dated 50.5–49.0 Ma (Clyde et al., 1997; Lindsay, 2001). The beginning of the Irdinmanhan Age probably corresponds to the terminal Early Eocene (Averianov and Godinot, 1998). This assumption is based on the Late Ypresian appearance of the fish assemblage from the Andarak 2 locality in Kyrgyzstan, which yielded a mammal fauna characteristic of the Irdinmanhan Age

(Averianov and Udovichenko, 1993; Averianov and Godinot, 1998). Rich assemblages of Middle Eocene small mammals are known from China and Mongolia (Russell and Zhai, 1987; Tong, 1997; Lopatin, 2003a). They demonstrate a new gradual shift of dominants in both entomophages and phytophages, which was marked by the appearance of many living groups. By the Middle Eocene, lagomorphs had become rather diverse (see Averianov and Lopatin, 2005; Lopatin and Averianov, 2006), whereas mixodonts gradually became extinct. The diversity of rodents sharply increased, in particular, about 20 families were recorded in the Middle Eocene (Hartenberger, 1996, 1998). The Asian faunas were dominated by primitive ctenodactyloids; however, a number of groups (Eomyidae, Gliridae, Zapodidae, and Cricetidae) that subsequently played the major role in rodent communities throughout the Northern Hemisphere appeared at the end of the Irdinmanhan Age (Tong et al., 1995; Tong, 1997; Dawson and Tong, 1998).

In the Late Eocene and Oligocene, the majority of early relicts became extinct, and the groups originating from Asia, including insectivores, lagomorphs, and rodents, began to determine the general pattern of new small mammal faunas of the Northern Hemisphere.

At the present state of knowledge, the Early Paleogene Asian land mammal ages are characterized by the following developmental features of small mammal faunas (Lopatin, 2004a; see also Table 5).

Shanghuanian Age. The primary development of endemic small mammal community dominated by anagalids and the first adaptive radiation of mixodonts among phytophages.

Nongshanian Age. The development of endemic community dominated by anagalids and mixodonts and emergence of allochtonous multituberculates among phytophages.

Gashatan Age. Transformation of endemic community dominated by mixodonts, the presence of anagalids and multituberculates and emergence of rodents among phytophages; domination of soricomorph insectivores among entomophages.

Bumbanian Age. Modernization of the community: rodents became dominants for the first time; radiation of eurymyloid mixodonts, soricomorphs, and erinaceids; appearance of lagomorphs.

Arshantan and Irdinmanhan ages. Development of the modernized endemic community of rodents, lagomorphs, and insectivores, which exerted a significant influence on the formation of Late Paleogene and Neogene small mammal faunas of the Northern Hemisphere.

The ecological structure of the Early Paleogene insectivore associations is characterized through the analysis of their taxonomic composition, revelation of dominant groups, estimation of the size structure of communities, and morphoecological analysis of particular species. The animal's sizes were estimated from the body mass, using the formulae based on the skull length (Thewissen and Gingerich, 1989) and length and width of teeth (Bloch et al., 1998). Body mass categories are delineated according to Strel'nikov (1970). For comparison purposes the same calculations were performed for all Paleogene Asian insectivores provided with adequate primary data.

Table 5. Changes in the composition of small mammal faunas in the Early Paleogene of Asia; designations: (D) dominants, (F) first appearance, and (L) last appearance

ALMA	Phytophages	Entomophages
Irdinmanhan	Rodentia (D) Lagomorpha Mixodontia (L)	Soricomorpha (D) Erinaceomorpha Didymoconida Palaeoryctida
Arshantan	Rodentia (D) Mixodontia	Soricomorpha (D) Erinaceomorpha Didymoconida
Bumbanian	Rodentia (D) Lagomorpha (F) Mixodontia Multituberculata (L) Rodentiaformes (L)	Soricomorpha (D) Erinaceomorpha (F) Didymoconida Didelphodonta Pantolesta
Gashatan	Mixodontia (D) Anagalida (L) Multituberculata Rodentiaformes (F) Rodentia (F)	Soricomorpha (D) Didymoconida Palaeoryctida (F) Pantolesta (F)
Nongshanian	Anagalida (D) Mixodontia Multituberculata (F)	Soricomorpha Didymoconida
Shanghuanian	Anagalida (D) Mixodontia (F)	Soricomorpha (F) Didymoconida (F)

CHAPTER 2. REVIEW OF EARLY PALEOGENE INSECTIVORE MAMMALS OF ASIA

The study of Early Paleogene insectivores of Asia started in 1925, when Matthew and Granger (1925a) described two new mammal genera and species named *Sarcodon pygmaeus* and *Hyracolestes ermineus* from the Upper Paleocene of the Gashato locality in Mongolia. Originally, the two taxa were not assigned to insectivores; *Sarcodon* was presumably regarded as a marsupial or a carnivore, while *Hyracolestes* was referred to creodonts. In the same year, Matthew and Granger (1925c) described *?Hapalodectes auctus* from the Middle Eocene Chinese Irdin Manha locality, which was subsequently assigned to Didymoconidae (Van Valen, 1966). To date, more than 60 species and more than 40 genera of 12 insectivore and insectivore-like families have been described from the Paleocene and Lower–Middle Eocene of Asia (Table 6). They are reviewed below in the systematic order.

Table 6. List of insectivore and insectivore-like taxa in the Paleocene–Middle Eocene of Asia; designations (SH) Shanghuanian, (N) Nongshanian, (G) Gashatan, (B) Bumbanian, (A) Arshantan, (I) Irdinmanhan, (SM) Sharamurunian, (E) Ergilian, (SG) Shandgolian, (T) Tabenbulukian

Taxon	Occurrence	References
SORICOMORPHA		
Micropternodontidae		
Sarcodontinae		
Carnilestes Wang et Zhai, 1995	Early Paleocene (SH): China	Wang and Zhai, 1995
Carnilestes palaeoasiaticus Wang et Zhai, 1995		
Carnilestes major Wang et Zhai, 1995		
Prosarcodon McKenna, Xue et Zhou, 1984	Early Paleogene (SH–B): China, Mongolia	McKenna et al., 1984; Lopatin and Kondrashov, 2004
Prosarcodon lonanensis McKenna, Xue et Zhou, 1984	Early Paleocene (SH): China	
Prosarcodon maturus Lopatin et Kondrashov, 2004	Early Eocene (B): Mongolia	
Sarcodon Matthew et Granger, 1925 (=*Opisthopsalis* Matthew, Granger et Simpson, 1929)	Late Paleocene (G): Mongolia and China	Matthew and Granger, 1925a; Szalay and McKenna, 1971; Meng et al., 1998; Huang, 2003; Lopatin and Kondrashov, 2004
Sarcodon pygmaeus Matthew et Granger, 1925 (=*Opisthopsalis vetus* Matthew, Granger et Simpson, 1929)	Late Paleocene (G): Mongolia and China	
Sarcodon minor Meng, Zhai et Wyss, 1998	Late Paleocene (G): China	
Sarcodon zhaii Huang, 2003	Late Paleocene (G): China	
Hyracolestes Matthew et Granger, 1925	Late Paleocene (G): Mongolia and China	Matthew and Granger, 1925a; Szalay and McKenna, 1971; Lopatin and Kondrashov, 2004
Hyracolestes ermineus Matthew et Granger, 1925		
Metasarcodon Lopatin et Kondrashov, 2004	Terminal Early Eocene to Middle Eocene (I): Kyrgyzstan and Mongolia	Averianov, 1994; Lopatin and Kondrashov, 2004
Metasarcodon udovichenkoi (Averianov, 1994) (=*Sarcodon udovichenkoi* Averianov, 1994)	Terminal Early Eocene (I): Kyrgyzstan	
Metasarcodon reshetovi Lopatin et Kondrashov, 2004	Middle Eocene (I): Mongolia	
Micropternodontinae		
Hsiangolestes Zheng et Huang, 1984	Early Eocene (B): China	Zheng and Huang, 1984
Hsiangolestes youngi Zheng et Huang, 1984		
Sinosinopa Qi, 1987	Terminal Early Eocene (A): China	Qi, 1987
Sinosinopa sinensis Qi, 1987		
Bogdia Dashzeveg et Russell, 1985	Middle Eocene (I): Mongolia	Dashzeveg and Russell, 1985
Bogdia orientalis Dashzeveg et Russell, 1985		
Geolabididae		
Gobigeolabis Lopatin, 2004	Late Paleocene (G): Mongolia	Lopatin, 2004e
Gobigeolabis verigranum Lopatin, 2004		
Nyctitheriidae		
Nyctitheriinae		
Yuanqulestes Tong, 1997	Middle (SM) or Late (E) Eocene: China	Tong, 1997
Yuanqulestes qiui Tong, 1997		

Table 6. (Contd.)

Taxon	Occurrence	References
Praolestinae sufam. nov.		
Praolestes Matthew, Granger et Simpson, 1929	Late Paleocene (G): Mongolia	Kondrashov et al., 2004
Praolestes nanus Matthew, Granger et Simpson, 1929		
Praolestes maximus Kondrashov, Lopatin et Lucas, 2004		
Bumbanius Russell et Dashzeveg, 1986	Early Eocene (B): China	Russell and Dashzeveg, 1986
Bumbanius rarus Russell et Dashzeveg, 1986		
Asionyctiinae		
Asionyctia Missiaen et Smith, 2005	Late Paleocene (G): China	Missiaen and Smith, 2005
Asionyctia guoi Missiaen et Smith, 2005		
Voltaia Nessov, 1987	Late Paleocene (G): Kazakhstan	Nessov, 1987; McKenna and Bell, 1997
Voltaia minuta Nessov, 1987		
Oedolius Russell et Dashzeveg, 1986	Early Eocene (B): Mongolia	Russell and Dashzeveg, 1986
Oedolius perexiguus Russell et Dashzeveg, 1986		
Bayanulanius Meng, Zhai et Wyss, 1998	Late Paleocene (G): China	Meng et al., 1998
Bayanulanius tenuis Meng, Zhai et Wyss, 1998		
Jarveia Nessov, 1987	Late Paleocene (G): Kazakhstan and Mongolia	Nessov, 1987; Averianov, 1995; Kondrashov et al., 2004
Jarveia minuscula Nessov, 1987	Late Paleocene (G): Kazakhstan	
Jarveia erronea Kondrashov, Lopatin et Lucas, 2004	Late Paleocene (G): Mongolia	
Edzenius lus gen. et sp. nov.	Early Eocene (B): Mongolia	Original data
Eosoricodontinae		
Eosoricodon Lopatin, 2005	Early Eocene (B): Mongolia	Lopatin, 2005b
Eosoricodon terrigena Lopatin, 2005		
Soricidae		
Soricolestinae		
Soricolestes Lopatin, 2002	Middle Eocene (I): Mongolia	Lopatin, 2002c
Soricolestes soricavus Lopatin, 2002		
Plesiosoricidae		
Butseliinae		
Pakilestes Russell et Gingerich, 1981	Basal Middle Eocene (I): Pakistan	Russell and Gingerich, 1981; Gingerich, 2003
Pakilestes lathrius Russell et Gingerich, 1981		
Ordolestes ordinatus gen. et sp. nov.	Early Eocene (B): Mongolia	Original data
Plesiosoricinae		
Ernosorex Wang et Li, 1990	Middle Eocene (I): China	Wang and Li, 1990; McKenna and Bell, 1997
Ernosorex jilinensis Wang et Li, 1990		
Apternodontidae		
Asiapternodontinae subfam. nov.		
Asiapternodus Lopatin, 2003	Middle Eocene (I): Mongolia	Lopatin, 2003b
Asiapternodus mackennai Lopatin, 2003		

Table 6. (Contd.)

Taxon	Occurrence	References
Apternodontidae indet.		
“cf. *Apternodus*” sp.	Middle Eocene (SM): China	Tong, 1997
ERINACEOMORPHA		
Erinaceidae		
Changlelestinae		
Changlelestes Tong et Wang, 1993	Early Eocene (B): China	Tong and Wang, 1993, 1998
Changlelestes dissetiformis Tong et Wang, 1993		
Tupaiodontinae		
Zaraalestes Storch et Dashzeveg, 1997	Middle Eocene (I): Mongolia; Oligocene (SG, T): China, Mongolia, Kazakhstan	Storch and Dashzeveg, 1997; McKenna and Bell, 1997
Zaraalestes russelli Storch et Dashzeveg, 1997	Middle Eocene (I): China and Mongolia	
Ictopidium Zdansky, 1930	Terminal Middle Eocene (SM) to Late Eocene (E): China and Kazakhstan	Tong, 1997
Ictopidium lechei Zdansky, 1930		
Galericinae		
Protogalericius averianovi gen. et sp. nov.	Terminal Early Eocene (I): Kyrgyzstan	Original data
Eogalericius Lopatin, 2004	Middle Eocene (I): Mongolia	Lopatin, 2004c
Eogalericius butleri Lopatin, 2004		
Microgalericulus esuriens gen. et sp. nov.	Middle Eocene (I): Mongolia	Original data
Eochenus Wang et Li, 1990	Middle Eocene (I): China	Wang and Li, 1990
Eochenus sinensis Wang et Li, 1990		
“*Tupaiodon*” *huadianensis* Wang et Li, 1990	Middle Eocene (I): China	Wang and Li, 1990; Tong, 1997
DIDYMOCONIDA		
Didymoconidae		
Kennatheriinae subfam. nov.		
Zeuctherium Tang et Yan, 1976	Early Paleocene (SH): China	Tang and Yan, 1976
Zeuctherium niteles Tang et Yan, 1976		
Kennatherium Mellett et Szalay, 1968	Middle Eocene (I): China and Mongolia	Mellett and Szalay, 1968; original data
Kennatherium shirense Mellett et Szalay, 1968		
Erlikotherium edentatum gen. et sp. nov.	Middle Eocene (I): Mongolia	Original data
Ardynictinae		
Archaeoryctes Zheng, 1979	Late Paleocene (N, G): China, Mongolia; terminal Early Eocene (A): China	Zheng, 1979; Meng, 1990; Lopatin, 2001a
Archaeoryctes notialis Zheng, 1979	Late Paleocene (N): China	
Archaeoryctes euryalis Lopatin, 2001	Late Paleocene (G): Mongolia	
Archaeoryctes borealis Meng, 1990	Terminal Early Eocene (A): China	

Table 6. (Contd.)

Taxon	Occurrence	References
Wanolestes Huang et Zheng, 2002	Late Paleocene (G): China	Huang and Zheng, 2002; Lopatin, 2004a
Wanolestes lii Huang et Zheng, 2002		
Hunanictis Li, Chiu, Yan et Hsien, 1979	Early Eocene (B): China	Li et al., 1979; Gingerich, 1981
Hunanictis inexpectatus Li, Chiu, Yan et Hsien, 1979		
Jiajianictis Tong, 1997	Middle Eocene (I): China	Tong, 1997
Jiajianictis muricatus Tong, 1997		
Ardynictis Matthew et Granger, 1925	Middle Eocene (I): Mongolia, China; Late Eocene (E): Mongolia, eastern Kazakhstan	Matthew and Granger, 1925c; Gabounia and Chkhikvadze, 1997; Lopatin, 1997, 2003c; Tong, 1997
Ardynictis captor Lopatin, 2003	Middle Eocene (I): Mongolia	
Ardynictis zhaii Tong, 1997	Middle Eocene (I): China	
Mongoloryctes Van Valen, 1966	Middle Eocene (I): China	Matthew and Granger, 1925b; Van Valen, 1966
Mongoloryctes auctus (Matthew et Granger, 1925)		
Didymoconinae		
Khaichinula lupula gen et sp. nov.	Middle Eocene (I): Mongolia	Original data
LEPTICTIDA		
Leptictidae		
?Leptictidae gen. et sp. indet.	Late Paleocene (G): China	Meng et al., 1998
DIDELPHODONTA		
Cimolestidae		
Naranius Russell et Dashzeveg, 1986	Early Eocene (B): Mongolia	Russell and Dashzeveg, 1986
Naranius infrequens Russell et Dashzeveg, 1986		
Tsaganius Russell et Dashzeveg, 1986	Early Eocene (B): Mongolia	
Tsaganius ambiguus Russell et Dashzeveg, 1986		
Bagalestes trofimovi gen. et sp. nov.	Early Eocene (B): Mongolia	Original data
PALAEORYCTIDA		
Palaeoryctidae		
Pinoryctes collector gen. et sp. nov.	Late Paleocene (G): Mongolia	Original data
Nuryctes Tong, 2003	Terminal Early Eocene–Middle Eocene (I): Kyrgyzstan, Mongolia, China	Tong, 1997; Lopatin and Averianov, 2004b
Nuryctes alayensis Lopatin et Averianov, 2004	Terminal Early Eocene (I): Kyrgyzstan	
Nuryctes gobiensis Lopatin et Averianov, 2004	Middle Eocene (I): Mongolia	
Nuryctes qinlingensis (Tong, 1997)	Middle Eocene (I): China	
Palaeoryctidae gen. et sp. indet.	Terminal Early Eocene (I): Kyrgyzstan	Original data
PANTOLESTA		
Pantolestidae		
Zhigdenia nemegetica gen. et sp. nov.	Late Paleocene (G): Mongolia	Original data
Pantolestidae gen. et sp. indet.	Early Eocene (B): Mongolia	Russell and Dashzeveg, 1986

Micropternodontidae. The family Micropternodontidae comprises the North American genera *Micropternodus* (Late Eocene–Oligocene) and *Clinopternodus* (Late Eocene) and several Paleocene and Eocene Asian genera, the taxonomic position of which was considered uncertain for a long time. The genera *Carnilestes, Sarcodon, Prosarcodon, Metasarcodon*, and *Hyracolestes* were recently combined in the subfamily Sarcodontinae, while *Sinosinopa* and *Hsiangolestes* were assigned to the subfamily Micropternodontinae (Lopatin and Kondrashov, 2004).

Sarcodon pygmaeus was originally described from the terminal Paleocene of Mongolia (Matthew and Granger, 1925a) based on the only isolated M^1 from the Gashato locality. It was impossible for the authors to determine the taxonomic position of the new taxon and proposed it was a marsupial or a carnivore. Soon after that, Matthew, Granger, and Simpson (1929) described a skull fragment with its lower jaw from the same beds and named it *Opisthopsalis vetus* of uncertain taxonomic position.

Van Valen (1967) noted that *Sarcodon* is similar to *Micropternodus* and placed it in the family Micropternodontidae. Szalay and McKenna (1971) redescribed *Sarcodon pygmaeus* and studied the skull fragment of *Opisthopsalis vetus*, which was better prepared by that time, and showed that it is conspecific with *Sarcodon pygmaeus.* Thus, the lower jaw fragment containing a canine, P_4, M_1, alveoli of P_1–P_3, and M_2 were also assigned to *Sarcodon*. Szalay and McKenna also marked that *Sarcodon* is similar to *Micropternodus*, but concluded that this was a result of convergent development. They believed that *Sarcodon* and *Hyracolestes* of the same age belong to the family Deltatheridiidae. Szalay and McKenna defined the formula of the cheek teeth of *Sarcodon* as $P^4/_4$ $M^2/_2$.

Subsequently, *Sarcodon pygmaeus* was repeatedly recorded in Late Paleocene localities of Mongolia and China (Beliajeva et al., 1974; Reshetov, 1976; Zhou et al., 1976; Dashzeveg and McKenna, 1977; Chow and Qi, 1978; Li and Ting, 1983; Meng et al., 1998; Lopatin and Kondrashov, 2004). Meng et al. (1998) determined an upper jaw fragment with P^4 and M^1 and a lower jaw fragment without teeth from the Late Paleocene Bayan Ulan locality in Inner Mongolia (China) as *?Sarcodon pygmaeus.* This was based on a similar morphology and approximately identical dimensions. From the same locality, Meng et al. described a new species, *Sarcodon minor*, which was represented by an isolated M^1 and an upper jaw fragment with P^3 and P^4. This species is characterized by its very small size. Recently, Huang (2003) described from the Upper Paleocene of China (Jiashan, Anhui Province) a lower jaw fragment with the talonid of M_1 and complete M_2 of a new micropternodontid species named *Sarcodon? zhaii.* Certain doubt in the generic identification is caused by the narrower talonid of molars in the new species than in *S. pygmaeus.*

Hyracolestes ermineus was described by Matthew and Granger (1925a) and, for more than 75 years after its discovery, was regarded as a mysterious taxon of uncertain taxonomic position. During this time, the knowledge of its morphology remained almost the same. In the original description, *Hyracolestes* was characterized as a carnivore of approximately the same size as shrew and was tentatively assigned to Creodonta. Van Valen (1967) placed *Hyracolestes* along with *Sarcodon* in the family Micropternodontidae. Szalay and McKenna (1971) proposed that *Hyracolestes* belongs to a special lineage of Asian Palaeoryctoidea and assigned it to Deltatheridiidae. Qiu and Li (1977) determined *Hyracolestes* as Deltatheridia family indet. In subsequent studies (Russell and Dashzeveg, 1986; Russell and Zhai, 1987), the position of *Hyracolestes* was determined as family and order indet. Meng et al. (1998) regarded *Hyracolestes* as Insectivora incertae sedis and indicated that it is most similar morphologically to *Sarcodon*. As the genera *Sarcodon, Carnilestes, Prosarcodon*, and *Metasarcodon* were referred to the subfamily Sarcodontinae (Lopatin and Kondrashov, 2004), *Hyracolestes* was presumably included in this group.

The genus *Prosarcodon*, including the only species *P. lonanensis*, was established by McKenna et al. (1984) based on an incomplete skull with a lower jaw from the Lower Paleocene of Shaanxi Province (China). The cranial morphology allowed the authors to assign *Prosarcodon* to micropternodontid insectivores.

The second species of *Prosarcodon, P. maturus*, was recently described from the Lower Eocene of the Tsagan-Khushu locality in Mongolia (Lopatin and Kondrashov, 2004). This discovery enlarged the period of existence of this genus from the Early Paleocene to the Early Eocene.

Early Eocene *Hsiangolestes youngi* Zheng et Huang, 1984 from China was originally referred to the subfamily Wyolestinae of the family Didymoconidae (Zheng and Huang, 1984; Russell and Zhai, 1987), but was later transferred to Micropternodontidae (Ting and Li, 1987; Ting, 1998). McKenna and Bell (1997) placed *Hsiangolestes* in Wyolestinae, which was considered within the order Cimolesta. Like *Micropternodus, Hsiangolestes* has three upper molars (lower teeth have not been found).

Bogdia orientalis Dashzeveg et Russell, 1985 from the Middle Eocene of Mongolia was initially assigned to Pantolestidae (Dashzeveg and Russell, 1985, p. 872), and its taxonomic position has not been revised till now (see Dashzeveg and Russell, 1992; McKenna and Bell, 1997; Lucas, 2004). At the same time, as was indicated in the original description (Dashzeveg and Russell, 1985, p. 875), which was based on P^4, M^1, and alveoli of M^2 and M^3, a number of morphological characters of M^1 prevent the assignment of this species to the Pantolestidae; in particular, these characters include the high paracone and metacone which are fused at the base, the well-developed stout metastylar crest, continuous lingual cingulum, and very large hypoconal shelf with a small cusp. Based on these characters and the very poor knowledge of Early Paleogene Asian insectivores at that time, Russell and Dashzeveg assumed that *Bogdia* was an aberrant pantolestid that possibly represented a distinct Asian subfamily (which, however, was not formally established). To date, it is evident that all the listed "aberrant characters" of M^1 of *Bogdia* are characteristic of Asian micropternodontids; a continuous lingual cingulum was marked in *Hsiangolestes youngi* (Zheng and Huang, 1984) and *Prosarcodon maturus* (Lopatin and Kondrashov, 2004), the twinned labial cusps, stout metastylar crest, and large hypoconal shelf of the same structure are characteristic of all members of the family. Other structural characters of the upper teeth and jaw also agree with the assignment of this genus to Micropternodontidae, while the presence of M^3 and the hypoconal shelf on P^4 suggest that it should be included along with *Sinosinopa* and *Hsiangolestes* among the Asian representatives of Micropternodontinae.

Sinosinopa sinensis Qi, 1987 was described from the Arshanto Formation of Inner Mongolia (upper Lower Eocene, China) based on fragments of a skull and lower jaw with teeth (Qi, 1987). This genus was assigned to Micropternodontidae. *Sinosinopa* has three upper and lower molars on each side.

Early Paleocene *Carnilestes palaeoasiaticus* and *C. major* were described from China (Nanxiong Basin) as Lipotyphla incertae sedis based on fragments of the upper and lower jaws with complete tooth rows (Wang and Zhai, 1995). *Carnilestes* has the same formula of cheek teeth as *Sarcodon* and *Prosarcodon*, similar structure of molars and premolars, but its upper molars are less expanded transversely and their labial cusps are not fused at the base.

Averianov (1994a) described a new species, *Sarcodon udovichenkoi*, from the uppermost Lower Eocene of Kyrgyzstan, based on an isolated upper molar and a lower jaw fragment without teeth. Subsequently, *S. udovichenkoi* along with a new species, *Metasarcodon reshetovi*, from the Middle Eocene of Mongolia were placed in a new genus, *Metasarcodon* (Lopatin and Kondrashov, 2004). The Middle Eocene *Metasarcodon reshetovi* from Khaychin-Ula is the latest known member of the subfamily Sarcodontinae (Lopatin and Kondrashov, 2004).

Geolabididae. This extinct family of soricomorph insectivores was widespread in North America from the onset of the Eocene to the Early Miocene (Bown and Schankler, 1982; Korth, 1992). At present, it includes the North American genera *Batodon* (Late Cretaceous), *Centetodon* (Early Eocene–Early Miocene, Wasatchian–Arikareean), *Marsholestes* (Middle Eocene, Bridgerian), and *Batodonoides* (Early–Middle Eocene, Wasatchian–Uintan) (McKenna and Bell, 1997; Bloch et al., 1998) and Asian *Gobigeolabis* from the Upper Paleocene of Mongolia (Lopatin, 2004e).

When describing Early Eocene insectivores of Mongolia, Russell and Dashzeveg (1986) assumed that an animal designated "Lipotyphla indet." and represented by a maxillary fragment with molars from the Bumban Member of the Naran-Bulak Formation of the Tsagan-Khushu locality (Russell and Dashzeveg, 1986, text-fig. 6) might have belonged to Geolabididae. In my opinion, this specimen represents a member of Nyctitheriidae.

Recently, the first reliable Asian geolabidid assigned to a new genus and species, *Gobigeolabis verigranum*, from the Upper Paleocene Zhigden Member of the Naran-Bulak Formation of the Tsagan-Khushu locality was described (Lopatin, 2004e). It is completely characterized in Chapters 3 and 5.

Nyctitheriidae. The family Nyctitheriidae comprises primitive soricomorph insectivores, which are common in the Paleocene and Eocene of North America and Eurasia; in Europe, they persisted up to the Early Oligocene. For a long time, nyctitheriids were only known from the Paleogene of North America (Simpson, 1928; McKenna, 1968; Krishtalka, 1976b) and Western Europe (see Sigé, 1976). The first Asian nyctitheriids were found by Russell and Dashzeveg (1986), who described *Bumbanius rarus* and *Oedolius perexiguus* from the Lower Eocene of the Tsagan-Khushu locality in Mongolia. Subsequently, Averianov (1995) redescribed *Jarveia minuscula* from the Upper Paleocene of Kazakhstan (Dzhilga locality) as a nyctitheriid (in the original description, it was determined ?Palaeoryctidae, see Nessov, 1987). *Yuanqulestes qiui* from China (Shanxi Province, Yuanqu Basin) comes from the Zaili Member of the Hedi Formation dated to the end of the Middle Eocene–Late Eocene (Tong, 1997). *Bayanulanius tenuis* was described from the Upper Paleocene of the Bayan Ulan locality in Inner Mongolia, China (Meng et al., 1998); *Jarveia erronea* was described from the Upper Paleocene of Tsagan-Khushu (Kondrashov et al., 2004a); and *Eosoricodon terrigena* was described from the Lower Eocene of Tsagan-Khushu and assigned to a distinct subfamily, the Eosoricodontinae (Lopatin, 2005a). Recently, Missiaen and Smith (2005) described *Asionyctia guoi* from the Upper Paleocene of China (and proposed to regard the newly established *Asionyctia* as the type genus of the new Asian subfamily Asionyctiinae).

Thus, the study of Asian Nyctitheriidae lasts for about 20 years. However, in fact, the first data on Asian nyctitheriids were obtained half a century earlier. In 1929, *Praolestes nanus* from the Upper Paleocene Gashato Formation in Mongolia was described based on a lower jaw fragment and assigned with caution to Leptictidae (Matthew et al., 1929). Later, it was proposed to place *Praolestes* in Geolabidinae (Van Valen, 1967), Zalambdalestidae (Szalay and McKenna, 1971; Ting, 1998), Anagalida fam. indet. (Carroll, 1988), Leptictida incertae sedis (McKenna and Bell, 1997), or Insectivora indet. (Meng et al., 1998).

The finding of more complete specimens of *Praolestes nanus* in the Upper Paleocene Zhigden Member of the Naran-Bulak Formation of the Tsagan-Khushu and Naran-Bulak localities and the description of a new species, *P. maximus*, provided evidence for the assignment of *Praolestes* to Nyctitheriidae (Kondrashov et al., 2004a).

Thus, two Early Paleogene Asian genera of uncertain position, *Praolestes* and *Jarveia*, have been shown to belong to the family Nyctitheriidae. Another taxon of this kind is *Voltaia*. The genus *Voltaia* with the only species *V. minuta* from the Upper Paleocene of Kazakhstan (Dzhilga locality) was originally assigned to ?Palaeoryctidae (Nessov, 1987). McKenna and Bell (1997, p. 286) placed without comment *Voltaia* in the family Nyctitheriidae. Missiaen and Smith (2005) assigned this genus to the newly established subfamily Asionyctiinae. *Voltaia minuta* was described based only on the holotype, a well-preserved lower jaw fragment with teeth (Nessov, 1987). This specimen was additionally prepared and reexamined; the assignment of *Voltaia* to the subfamily Asionyctiinae of Nyctitheriidae was corroborated (see Chapters 3 and 5). In addition, a new nyctitheriid, *Edzenius lus* gen. et sp. nov., from the Lower Eocene of Mongolia is described in the present study (see Chapter 3).

Soricidae. The fossil record of the family Soricidae starts in the Middle Eocene of Asia (Irdinmanhan) and North America (Late Uintan). Until recently, the pre-Oligocene Soricidae have not been recorded in Asia. *Ernosorex jilinensis* from the Middle Eocene of China was originally assigned to Soricidae (Wang and Li, 1990), but subsequently transferred to the family Plesiosoricidae (McKenna and Bell, 1997). *Cretasorex arkhangelskyi* Nessov et Gureev, 1981 from Uzbekistan was originally dated Late Cretaceous (Nessov and Gureev, 1981); however, it is presently regarded as a Late Cenozoic member of Soricidae, the remains of which were transported in the Upper Cretaceous strata (Nessov et al., 1994; Nessov, 1997; Storch et al., 1998). The reexamination of the holotype of *C. arkhangelskyi* (TsNIGR Museum, no. 2/11758) suggests to assign this shrew to the tribe Soricini (Lopatin and Tesakov, 2004). This indirectly indicates that the age of this taxon is at most the Late Miocene.

Recently, I described the earliest shrew *Soricolestes soricavus* Lopatin, 2002 from the Middle Eocene of Mongolia. The lower molars of this animal are typical for Soricidae, but its dentition and ascending ramus of the lower jaw are very primitive (Lopatin, 2002c; see Chapters 3 and 5). *Soricolestes* is placed in a special subfamily, the Soricolestinae. It is presumably similar to the common ancestor of all Soricidae (Lopatin, 2002c).

Plesiosoricidae. This small family of soricomorph insectivores occurs in the Eocene–Miocene of Asia, the Oligocene–Miocene of Europe, and the Miocene of North America (McKenna and Bell, 1997). The earliest members are *Pakilestes lathrius* from the basal Middle Eocene of Pakistan (Russell and Gingerich, 1981; Gingerich, 2003) and *Ernosorex jilinensis* from the Middle Eocene of China (Wang and Li, 1990). *Pakilestes* is similar in dental structure to *Butselia biveri* Quinet et Misonne, 1965 from the Lower Oligocene of Europe (see Butler, 1972, 1988), while *Ernosorex* is similar to more typical plesiosoricids, mostly the Neogene genera *Plesiosorex* and *Meterix* with their somewhat erinaceoid molars. In the present study, an even earlier representative of Plesiosoricidae, *Ordolestes ordinatus* gen. et sp. nov., from the basal Eocene of Mongolia, is described; it demonstrates clear similarity to *Butselia* and *Pakilestes* and along with them assigned to the subfamily Butseliinae.

Apternodontidae is a group of zalambdodont soricomorph insectivores, which was widespread in North America from the Late Paleocene to the Early Oligocene. At present, four apternodontid genera are known from the Paleogene of North America: the Early Eocene *Parapternodus* and *Koniaryctes*, the Early Eocene–Early Oligocene *Oligoryctes*, and the Middle Eocene–Early Oligocene *Apternodus* (Matthew, 1903; Hough, 1956; Bown and Schankler, 1982; Stucky, 1992; McKenna and Bell, 1997; Robinson and Kron, 1998; Asher et al., 2002). In addition, remains of various Apternodontidae indet. were found in the Upper Paleocene and Eocene of North America (McKenna et al., 1962; Edinger, 1964; Jepsen and Woodburne, 1969; Sloan, 1969; West and Atkins, 1970; Galbreath, 1979; Rose, 1981; Savage and Russell, 1983; Emry, 1990; McKenna and Bell, 1997; Wood et al., 2000; Asher et al., 2002).

The first data on the Apternodontidae from the Paleogene of Asia were based on a zalambdodont insectivore found in the Eocene of the Khaychin Formation of the Khaychin-Ula 2 locality in Mongolia (collected in 1973 by YuGO SSMPE headed by V.Yu. Reshetov). M. McKenna (AMNH) assigned this insectivore to Apternodontinae and Tenrecoidea (a label written by him is preserved). Subsequently, this specimen was mentioned as Tenrecoidea gen. et sp. nov. (Badamgarav and Reshetov, 1985) or Apternodontidae indet. (Russell and Zhai, 1987; McKenna and Bell, 1997, p. 285) and, then, was described as the holotype of *Asiapternodus mackennai* (Lopatin, 2003b) (see Chapters 3 and 5).

From the Middle Eocene of China, Tong (1997) described several zalambdodont insectivores, including cf. *Apternodus* sp. (Apternodontidae), *Iconapternodus qii* Tong, 1997, cf. *Iconapternodus* sp. I and cf. *Iconapternodus* sp. 2 (?Apternodontidae). The first species undoubtedly belongs to apternodontids; however, its subfamilial and generic positions are not clear. The assignment of *Iconapternodus* to any group of zalambdodont insectivores or insectivore-like placentals is problematic. This taxon does not belong to the family Apternodontidae, but resembles Palaeoryctidae (see Lopatin, 2003b) and some Tenrecidae in the structure of the upper and lower molars.

Erinaceidae. The earliest Asian erinaceids are known from the Early Eocene Wutu Fauna (China), where they are represented by "Erinaceidae gen. et sp. nov. (cf. *Litolestes*)," *Changlelestes dissetiformis* Tong et Wang, 1993 (Changlelestinae), and "Changlelestidae gen. et sp. nov." (Tong and Wang, 1993, 1998). Judging from the structure of the dentition (Tong and Wang, 1998, pp. 34, 35), the last taxon belongs to Tupaiodontinae. The Middle Eocene of Central Asia has yielded *Zaraalestes russelli* Storch et Dashzeveg, 1997 (Tupaiodontinae), *"Tupaiodon" huadianensis* Wang et Li, 1990, *Eochenus sinensis* Wang et Li, 1990, and *Eogalericius butleri* Lopatin, 2004 (Galericinae) (Wang and Li, 1990; Storch and Dashzeveg, 1997; Lopatin, 2004c). In addition, two new taxa of Galericinae are described below, i.e., *Microgalericulus esuriens* gen. et sp. nov. from the Middle Eocene of Mongolia and *Protogalericius averianovi* gen. et sp. nov. from the uppermost Lower Eocene of Kyrgyzstan (see Chapter 3).

Didymoconidae. Didymoconids compose an endemic Paleogene Asian family of uncertain phylogenetic relationships, which was recently ranked as a separate order, Didymoconida, of the superorder Insectivora (Lopatin, 2001a). Based on the structure of the dentition, the Didymoconidae are divided into the subfamilies Didymoconinae and Ardynictinae (Lopatin, 1997, 2003c; Tong, 1997; Morlo and Nagel, 2002).

The earliest known member of this family is the Early Paleocene *Zeuctherium niteles* Tang et Yan, 1976 from the Shanghuanian of China (Tang and Yan, 1976), which was described on the basis of the only maxillary fragment. The Late Paleocene ardynictine *Archaeoryctes notialis* Zheng, 1979 from the Nongshanian of China and *A. euryalis* Lopatin, 2001 from the Gashatan of Mongolia are known better, the first was described based on upper and lower jaw fragments, while the second was represented by an almost complete skull without lower jaw (Zheng, 1979; Lopatin, 2001a).

A new insectivore genus and species, *Wanolestes lii*, from the Upper Paleocene of China was recently described; it was assigned to Soricomorpha and ?Micropternodontidae and considered to be similar to *Hyracolestes* (Huang and Zheng, 2002). It has a reduced paraconid and a high trigonid with twinned protoconid and metaconid on M_1 and M_2 and lacks a metaconid on P_4 and entoconid on M_1 and M_2. These characters suggest that *Wanolestes* is similar to *Archaeoryctes* and belongs to Didymoconidae rather than Micropternodontidae or Soricomorpha in general (see Zheng, 1979; Meng, 1990; Lopatin, 2001a, 2004a).

The ardynictine *Hunanictis inexpectatus* Li, Chiu, Yan et Hsien, 1979 from the Lower Eocene China (Hunan, Lingcha Formation) was described based on the anterior region of a skull with strongly damaged teeth (Li et al., 1979; Gingerich, 1981). In addition, a fragmentary skull of *Hunanictis* sp. (Meng et al., 1994a) was described from the Yuhuangding Formation dated the end of the Early Eocene–beginning of the Middle Eocene (Hubei, China).

Five genera and six species of the Didymoconidae are known from the upper Lower Eocene and the Middle Eocene (Arshantan and Irdinmanhan) of Central Asia: *Archaeoryctes borealis* Meng, 1990, *Mongoloryctes auctus* (Matthew et Granger, 1925), *Kennatherium shirense* Mellett et Szalay, 1968 (China, Inner Mongolia, Arshanto, Irdin Manha, and Ulan Shireh formations, respectively), *Jiajianictis muricatus* Tong, 1997, *Ardynictis zhaii* Tong, 1997 (China, Henan, Hetaoyuan Formation), *A. captor* Lopatin, 2003 (Mongolia, Khaychin-Ula 2 locality, Khaychin Formation). The majority of these taxa were described based on isolated finds of fragmentary specimens: *Archaeoryctes borealis* is represented by a lower jaw fragment with P_4 and poorly preserved molars (Meng, 1990); *Mongoloryctes* was based on an isolated M^1 (Matthew and Granger, 1925c); *Kennatherium*, on the posterior part of the lower jaw with a heavily worn M_1 (Mellett and Szalay, 1968); *Jiajianictis*, on a dentary fragment with teeth; and *Ardynictis zhaii*, on an isolated M_2 (Tong, 1997). Exception is *Ardynictis captor* from the Middle Eocene of Mongolia, which was originally described based on rather extensive material, including almost two dozen jaw fragments, several isolated teeth, and a fragmentary humerus (Lopatin, 2003c). In addition, the Khaychin Fauna yielded three representatives of Didymoconidae, including *Kennatherium shirense* and two new taxa, *Khaichinula lupula* gen. et sp. nov. and *Erlikotherium edentatum* gen. et sp. nov.

Leptictidae. The family Leptictidae was earlier assigned to insectivores or proteutherians, but then was placed in the order Leptictida of the superorder Insectivora (Novacek, 1986) or regarded as a distinct superorder (McKenna and Bell, 1997). This group was widespread in the Paleogene of North America and Europe. In Asia, leptictids are scarce. "?Leptictidae gen. et sp." were tentatively recorded in the Upper Paleocene of China (Meng et al., 1998, p. 162). A later representative of leptictids, *Ongghonia dashzevegi* was described from the Lower Oligocene of Mongolia (Kellner and McKenna, 1996).

Cimolestidae. The family Cimolestidae comprises primitive insectivore-like placentals recorded in the Late Cretaceous of North America and the Early Paleogene of North America, Eurasia, and North Africa. For a long time, they were regarded as a subfamily (named Didelphodontinae) of the family Deltatherididae or Palaeoryctidae in the broad sense. At present, the family Cimolestidae is assigned to the suborder Didelphodonta of the order Cimolesta of the superorder Ferae (McKenna and Bell, 1997; Kielan-Jaworowska et al., 2004). *Naranius infrequens* Russell et

Dashzeveg, 1986 and *Tsaganius ambiguus* Russell et Dashzeveg, 1986 were described from Asia. They are rather common in the Lower Eocene Bumban Member of the Naran-Bulak Formation of the Tsagan-Khushu locality in Mongolia (Russell and Dashzeveg, 1986; see Chapter 3). In addition, a new cimolestid, *Bagalestes trofimovi* gen. et sp. nov., from these beds is described below.

Palaeoryctidae. This Early Paleogene family of small primitive placentals of uncertain taxonomic position was assigned to Insectivora (Matthew, 1913; Gingerich, 1982; Thewissen and Gingerich, 1989; Tong, 1997; Bloch et al., 2004; Fox, 2004), Zalambdodonta (Vandebroek, 1961), Deltatheridia (Van Valen, 1966, 1967), Proteutheria (Romer, 1966; Butler, 1972; Kielan-Jaworowska, 1981; Bown and Schankler, 1982), Kennalestida (McKenna, 1975a), Leptictimorpha (Szalay, 1977), Soricomorpha (McKenna et al., 1984), Cimolesta (McKenna and Bell, 1997), or Eutheria incertae sedis (Scott et al., 2002).

Initially, the point of view that Palaeoryctidae belong to zalambdodont Insectivora prevailed (Matthew, 1913; Simpson, 1945). Subsequently, palaeoryctids were excluded from Zalambdodonta and even from Lipotyphla (McDowell, 1958; Butler, 1988), but were retained in the superorder Insectivora sensu Novacek, 1986, outside the orders Lipotyphla and Leptictida (Thewissen and Gingerich, 1989; MacPhee and Novacek, 1993; Bloch et al., 2004; Fox, 2004). The similarity in dental structure between *Palaeoryctes* and *Cimolestes* (see Butler, 1988) suggests that palaeoryctids possibly belong to Proteutheria or Cimolesta suborder indet. (McKenna and Bell, 1997). Averianov (2003) placed without comment Palaeoryctidae in the separate order Palaeoryctida, which along with Cimolesta was assigned to the superorder Carnivora. However, the dental structure of palaeoryctids suggests that they compose a special group of cimolestans; therefore, Palaeoryctida are considered here as a suborder of the order Cimolesta.

Earlier, Deltatheridiinae, Didelphodontinae, Micropternodontinae, and Asioryctinae were also included in Palaeoryctidae (see Van Valen, 1966, 1967; Kielan-Jaworowska, 1975, 1981; Fox, 1979, 1983); subsequently, they were excluded from this family for some reasons (Butler, 1972; Butler and Kielan-Jaworowska, 1973; Wilson, 1985; Thewissen and Gingerich, 1989; MacPhee and Novacek, 1993; Gunnell, 1994; McKenna and Bell, 1997). At the present state of knowledge, palaeoryctids (Palaeoryctinae sensu McKenna, 1975a; Thewissen and Gingerich, 1989; Bloch et al., 2004; Palaeoryctidae sensu Kellner and McKenna, 1996; McKenna and Bell, 1997; Fox, 2004; Lopatin and Averianov, 2004b) include six genera: *Palaeoryctes* (Paleocene of North America), *Aaptoryctes, Lainoryctes* (Late Paleocene–Early Eocene of North America and North Africa), *Eoryctes, Ottoryctes* (Early Eocene of North America), and *Nuryctes* (end of the Early Eocene–Middle Eocene of Asia).

The Asian *Nuryctes qinlingensis* (Tong, 1997) from the Middle Eocene of China was originally described under the generic name *Neoryctes*. However, this was a preoccupied name, *Neoryctes* Arrow, 1908 (Insecta, Coleoptera, Scarabaeidae) (Arrow, 1908, p. 342), subsequently replaced by the name *Nuryctes* (Tong, 2003). Two Eocene species of *Nuryctes* were recently described from Asia, i.e., *N. alayensis* Lopatin et Averianov, 2004 from the upper Lower Eocene of Kyrgyzstan (Andarak 2 locality) and *N. gobiensis* Lopatin et Averianov, 2004 from the Middle Eocene of Mongolia (Khaychin-Ula 2 locality) (Lopatin and Averianov, 2004b). *Pinoryctes collector* gen. et sp. nov. from the Upper Paleocene of Mongolia and Palaeoryctidae gen. et sp. indet. from of the uppermost Lower Eocene of Kyrgyzstan is described below.

Pantolestidae. This family was earlier assigned to Insectivora sensu lato; at present, it is placed in the suborder Pantolesta (along with Paroxyclaenidae and Ptolemaiidae) of the order Cimolesta (McKenna and Bell, 1997). It was widespread in the Paleogene of North America and Europe (Van Valen, 1967, 1978; Jaeger, 1970; Dorr, 1977; Gingerich, 1980; Koenigswald, 1980; Bown and Schankler, 1982; Krause and Gingerich, 1983; Mathis, 1989; McKenna and Bell, 1997; Smith R., 1997, 2001; etc.). Pantolestidae scarcely occur in Asia. Pantolestidae indet. are described from the Lower Eocene of Mongolia (Tsagan-Khushu locality, Bumban Member of the Naran-Bulak Formation: Russell and Dashzeveg, 1986) also were determined from the Middle Eocene of China (Irdin Manha: Russell and Zhai, 1987). It should be noted that, among specimens from the Bumban Member of the Tsagan-Khushu locality, Pantolestidae indet. are represented not only by the specimens described under this name (Russell and Dashzeveg, 1986, text-figs. 9a, 9g, 9h), but also the upper cheek tooth determined by Russell and Dashzeveg as M^1 of Nyctitheriidae gen. indet. (Ibid., fig. 9f), which is in fact DP^4 of Pantolestidae (see Mathis, 1989, text-fig. 13).

Later pantolestids are known from the Upper Eocene of eastern Kazakhstan, such as *Kiinkerishella zaisanica* (Gabunia and Biryukov, 1978) and the pantolestine *Oboia argillaceous* (Gabunia, 1989), and from the basal Oligocene of Mongolia, the dyspternine *Gobiopithecus khan* (Dashzeveg and Russell, 1992). *Kiinkerishella* was originally described as an arctocyonid condylarth (Gabunia and Biryukov, 1978) and subsequently placed in Paroxyclaenidae (Russell and Zhai, 1987; Russell and Godinot, 1988; McKenna and Bell, 1997); at present, it is assigned to the subfamily Dyspterninae of the family Pantolestidae (Dashzeveg and Russell, 1992; Lucas, 2004).

In the present study, a new pantolestine, *Zhigdenia nemegetica* gen. et sp. nov., from the Upper Paleocene

Zhigden Member of the Naran-Bulak Formation of the Tsagan-Khushu locality (Mongolia) is described.

Representatives of Lipotyphla, Didymoconidae, Cimolestidae, Palaeoryctidae, and Pantolestidae from the Upper Paleocene–Middle Eocene of Mongolia, the Upper Paleocene of Kazakhstan, and the uppermost Lower Eocene of Kyrgyzstan are described below.

CHAPTER 3. SYSTEMATIC PALEONTOLOGY

SUPERORDER INSECTIVORA BOWDICH, 1821

Insectivora: Bowdich, 1821, p. 24.

Diagnosis. Small carnivorous (zoophagous) epitherian mammals adapted for terrestrial, semiaquatic, or fossorial modes of life and feeding mostly on invertebrates. Head relatively large, neck short, body compact. Limbs short, usually pentadactyl, plantigrade or semidigitigrade, with claws.

In cranial structure: jugal bone reduced; maxilla and frontal coming in extensive contact in facial region and close position or contact between these bones within orbit; relatively short infraorbital canal; large common depression for sphenopalatine and dorsal palatine foramina; lacrimal lacking facial process; well-developed Glaserian fissure; distinct medial crest on promontory; large mastoid tubercle near lateral margin of promontory, including tympanohyal, with clear ventral fossa; and sharp sigmoid outlines of anterior margin of ventral surface of occipital condyle.

In dentition: presence of relatively low-crowned teeth with roots and moderately developed adaptation for vertical cutting. Dental formula, $I^{3-2}/_{3-0}C^{1}/_{1}P^{5-2}/_{5-1}M^{3-2}/_{3-2}$, usually with tendency toward reduction of last molars and teeth between increased anterior incisor or canine and last premolar. Cheek teeth tuberculosectorial, cuspidate. Upper molars diverse in structure, but always expanded considerably transversely, having elongated labial lobe and short lingual lobe, paracone, styles, and at least one pair of long, subtransversely or diagonally directed crests. Lower molars clearly divided into trigonid and talonid, with trigonid dominated by protoconid or twinned protoconid and metaconid and obligatory presence of paraconid located relatively lowly and sharp protocristid.

Composition. Three orders: Lipotyphla Haeckel, 1866, Upper Cretaceous–Recent, Northern Hemisphere, Africa, northern part of South America; Leptictida McKenna, 1975, Upper Cretaceous–Oligocene of the Northern Hemisphere; and Didymoconida Lopatin, 2001, Paleogene of Asia.

Comparison and remarks. The differences from other placentals in body, skeleton, and skull are evident from the diagnosis. Insectivores are similar in the structure of the dentition to some primitive members of the superorders Ferae (Cimolestidae, Palaeoryctidae, Pantolestidae, and Apatemyidae) and Archonta (Chiroptera, Dermoptera, and Primates); sometimes, it is impossible to distinguish with certainty isolated teeth and even jaw fragments of the groups listed. In general, the basic difficulties in the identification of Paleogene remains of insectivores and insectivore-like placentals can be overcome based on the following. The Cimolestidae (Cimolesta) are similar in the structure of upper molars to protodilambdodont insectivores (primitive Geolabididae and Nyctitheriidae), but differ from them in the absence of paracrista and, particularly clearly, in the structure of lower molars characterized by the high position of the paraconid and clearly detached talonid. The Palaeoryctidae (Cimolesta) resemble the Apternodontidae in the zalambdomorph morphology of their molars, but differ from them in the protozalambdomorph structural type (in particular, they preserve the metacone on the upper molars and a long talonid of the lower molars). Primitive Pantolestidae (Cimolesta), resembling in dental structure primitive Paleogene eudilambdodont insectivores (for example, Micropternodontidae and Nyctitheriidae) are distinguished by the presence of weakly developed styles, short metacrista, and massive hypocone on the upper molars and the paraconid positioned close to the metaconid on the lower molars; additional evidence for the assignment of fragmentary teeth and dentaries of insectivore-like mammals to Pantolestidae is the presence of the entoconulid and the position of the posterior mental foramen under M_1–M_2.

ORDER LIPOTYPHLA HAECKEL, 1866

Lipotyphla: Haeckel, 1866, p. 160.

Diagnosis. Insectivores characterized by absence or strong reduction of jugal bone (to insignificant element of zygomatic arch between processes of maxilla and squamosal, lacking contact with lacrimal) and presence of large orbital process of maxilla coming in contact with frontal inside orbit and preventing contact between palatine and lacrimal. Tympanic bulla absent or formed by petrosal and basisphenoid.

Dental formula, $I^{3-2}/_{3-1}C^{1}/_{1}P^{4-2}/_{4-1}M^{3-2}/_{3-2}$. Anterior incisors usually enlarged, canines frequently reduced. Lower molars characterized by well-developed paraconid with distinct paracristid and by presence of protoconid and metaconid considerably separated in upper part.

Composition. Three suborders: Soricomorpha Gregory, 1910, Upper Cretaceous–Recent, Northern Hemisphere, Africa, northern part of South America; Erinaceomorpha Gregory, 1910, Paleocene–Recent, Northern Hemisphere and Africa; Chrysochloridea Broom, 1915, Lower Miocene–Recent, Africa.

Comparison. Lipotyphla differ from Didymoconida in the structure of the tympanic bulla and external auditory meatus (in Didymoconida, the tympanic bulla completely ossified, formed by fused tympanic bones, while the walls of the external auditory meatus are formed by the squamosal and mastoid), the absence of a bony rostrum formed by the nasals and premaxillae, the weaker development of canines, and in the structure of the trigonid of lower molars (in Didymoconida, the protoconid and metaconid are twinned along almost the entire height, while the paraconid is considerably reduced). Lipotyphla are distinguished from Leptictida by the more reduced jugal bone (in Leptictida, it adjoins the lacrimal), the presence of contact between the maxilla and the frontal and the absence of contact between the palatine and the lacrimal inside the orbit, by the structure of the tympanic bulla (in Leptictida, it is formed by the expanded entotympanic bone), the parietal not participating in the formation of the occipital region, and the absence of a large suprameatal foramen of the squamosal (foramen suprameatus). Certain distinctions are also observed in the dental formula; Lipotyphla never display complete reduction of lower incisors (characteristic of some Didymoconidae, see below) and never have five premolars (in contrast to Cretaceous leptictids of the family Gypsonictopidae: see Lillegraven, 1969; Clemens, 1973; Novacek, 1977).

SUBORDER SORICOMORPHA GREGORY, 1910

Soricomorpha: Gregory, 1910, p. 465.

Diagnosis. Widely adapted insectivores. Orbits small, optic foramen small, infraorbital canal short, jugal bone usually absent, zygomatic arches narrow or absent, ectopterygoid processes of alisphenoid partially or completely reduced. Alisphenoid canal long, with nonossifying medial wall. Jugular foramen usually extending anteriorly in shape of fissure between mastoid process of petrosal and basioccipital. Mandibular condyle expanded. Dentition varying, including zalambdomorph types.

Composition. Two infraorders: Soricota Kalandadze et Rautian, 1992, Upper Cretaceous–Recent, Northern Hemisphere, Africa, northern part of South America; Tenrecomorpha Butler, 1972, Upper Eocene–Recent, Africa.

Comparison. Soricomorpha differ from Erinaceomorpha and Chrysochloridea in the greater range of adaptations (among erinaceids, there are no subterranean or semiaquatic forms, while among golden moles, there are no terrestrial or semiaquatic forms), the greater (or complete) reduction of the zygomatic arch, the structure of the jugular foramen, the shape of the mandibular condyle, and in the greater diversity of types of dental structure, including both dilambdomorphy (in contrast to golden moles) and zalambdomorphy (in contrast to erinaceomorphs). In addition, Soricomorpha differ from Erinaceomorpha in the structure of the alisphenoid canal, usual absence of the jugal bone and midcranial constriction, and from Chrysochloridea, in the absence of a rudimentary entotympanicum (see MacPhee and Novacek, 1993) and the position of the temporomandibular joint (in the Chrysochloridea, it is located posterodorsal to the external auditory meatus).

INFRAORDER SORICOTA
KALANDADZE ET RAUTIAN, 1992

Soricota: Kalandadze and Rautian, 1992, p. 55.

Solenodonta (partim): Kalandadze and Rautian, 1992, p. 54.

Diagnosis. Dilambdodont and zalambdodont soricomorph insectivores. Zygomatic arches present or absent. Postpalatine torus massive. Tympanic process of basisphenoid rudimentary or absent (except for Talpoidea, in which it contributes to formation of tympanic bulla). Piriform fenestra large. Deciduous tooth generation reduced or absent.

Composition. Five superfamilies: Micropternodontoidea Stirton et Rensberger, 1964, Paleocene–Middle Eocene of Asia, Upper Eocene–Oligocene of North America; Nesophontoidea Anthony, 1916, Upper Cretaceous, Eocene–Lower Miocene of North America, Upper Paleocene of Asia, Pleistocene–Holocene of the Antilles; Soricoidea Fischer von Waldheim, 1817, Paleocene–Recent, Northern Hemisphere, Africa, northern part of South America; Talpoidea Fischer von Waldheim, 1817, Middle Eocene–Recent, Northern Hemisphere; Solenodontoidea Gill, 1972, Eocene–Oligocene, North America and Asia, Pleistocene–Recent of the Antilles.

Comparison. Soricota differ from Tenrecomorpha in the absence or rudimentary character of the tympanic process of the basisphenoid (except for Talpoidea), the large piriform fenestra, well-developed postpalatine torus, reduced deciduous tooth generation, predominantly dilambdomorph structure of molars (except for Solenodontoidea), and in the presence of zygomatic arches in some representatives (Talpidae, Geolabididae, Nyctitheriidae, and Heterosoricinae).

SUPERFAMILY MICROPTERNODONTOIDEA
STIRTON ET RENSBERGER, 1964

Micropternodidae: Stirton and Rensberger, 1964, p. 59.

Micropternodontidae: Van Valen, 1965b, p. 636.

Micropternodontinae: Van Valen, 1966, p. 110.

Diagnosis. Small and medium-sized dilambdodont soricotan insectivores. Zygomatic arches absent. Dental formula, $I^3/_3C^1/_1P^4/_4M^{3-2}/_{3-2}$. Incisors small, $I^1/_1$ sometimes enlarged; canines large, of carnivorous type. Molars protodilambdomorph or eudilambdomorph, with carnassial specialization, i.e., long and strong metastylar crest and paracristid. Paracone and metacone usually twinned. P_4 semimolariform, with well-developed metaconid.

Composition. One family, Micropternodontidae Stirton et Rensberger, 1964, Paleocene–Middle Eocene of Asia, Upper Eocene–Oligocene of North America.

Comparison and remarks. Micropternodontidae are ranked here as a superfamily based on the significant differences from the other superfamilies of the infraorder Soricota (Nesophontoidea, Solenodontoidea, Soricoidea, and Talpoidea), which are primarily displayed in the prominent carnassial specialization of canines and molars. In addition, they differ from Solenodontoidea in the dilambdomorph structure of molars.

FAMILY MICROPTERNODONTIDAE STIRTON ET RENSBERGER, 1964

Micropternodidae: Stirton and Rensberger, 1964, p. 59.

Micropternodontidae: Van Valen, 1965b, p. 636.

Micropternodontinae: Van Valen, 1966, p. 110.

Type genus. *Micropternodus* Matthew, 1903, Upper Eocene–Upper Oligocene of North America.

Diagnosis. The same as in the superfamily Micropternodontoidea.

Composition. Two subfamilies: Sarcodontinae Lopatin et Kondrashov, 2004, Lower Paleocene–Middle Eocene of Asia; Micropternodontinae Stirton et Rensberger, 1964, Middle Eocene of Asia, Upper Eocene–Upper Oligocene of North America.

SUBFAMILY SARCODONTINAE LOPATIN ET KONDRASHOV, 2004

Sarcodontinae: Lopatin and Kondrashov, 2004, p. 178.

Type genus. *Sarcodon* Matthew et Granger, 1925, Upper Paleocene of Asia.

Diagnosis. Micropternodontids with following dental formula: $I^3/_3C^1/_1P^4/_4M^2/_2$. P^4 and M^2 without hypoconal shelf.

Generic composition. *Sarcodon* Matthew et Granger, 1925, Upper Paleocene (Gashatan) of Mongolia and China; *Carnilestes* Wang et Zhai, 1995, Lower Paleocene of China; *Prosarcodon* McKenna, Xue et Zhou, 1984, Lower Paleocene of China, Lower Eocene (Bumbanian) of Mongolia; *Hyracolestes* Matthew et Granger, 1925, Upper Paleocene (Gashatan) of Mongolia and China; *Metasarcodon* Lopatin et Kondrashov, 2004, uppermost Lower Eocene (Irdinmanhan) of Kyrgyzstan, Middle Eocene (Irdinmanhan) of Mongolia.

Comparison. Sarcodontinae differ from Micropternodontinae (composed of *Micropternodus* Matthew, 1903, *Clinopternodus* Clark, 1937, *Hsiangolestes* Zheng et Huang, 1984, *Bogdia* Dashzeveg et Russell, 1985, and *Sinosinopa* Qi, 1987) in the absence of $M^3/_3$ and a hypoconal shelf in P^4 and M^2.

Genus *Sarcodon* Matthew et Granger, 1925

Sarcodon: Matthew and Granger, 1925a, p. 11; Szalay and McKenna, 1971, p. 286; Lopatin and Kondrashov, 2004, p. 178.

Opisthopsalis: Matthew et al., 1929, p. 8.

Type species. *Sarcodon pygmaeus* Matthew et Granger, 1925, Upper Paleocene of Mongolia and China.

Diagnosis. Small sarcodontines with strongly transversely expanded upper molars. Protocone of P^3 well developed. M^1 with clear medial constriction subdividing crown into labial and lingual parts. Labial cusps twinned, metastylar lobe strongly projecting posterolabially, parastyle reduced, hypoconal shelf and hypocone large. M^1 and M^2 lacking precingulum, M_1 and M_2 lacking precingulid. Metaconid of P_4 small, talonid without longitudinal shearing crest. Trigonid of M_1 compressed longitudinally; talonid relatively long, with well-developed basin.

Species composition. *S. pygmaeus* Matthew et Granger, 1925, Upper Paleocene of Mongolia and China; *S. minor* Meng, Zhai et Wyss, 1998, *S. zhaii* Huang, 2003, Upper Paleocene of China.

Comparison. *Sarcodon* differs from *Prosarcodon* in the larger protocone of P^3, in the structural details of M^1 (the metastylar lobe projects more strongly posterolabially, the parastyle is reduced, the hypoconal shelf is better developed, and the hypocone is large), in the absence of precingulum on M^1 and M^2, the absence of precingulid on M_1 and M_2, and the absence of a shearing crest on the talonid of P_4. *Sarcodon* has wider upper molars than *Carnilestes* and differs from it in the twinned labial cusps of M^1 and M^2, the large hypoconal shelf, the strongly developed metastylar lobe, the reduced parastyle of M^1, and the absence of precingulum on M^1 and M^2 and precingulid on M_1 and M_2. *Sarcodon* differs from *Metasarcodon* in the more expanded, less massive M^1 with a well-pronounced medial constriction and less developed hypoconal shelf; the shorter trigonid of the lower teeth; and in the better developed talonid and the absence of a precingulid on M_1. *Sarcodon* differs from *Hyracolestes* in the smaller metaconid, the absence of a talonid crest on P_4, and in the larger talonid with a well-developed basin and a prominent entoconid on M_1.

Sarcodon pygmaeus Matthew et Granger, 1925

Plate 1, fig. 1

Sarcodon pygmaeus: Matthew and Granger, 1925a, p. 11, text-fig. 14; Szalay and McKenna, 1971, p. 288, text-figs. 4–13; Lopatin and Kondrashov, 2004, p. 178, text-figs. 1 and 2.

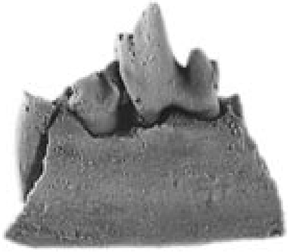
Opisthopsalis vetus: Matthew et al., 1929, p. 8, text-fig. 6.

Holotype. AMNH, no. 20427, left M^1; Mongolia, Gashato locality; Upper Paleocene, Gashato Formation.

Description (Fig. 5). The horizontal ramus of the lower jaw is relatively high and massive, with a curved lower margin. The angular process is relatively long, projects posteroventrally. The P_4 fragment preserved suggests that the talonid was short, narrow, unicuspid. Judging from the alveoli, M_1 is shorter than M_2.

The trigonid of M_2 is large and high, the talonid is almost as long as, but substantially narrower and lower than the trigonid. The paracristid is directed anterolingually, has a well-pronounced notch. The trigonid basin is narrow, relatively deep, open lingually. The protoconid is longitudinally compressed, fused with the metaconid at the base. The labial wall of the protoconid is strongly convex, while the lingual wall is very steep. The hypoflexid is deep, but narrow. The talonid basin is deep, narrow, open lingually. The hypoconid is massive, but lower than the hypoconulid. The cristid oblique is short, extends to the middle of the posterior wall base of the trigonid. The entoconid is small, elon-

Plate 1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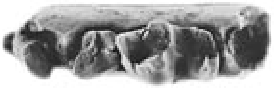
2c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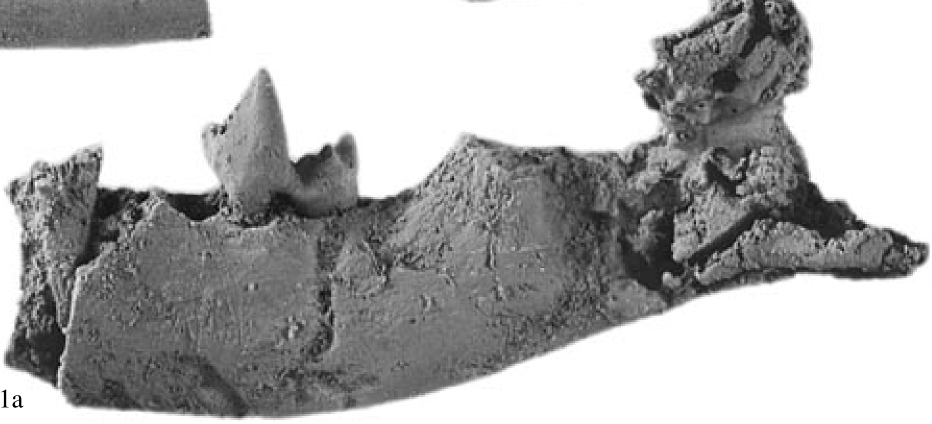
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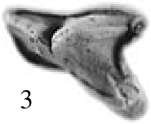
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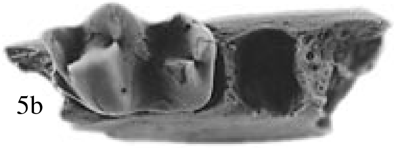
5a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6


7a


7b


8

gated, compressed transversely, positioned far from the metaconid, and is separated from the hypoconulid by a small valley. The hypoconulid is relatively large, high, conical, projects strongly posteriorly, is connected by a weak crest to the apex of the hypoconid.

Measurements, mm. Total length of M_2, 3.25; trigonid length, 1.75; trigonid width, 2.0; talonid width, 1.25; depth of the horizontal ramus of the lower jaw under M_1, 4.6; under M_2, 4.7 (specimen PIN, no. 3104/771).

Comparison. *Sarcodon pygmaeus* is approximately 30% larger than *S. minor* and differs from it in the better developed hypoconal shelf and better developed metastylar wing of M^1. It differs from *S. zhaii* in the wider talonid of M_1 and M_2.

Occurrence. Upper Paleocene (Gashatan) of Mongolia and China.

Material. Left dentary fragment with fragmentary P_4, alveoli of M_1 and complete M_2 (specimen PIN, no. 3104/771) from the Zhigden Member of the Naran-Bulak Formation of the Tsagan-Khushu locality.

Genus *Hyracolestes* Matthew et Granger, 1925

Hyracolestes: Matthew and Granger, 1925a, p. 10; Szalay and McKenna, 1971, p. 293; Lopatin and Kondrashov, 2004, p. 182.

Type species. *Hyracolestes ermineus* Matthew et Granger, 1925, Upper Paleocene of Mongolia and China.

Diagnosis. Small sarcodontines, with large metaconid and shearing talonid crest on P_4, and short paracristid, weak precingulid, considerably reduced entoconid, and small talonid basin on M_1.

Species composition. Type species.

Comparison. *Hyracolestes* differs from *Sarcodon* in the shearing talonid crest and the larger metaconid on P_4, and the short paracristid, more reduced entoconid, and less developed talonid basin on M_1. These characters of M_1 and the absence of a well-developed precingulid distinguish *Hyracolestes* from *Carnilestes, Prosarcodon*, and *Metasarcodon*.

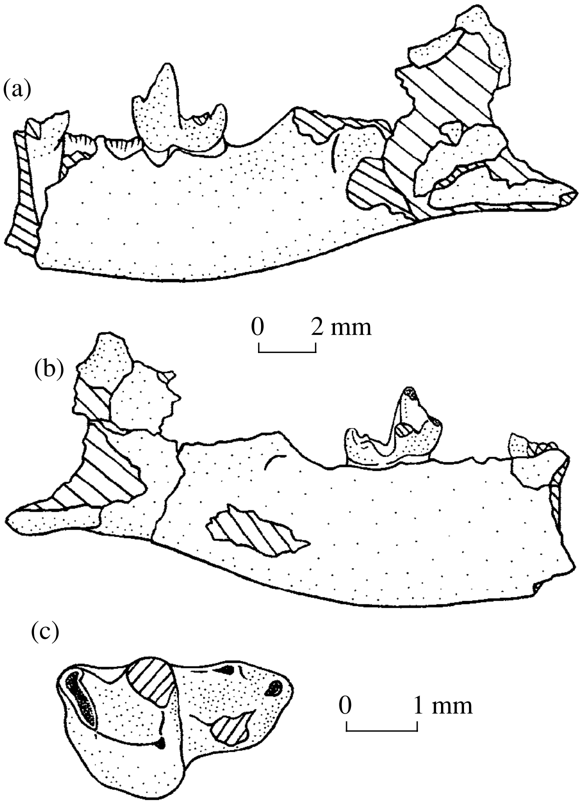


Fig. 5. *Sarcodon pygmaeus* Matthew et Granger, 1925, specimen PIN, no. 3104/771, left dentary fragment with fragmentary P_4, alveoli of M_1, and complete M_2: (a) labial and (b) lingual views and (c) M_2, occlusal view; Tsagan-Khushu locality, Mongolia; Zhigden Member, Naran-Bulak Formation, Upper Paleocene.

Hyracolestes ermineus Matthew et Granger, 1925

Plate 1, fig. 2

Hyracolestes ermineus: Matthew and Granger, 1925a, p. 10, text-fig. 13; Szalay and McKenna, 1971, p. 294, text-figs. 14–18; Qiu, Li, 1977, p. 98, pl. 1, fig. 3; Lopatin and Kondrashov, 2004, p. 182, text-figs. 7 and 8.

Hyracolestes sp., cf. *H. ermineus*: Meng et al., 1998, p. 161, text-fig. 6.

Explanation of Plate 1

Fig. 1. *Sarcodon pygmaeus* Matthew et Granger, 1925, specimen PIN, no. 3104/771, left dentary fragment with fragmentary P_4, alveoli of M_1, and complete M_2, ×6: (1a) labial and (1b) occlusal views; Mongolia, Tsagan-Khushu locality; Upper Paleocene, Naran-Bulak Formation, Zhigden Member.

Fig. 2. *Hyracolestes ermineus* Matthew et Granger, 1925: (2) specimen PIN, no. 3104/772, left dentary fragment with partially preserved P_4 and complete M_1: (2a) labial and (2b) occlusal views, ×6; (2c) talonid of P_4 and M_1, occlusal view, ×12; Mongolia, Tsagan-Khushu locality; Upper Paleocene, Naran-Bulak Formation, Zhigden Member.

Figs. 3–5. *Prosarcodon maturus* Lopatin et Kondrashov, 2004: (3) specimen PIN, no. 3104/777, right P^3, occlusal view, ×6; (4) holotype PIN, no. 3104/778, right M^1–M^2, occlusal view, ×6; (5) specimen PIN, no. 3104/782, left dentary fragment with M_1, ×6: (5a) labial and (5b) occlusal views; Mongolia, Tsagan-Khushu locality; Lower Eocene, Naran-Bulak Formation, Bumban Member.

Figs. 6 and 7. *Metasarcodon reshetovi* Lopatin et Kondrashov, 2004: (6) holotype PIN, no. 3107/401, left maxillary fragment with M^1 and alveoli of P^4, occlusal view, ×6; (7) specimen PIN, no. 3107/403, right M_1, ×6: (7a) labial and (7b) occlusal views; Mongolia, Khaychin-Ula 2 locality; Middle Eocene, Khaychin Formation.

Fig. 8. *Gobigeolabis verigranum* Lopatin, 2004, holotype PIN, no. 3104/776, right dentary fragment with P_4–M_2, labial view, ×12; Mongolia, Tsagan-Khushu locality; Upper Paleocene, Naran-Bulak Formation, Zhigden Member.

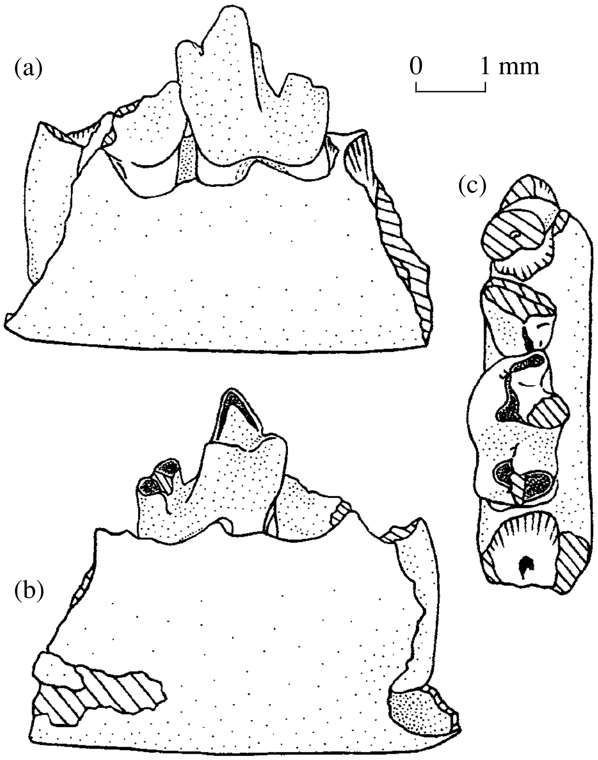


Fig. 6. *Hyracolestes ermineus* Matthew et Granger, 1925, specimen PIN, no. 3104/772, left dentary fragment with partially preserved P_4 and complete M_1: (a) labial, (b) lingual, and (c) occlusal views; Tsagan-Khushu locality, Mongolia; Zhigden Member, Naran-Bulak Formation, Upper Paleocene.

Holotype. AMNH, no. 20425, right dentary fragment with P_3–M_1, and alveoli of C_1, P_1, P_2, and M_2; Mongolia, Gashato locality; Upper Paleocene, Gashato Formation.

Description (Fig. 6). The horizontal ramus of the lower jaw is low, a little deeper than the crown height of M_1.

P_4 is slightly shorter in length than M_1. The talonid of P_4 is relatively small (but much better developed than that of P_3), trenchant, with a single small conical cusp at the posterior margin. The talonid crest reaches the base of the protoconid. The hypoflexid is relatively wide. The posterior wall of the talonid is straight.

The trigonid of M_1 is much longer and higher than the talonid. The paraconid is high. The paracristid is short, directed anterolingually. A deep paracristid notch is present. The trigonid basin is superficial, open lingually. The precingulid is a weak prominence in line with the paraconid, posterolabial to the anterior fold containing the end of the talonid of P_4. The protoconid and metaconid are positioned opposite to each other. The protoconid is a little larger than the metaconid, fused with it at the base for approximately two-thirds of the height. The protocristid notch is well-pronounced. The posterior wall of the trigonid is almost vertical. The talonid is narrow; the talonid basin is small, widely open lingually. The hypoflexid is relatively deep and narrow. The hypoconid is relatively large, massive, and high. The cristid oblique is short and low, its anterior portion ascends a little on the posterior wall of the trigonid under the protocristid notch. The hypoconulid is low, but very wide, positioned close to the posterolingual wall of the hypoconid. The entoconid is reduced, represented by an expansion of the posterolingual corner of the talonid.

Measurements, mm. Specimen PIN, no. 3104/772: length of P_4, ca. 2.2; talonid length, 0.55; talonid width, 0.9; total length of M_1, 2.3; trigonid length, 1.5; trigonid width, 1.35; talonid width, 1.15; depth of the horizontal ramus of the lower jaw under P_4, 3.0, and under M_1, 2.9.

Remarks. Russell and Dashzeveg (1986, p. 289, text-figs. 9d, 9e) assigned one lower molar ("M_1 or M_2") from the Lower Eocene Bumban Member of the Naran-Bulak Formation of the Tsagan-Khushu locality to cf. *Hyracolestes* sp. However, this molar is distinct from the lower teeth of *Hyracolestes* in the trigonid structure, the well-developed talonid basin, and the prominent entoconid; thus, it should not be assigned to this genus (Lopatin and Kondrashov, 2004). It is determined below as M_1 of *Ordolestes ordinatus* gen. et sp. nov. (Plesiosoricidae).

Occurrence. Upper Paleocene (Gashatan) of Mongolia and China.

Material. A left dentary fragment with partially preserved P_4 and complete M_1 (specimen PIN, no. 3104/772) from the Zhigden Member of the Naran-Bulak Formation of the Tsagan-Khushu locality.

Genus *Prosarcodon* McKenna, Xue et Zhou, 1984

Prosarcodon: McKenna et al., 1984, p. 4; Lopatin and Kondrashov, 2004, p. 179.

Type species. *Prosarcodon lonanensis* McKenna, Xue et Zhou, 1984, Lower Paleocene of China.

Diagnosis. Relatively small sarcodontines with moderately transversely expanded upper molars. Protocone of P^3 small. M^1 with clear medial constriction. Labial cusps twinned at base, metastylar lobe weakly projecting posterolabially, parastyle large, hypoconal shelf moderately developed, hypocone small. M^1 and M^2 having precingulum and M_1 and M_2 having precingulid. Metaconid of P_4 small, talonid with longitudinal shearing crest. Trigonid of M_1 compressed longitudinally; talonid relatively long, with well-developed basin.

Species composition. *P. lonanensis* McKenna, Xue et Zhou, 1984, Lower Paleocene of China; *P. maturus* Lopatin et Kondrashov, 2004, Lower Eocene of Mongolia.

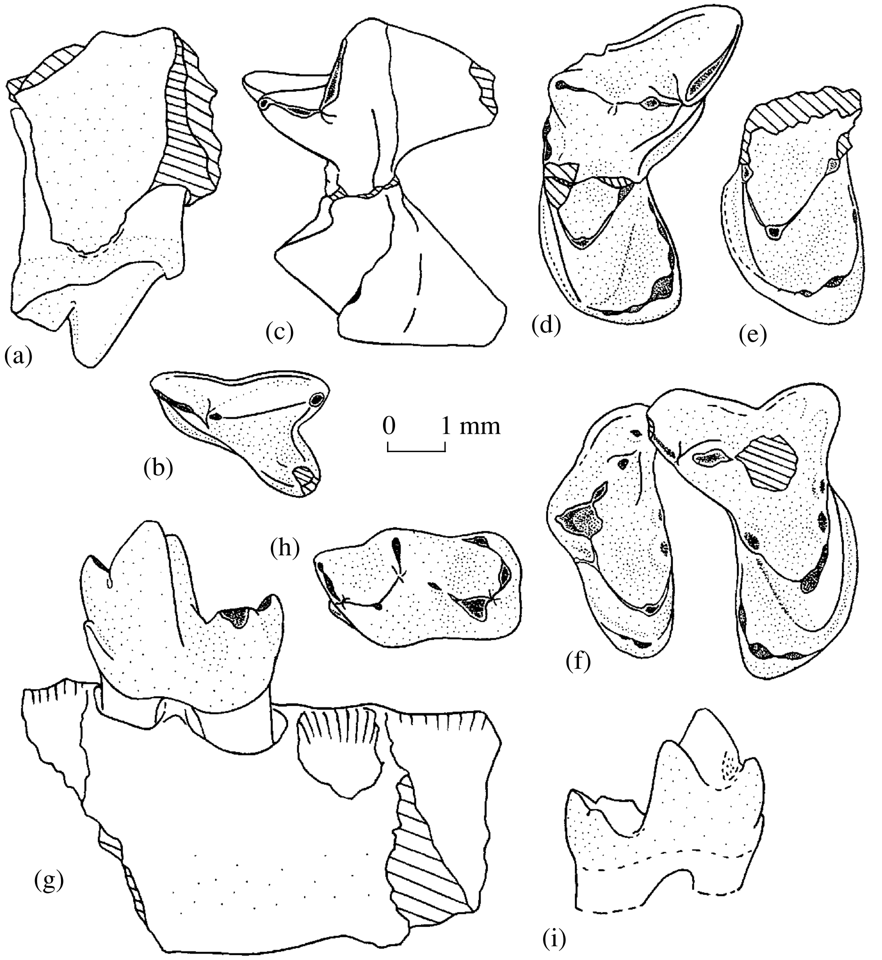


Fig. 7. *Prosarcodon maturus* Lopatin et Kondrashov, 2004: (a, b) specimen PIN, no. 3104/777, right P^3: (a) labial and (b) occlusal views; (c, d) specimen PIN, no. 3104/779, left M^1: (c) posterior and (d) occlusal views; (e) specimen PIN, no. 3104/780, fragmentary left M^1, occlusal view; (f) holotype PIN, no. 3104/778, M^1–M^2, occlusal view; (g–i) specimen PIN, no. 3104/782, left dentary fragment with M_1: (g) labial view, (h) M_1, occlusal view, and (i) M_1, lingual view; Tsagan-Khushu locality, Mongolia; Bumban Member, Naran-Bulak Formation, Lower Eocene.

Comparison. *Prosarcodon* differs from *Sarcodon* and *Metasarcodon* in the less developed hypoconal shelf, and in the well-developed precingulum and the large parastyle of M^1. It also differs from *Sarcodon* in the smaller protocone of P^3 and the presence of the precingulid on M_1 and M_2, and from *Metasarcodon* in the shorter trigonid of M_1 and less developed paracristid. It differs from *Carnilestes* in the greater transverse expansion of the upper molars, in the labial cusps fused at the base, the larger hypoconal shelf, and the larger metastylar lobe. It differs from *Hyracolestes* in the better developed talonid basin, larger entoconid, and stronger precingulid of M_1.

Prosarcodon maturus Lopatin et Kondrashov, 2004

Plate 1, figs. 3–5

Prosarcodon maturus: Lopatin and Kondrashov, 2004, p. 179, text-figs. 3 and 4.

Holotype. PIN, no. 3104/778, right maxillary fragment with M^1 and M^2; Mongolia, Tsagan-Khushu locality; Lower Eocene, Naran-Bulak Formation, Bumban Member.

Description (Fig. 7). P^3 is three-rooted, with strongly projecting parastyle, metastyle, and the protocone lobe. The labial side of the crown is slightly concave in the middle region. The parastyle is low, but distinct, projects far anteriorly, and is connected by a narrow crest to the apex of the paracone. The paracone is high, conical, separated from the metastylar wing by a deep carnassial notch. The metastylar wing projects posterolabially. The cusp of the metastyle is indistinct. The metastylar crest is strong, high, relatively long, about one-third of the labial crown length. The protocone lobe projects anterolingually. The protocone is small, but prominent, conical in shape. A narrow crest extends from the apex to the lingual base of the paracone. The cingula are well-developed. The ectocingu-

Table 7. Measurements of the upper cheek teeth in *Prosarcodon maturus* Lopatin et Kondrashov, 2004

Specimen PIN, no.	Tooth	Labial length	Lingual length	Posterior width
3104/777	P^3	3.1	–	2.2
3104/779	M^1	–	2.6	5.9
3104/780	M^1	–	2.5	–
3104/778 (holotype)	M^1	3.5	2.3	5.5
	M^2	2.9	1.6	4.6

Table 8. Measurements of M_1 of *Prosarcodon maturus* Lopatin et Kondrashov, 2004

Specimen PIN, no.	Total length	Trigonid length	Trigonid width	Talonid width
3104/782	3.8	2.0	2.25	2.0
3104/783	3.7	2.0	2.25	2.0
3104/798	4.0	2.3	2.5	2.1
3104/784	–	2.0	2.1	–

lum is relatively narrow, extends from the labial base of the parastyle to the metastyle. The precingulum is strong, extends from the parastyle to the protocone. The postcingulum is relatively broad at the level of the metastylar crest, becoming narrow and weak at the posterior base of the protocone lobe.

M^1 typical for sarcodontines, but has a well-developed parastylar wing, a relatively weakly developed hypoconal shelf, widely spaced labial cusps, and a relatively small metastylar wing. The parastylar lobe is rounded. The ectocingulum is narrow, extends from the parastyle to the labial base of the metastyle. The metastylar wing projects posterolabially, the metastylar crest is strong, but relatively low. The carnassial notch is well-developed, the cusp of the metastyle is indistinct. The paracone and metacone are conical, the first is slightly larger than the second. The notch between the paracone and metacone is relatively sharp and narrow, the opposite walls of the two cusps are positioned at an angle about 70°. The anterolabial slope of the paracone has a weak crest of the preparacrista, which ascends for three-fourths of the cusp height, terminating short of its apex. The centrocrista is narrow and sharp. The paraconule and metaconule are well-developed. The preparaconule crest is weak, extends to the parastyle. Weak, but distinct notches are seen between the lingual parts of conules and the labial margins of the preprotocrista and postprotocrista. The trigon basin is deep, expanded transversely. The protocone is strongly compressed longitudinally and has a pointed pyramidal apex. The precingulum originates at the base of the preparaconule crest and adjoins the hypoconal shelf at the anterolingual base of the protocone. The hypoconal shelf looks like a broad triangular lobe, its basin is relatively shallow. Posteriorly, in line with the metaconule, the hypoconal shelf is continued by a narrow postcingulum, which reaches the base of the metastylar wing in line with the carnassial notch. The hypocone is relatively large, displaced posterolingually. Some specimens have a supplementary cuspule anterolingual to the hypocone (Figs. 7d, 7e).

M^2 is substantially reduced. The parastylar lobe is large, projects labially. The cusp of the parastyle is indistinct. A small supplementary cusp is located in the center of the parastylar lobe. The metastylar wing is absent. The ectocingulum extends along the parastylar lobe and reaches the base of the anterolabial slope of the metacone. The paracone and metacone are conical, separated at the base, the paracone is approximately twice as massive as and twice as high as the metacone. A low paracrista extends from the supplementary cusp of the parastylar lobe to the apex of the paracone. The centrocrista is weak. The paraconule is large, located in the middle between the paracone and protocone, the preparaconule crest is well-developed. The metaconule is small, pyramidal. The premetaconule crest adjoins the lingual base of the metacone, the postmetaconule crest adjoins the posterolingual base of this cusp. A small cuspule is present at the point of contact between the postmetaconule crest and the metacone. The trigon basin is deep and narrow. The protocone is less compressed longitudinally than in M^1. The precingulum is narrow and weak. A hypoconal shelf, as such, is absent; however, the posterolingual wall of the protocone has a thickening connected to a short postcingulum.

M_1 is elongated, with a well-developed talonid. The paraconid is high. The paracristid short, blade-shaped, directed anterolingually. The paracristid and protocristid notches are well-pronounced. The protoconid and metaconid are widely spaced, the protoconid is more massive and higher than the metaconid. The apex of the metaconid is displaced slightly posteriorly in relation to the apex of the protoconid. The posterior wall of the trigonid is subvertical. The hypoflexid is relatively deep. The talonid is only slightly shorter and narrower than the trigonid. The hypoconid extends longitudinally, the cristid oblique adjoins the base of the metaconid and ascends to approximately midheight of the posterior wall of this cusp. The talonid basin is deep, open lingually. The entoconid is small, slightly elongated. The hypoconulid is relatively large, high, conical, projects slightly posteriorly, is connected by weak crests to the hypoconid and entoconid. A short, but strong precingulid is present in line with the paracristid notch.

Measurements, mm. Tables 7 and 8 show tooth measurements.

Comparison. *Prosarcodon maturus* differs from the type species in its larger size, less transverse expansion of the upper molars, in the anteriorly oblique protocone lobe of P^3, relatively smaller parastyle of M^1, smaller parastylar lobe of M^2, and in the lower trigonid of M_1.

Remarks. The differences between *Prosarcodon maturus* and *P. lonanensis* are rather significant. They are not regarded as generic characters because they primarily concern quantitative parameters, while important structural distinctions are absent.

Occurrence. Lower Eocene (Bumbanian) of Mongolia.

Material. In addition to the holotype, the type locality has yielded ten specimens housed in PIN: right maxillary fragment with P^3 (PIN, no. 3104/777), isolated left M^1 (PIN, no. 3104/779), fragments (lingual lobes) of M^1 (PIN, nos. 3104/780, 796) and M^2 (PIN, no. 3104/797), a fragment (metastylar lobe) of P^4 or M^1 (PIN, no. 3104/781), left dentary fragment with M_1 and alveoli of M_2 (PIN, no. 3104/782), three isolated M_1 (PIN, nos. 3104/783, 784, and 798).

Genus *Metasarcodon* Lopatin et Kondrashov, 2004

Metasarcodon: Lopatin and Kondrashov, 2004, p. 181.

Type species. *Metasarcodon reshetovi* Lopatin et Kondrashov, 2004, Middle Eocene of Mongolia.

Diagnosis. Large sarcodontines with massive M^1, slightly divided into labial and lingual lobes. Bases of paracone and metacone of M^1 fused, parastylar lobe considerably reduced, metastylar lobe large, hypoconal shelf well-developed, large, precingulum absent. Trigonid of M_1 large, elongated, paracristid strong, precingulid well-developed, talonid short, low.

Species composition. *M. reshetovi* Lopatin et Kondrashov, 2004, Middle Eocene of Mongolia; *M. udovichenkoi* (Averianov, 1994), uppermost Lower Eocene of Kyrgyzstan.

Comparison. *Metasarcodon* differs from *Sarcodon* and *Prosarcodon* in the more massive M^1, the labial and lingual lobes of which are less differentiated because of the poorly developed constriction in the middle region (lingual to the paracone and metacone, in line with the conules), and in the better developed hypoconal shelf of M^1. *Metasarcodon* differs from *Sarcodon* and *Hyracolestes* in the structure of its M_1, i.e., the more elongated paracristid and the presence of a massive precingulid. In addition, *Metasarcodon* differs from *Hyracolestes* in the well-developed entoconid and talonid basin of M_1. It is distinguished from *Prosarcodon* by the less developed parastyle and the absence of distinct precingulum on its M^1. The paracristid of M_1 of *Metasarcodon* is much stronger than in *Prosarcodon*. It differs from *Carnilestes* in the fused bases of the labial cusps, the larger hypoconal shelf and the larger metastylar lobe, in the reduced parastylar lobe and the absence of distinct precingulum on M^1, and in the larger trigonid, short talonid, and strong paracristid of M_1.

Metasarcodon udovichenkoi (Averianov, 1994)

Sarcodon udovichenkoi: Averianov, 1994a, p. 256, text-figs. 1 and 2.

Holotype. ZIN, no. 78969, isolated right M^1; Kyrgyzstan, Andarak 2 locality; uppermost Lower Eocene, lower part of the Alai Beds.

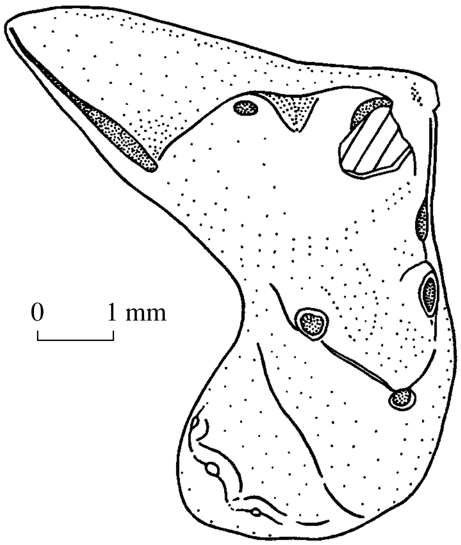


Fig. 8. *Metasarcodon udovichenkoi* (Averianov, 1994), holotype ZIN, no. 78969, right M^1, occlusal view; Andarak 2 locality, Kyrgyzstan; lower part of the Alai Beds, uppermost Lower Eocene.

Description (Fig. 8). M^1 is dissymmetrical, with a large, strongly projecting metastylar wing and a well-developed hypoconal shelf. The labial wall of the crown is almost straight. The ectocingulum is distinct. The parastyle is weak, reduced. The paracone and metacone are high, fused for three-fourths of their heights, the paracone is more massive than the metacone. The common base of the labial cusps is positioned apart from the external edge of the occlusal surface. The centrocrista is well-developed, the notch between the paracone and metacone is relatively shallow and wide. The metacone is compressed substantially transversely. The carnassial notch between the posterior slope of the metacone and the strong shearing metastylar crest is well-pronounced. The metastylar crest is very long, high, and steep. The precingulum is absent, but a very weak thickening is present at the base of the protocone in line with the notch between the paraconule and preprotocrista. The paraconule is relatively large, low, conical, oval in outline. The preparaconule crest is narrow. The metaconule is lower than the paraconule, but is also quite distinct. The trigon basin is relatively shallow. The protocone is massive. The postprotocrista is more massive than the preprotocrista. The hypoconal shelf extends strongly posterolingually. The basin of the hypoconal shelf is relatively deep and wide. The hypocone is well-developed, conical. In the holotype, the hypoconal shelf has two supplementary cuspules, one is located posterolabial to the hypocone apex, the second is anterolingual to it.

The horizontal ramus of the lower jaw curves substantially ventrally. The alveoli of P_4–M_2 are preserved; the posterior of them is long, which suggests that the talonid of M_2 was elongated. A distinct depression is observed in the dorsal part of the labial side of P_4 and M_1. The ventral margin of the coronoid region curves significantly dorsally. The masseteric fossa is moderately developed, the masseteric crest is sharp. The medial side of the coronoid process is slightly concave. The medial crest at the base of the coronoid process (bordering the attachment area for the profound portion of the temporal muscle) is well-developed, but relatively short. On the lingual side of the horizontal ramus, a distinct, moderately deep depression extends anteriorly from the coronoid region to P_4.

Measurements, mm. Holotype: labial length, 5.5; lingual length, 3.4; anterior width, 5.7; posterior width, 6.7.

Comparison. *Metasarcodon udovichenkoi* differs from *M. reshetovi* in the structure of M^1, i.e., in the less reduced parastyle, less widely spaced apices of the labial cusps (the angle between the crests of the centrocrista is about 45° versus 80° in *M. reshetovi*), the longer, higher, and steeper metastylar crest; and in the relatively large conules.

Occurrence. Uppermost Lower Eocene (Irdinmanhan) of Kyrgyzstan.

Material. In addition to the holotype, the collection of ZIN contains a right dentary fragment without teeth from the type locality (ZIN, no. 78970; collected by A.O. Averianov in 1993).

Metasarcodon reshetovi Lopatin et Kondrashov, 2004

Plate 1, figs. 6 and 7

Metasarcodon reshetovi: Lopatin and Kondrashov, 2004, p. 181, text-figs. 5 and 6.

Holotype. PIN, no. 3107/401, left maxillary fragment with M^1 and alveoli of P^4; Mongolia, Khaychin-Ula 2 locality; Middle Eocene, Khaychin Formation.

Description (Fig. 9). Judging from the alveoli, the crown of P^4 is T-shaped, longer and substantially narrower than the crown of M^1. The spaced between the upper teeth contain well-pronounced, deep, vascularized pits.

M^1 is massive, with a large, strongly projecting metastylar wing and a distinct hypoconal shelf. The labial wall of the crown is poorly concave in the central part. The ectocingulum is well-developed. The parastyle is very small. The paracone and metacone are high, pointed, twinned (fused for two-thirds of their height). The paracone is conical, slightly higher than the metacone. The centrocrista is weak and short. The notch between the paracone and metacone is deep and narrow. The metacone is somewhat shorter than the paracone, slightly compressed transversely. A well-developed carnassial notch is located between the posterior slope of the metacone and strong shearing metastylar crest. The precingulum is absent, but a weak thickening is observed at the base of the protocone in line with the preprotocrista. The paraconule is relatively large, low, triangular in outline. The preparaconule crest is narrow, connected to the parastyle. The metaconule is very weak, much lower than the paraconule. The trigon basin is shallow. The protocone is large and high. The preprotocrista reaches the lingual side of the paraconule. The postprotocrista is less developed than the preprotocrista. The hypoconal shelf projects strongly posterolingually. The basin of the hypoconal shelf is relatively wide and deep. The hypocone is well-developed, conical, half as long as the protocone. Specimen PIN, no. 3107/395 has three supplementary cuspules of the hypoconal shelf; two are located labial to the hypocone apex, while one is lingual to it. The holotype lacks a supplementary lingual cuspule on the hypoconal shelf, while the labial cuspules are worn and connected by a weak crest.

It is noteworthy that, in the holotype, the considerably worn protocone and conules are combined with relatively slightly worn apices of the paracone, metacone, and hypocone and metastylar crest.

M_1 is elongated, with a large trigonid and a short and low talonid. The paraconid is high. The paracristid is strong, blade-shaped, curved anterolabially, and has a large notch. In a worn tooth (specimen PIN, no. 3107/402), the anterolabial wall of the trigonid has a large, crescentic wear facet below the paracristid. It descends from the paracristid notch for a half height of the trigonid. The entire surface of the facet is covered with distinct vertical microscratches formed as a result of contact with the metastylar wing of P^4. The precingulid is strong, extends from the line of the paracristid notch to the anterior wall of the paraconid and terminates in a thickening. The trigonid basin is relatively deep, open widely lingually. The protoconid is substantially larger and higher than the metaconid; both cusp are relatively sharp. The protoconid is displaced slightly anteriorly. The protoconid has an apical wear facet, while the wear facet of the metaconid descends on its posterior wall. A well-developed protocristid notch is present. The posterior wall of the trigonid is vertical. The talonid is narrower than the trigonid, the hypoflexid is relatively deep and wide. The talonid has three well-developed cusps, separated by shallow, but distinct grooves. The largest cusp is the hypoconid; its base is widened and projects posterolabially. The cristid oblique is short and low, extends to the middle of the posterior wall of the trigonid in line with the protocristid notch. The entoconid is low, occupies the posterolingual region of the talonid. The hypoconulid is larger than the entoconid, projects slightly posteriorly. The talonid basin is deep and elongated, open widely lingually. The roots of M_1 are long, curved posteriorly; the posterior root is somewhat larger than the anterior root.

Measurements, mm. Labial length of M^1, 5.0; lingual length, 3.35; anterior width, 5.75; posterior width, 6.0 (holotype); lingual length of M^1 (specimen PIN, no. 3107/395), 3.7.

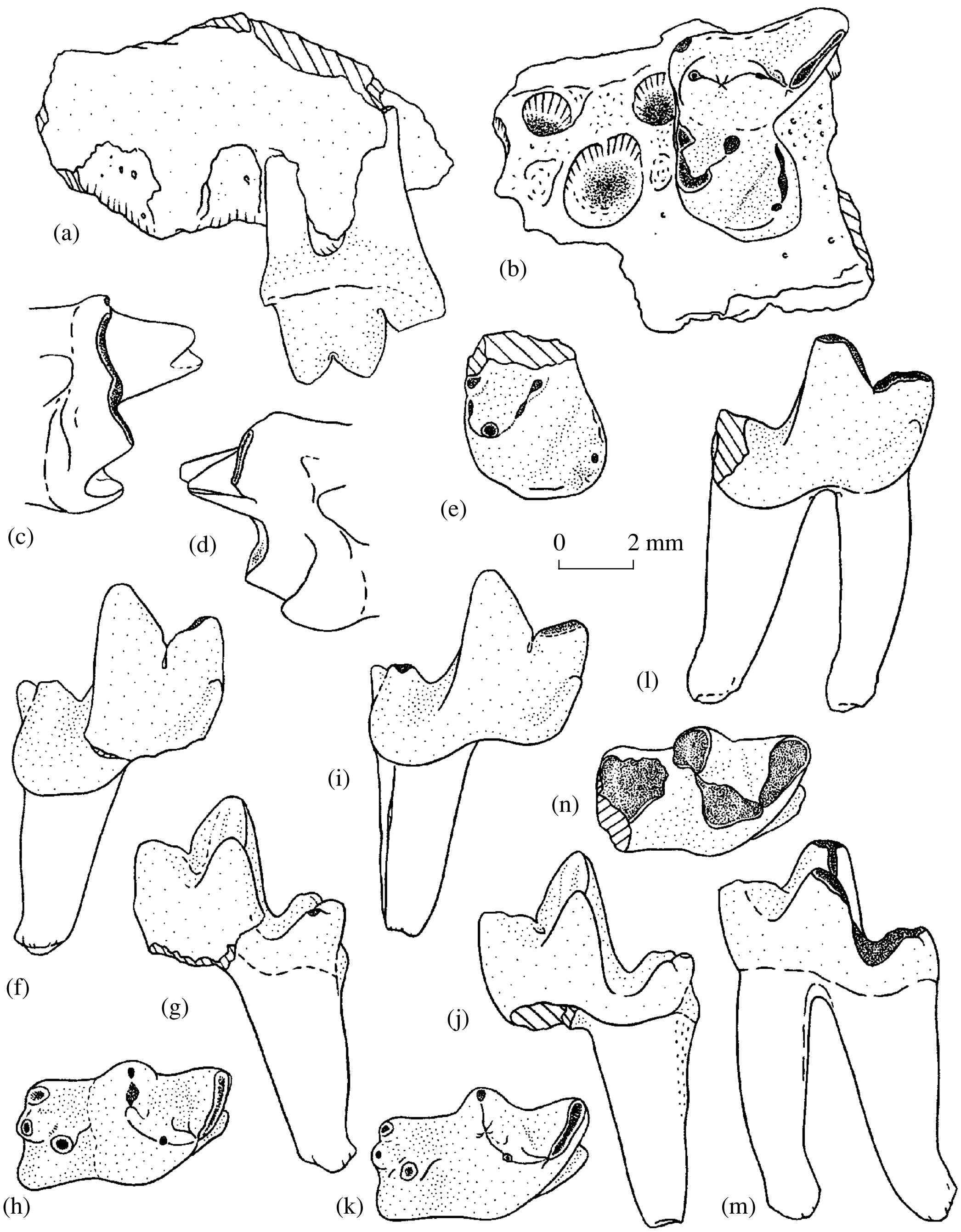


Fig. 9. *Metasarcodon reshetovi* Lopatin et Kondrashov, 2004: (a–d) holotype PIN, no. 3107/401, left maxillary fragment with M^1 and alveoli of P^4: (a) labial and (b) occlusal views, (c) M^1, anterior view, and (d) M^1, posterior view; (e) specimen PIN, no. 3107/395, fragmentary left M^1, occlusal view; (f–h) specimen PIN, no. 3107/404, right M_1: (f) labial, (g) lingual, and (h) occlusal views; (i–k) specimen PIN, no. 3107/403, right M_1: (i) labial, (j) lingual, and (k) occlusal views; (l–n) specimen PIN, no. 3107/402, right M_1: (l) labial, (m) lingual, and (n) occlusal views; Khaychin-Ula 2 locality, Mongolia; Khaychin Formation, Middle Eocene.

Measurements of M_1 crowns are shown in Table 9. Depth of the anterior root of M_1, 6.5 (specimen PIN, no. 3107/402); depth of the posterior root: 5.2 (specimen PIN, no. 3107/403), 5.4 (specimen PIN, no. 3107/404), 6.0 (specimen PIN, no. 3107/402).

Comparison. *Metasarcodon reshetovi* differs from *M. udovichenkoi* in the structure of M^1, i.e., in the more reduced parastyle, more widely spaced apices of the labial cusps (the angle between the crests of the centrocrista is about 80° versus 45° in *M. udovichenkoi*),

Table 9. Measurements of M_1 of *Metasarcodon reshetovi* Lopatin et Kondrashov, 2004

Specimen PIN, no.	Total length	Trigonid length	Trigonid width	Talonid width
3104/402	6.0	3.7	3.5	2.7
3104/403	5.9	3.5	3.5	2.8
3104/404	6.1	3.7	3.4	2.9

the shorter, lower, and less steep metastylar crest, and in the relatively small conules.

Occurrence. Middle Eocene (Irdinmanhan) of Mongolia.

Material. In addition to the holotype, the collection of PIN contains four isolated teeth from the type locality: a fragmentary left M^1 (PIN, no. 3107/395) and three right M_1 (PIN, nos. 3107/402, 403, and 404).

SUPERFAMILY NESOPHONTOIDEA ANTHONY, 1916

Nesophontidae: Anthony, 1916, p. 728.

Nesophontoidea: Saban, 1954, p. 428.

Diagnosis. Small and very small dilambdodont soricotan insectivores. Dental formula $I^3/_3C^1/_1P^{4-3}/_{4-3}M^3/_3$. I^1 slightly increased. $C^1/_1$ medium-sized. P^4 semimolariform, usually without metacone (rudimentary metacone present only in *Batodon*). Molars protodilambdomorph, eudilambdomorph, or metadilambdomorph. Upper molars with well-developed styles, conules reduced or absent, postcingulum or hypoconal shelf present. Lower incisors small, lower premolars usually double-rooted (except for P_1 of *Batodon* and *Batodonoides vanhouteni*). P_3 smaller than P_2. P_4 semimolariform, semimolarized or partially molarized, with trenchant talonid. Hypoconulid of lower molars displaced lingually, positioned close to, or fused with entoconid.

Composition. Two families: Geolabididae McKenna, 1960, Upper Cretaceous, Lower Eocene–Lower Miocene of North America, Upper Paleocene of Asia; Nesophontidae Anthony, 1916, Pleistocene–Holocene of the Antilles.

Comparison. The Nesophontoidea differ from the Solenodontoidea in the dilambdomorph molars; from Micropternodontoidea in the nonreduced dental formula of molars, the absence of predatory specialization in canines or molars, and structural characters of upper and lower molars listed in the diagnosis. The Nesophontoidea differ from the Soricoidea and Talpoidea in the absence of ectodilambdomorphy, relatively small incisors, predominant reduction of P_3 (rather than P_2), obligatory semimolariform $P^4/_4$, and relatively weakly developed hypoconal shelf of the upper molars.

FAMILY GEOLABIDIDAE MCKENNA, 1960

Metacodontidae: Butler, 1948, p. 491.

Geolabidinae: McKenna, 1960, p. 134.

Geolabididae: Butler, 1972, p. 261.

Type genus. *Centetodon* Marsh, 1872 (= *Geolabis* Cope, 1884), Lower Eocene–Lower Miocene of North America.

Diagnosis. Small nesophontoid insectivores. Zygomatic arches present. Dental formula, $I^3/_3C^1/_1P^4/_4M^3/_3$. $P^1/_1$ present. P^4 with very high paracone. Molars of protodilambdomorph or eudilambdomorph type. Upper molars strongly widened, with closely positioned paracone and metacone, reduced conules, and well-developed postcingulum (hypoconal shelf). Late representatives showing tendency to bifurcation of lingual root of upper molars. P_4 semimolarized, with conical paraconid, large protoconid, large metaconid, and simplified narrow trenchant talonid having small lingual basin. Lower molars with high, closely positioned cusps of trigonid and low cusps of talonid; hypoconulid frequently fused with entoconid.

Generic composition. *Batodon* Marsh, 1892, Upper Cretaceous (Maastrichtian) of North America; *Gobigeolabis* Lopatin, 2004, Upper Paleocene (Gashatan) of Mongolia; *Centetodon* Marsh, 1872 (= *Embassis* Cope, 1873; *Geolabis* Cope, 1884; *Protictops* Peterson, 1934; *Metacodon* Clark, 1936; *Hypacodon* McKenna, 1960), Lower Eocene–Lower Miocene (Wasatchian–Arikareean) of North America; *Marsholestes* McKenna et Haase, 1992, Middle Eocene (Bridgerian) of North America; *Batodonoides* Novacek, 1976, Lower–Middle Eocene (Wasatchian–Uintan) of North America.

Comparison and remarks. The Geolabididae differ from the Nesophontidae in the presence of zygomatic arches, the type of molar structure (in Nesophontidae, they are metadilambdomorph), the presence of $P^1/_1$, more widened upper molars with closely positioned labial cusps, better developed postcingulum, bifurcating lingual root (in post-Early Eocene taxa), the presence of the metaconid and narrow talonid of P_4, closely positioned cusps of the trigonid, and frequent fusion between the hypoconulid and the entoconid on the lower molars. As compared to other Paleogene families of Soricomorpha, the Geolabididae differ from the Apternodontidae in the dilambdomorph molars; from the Micropternodontidae, in the absence of predatory specialization of canines and molars; from the Nyctitheriidae, Plesiosoricidae, Soricidae, Proscalopidae, Dimylidae, and Talpidae, in the twinned labial cusps of the upper molars and the twinned protoconid and metaconid of the lower molars; from the Soricidae, Proscalopidae, and Talpidae, in the nonreduced premolars, the absence of metacone of P^4, and in the semimolariform P_4.

The replacement of the family name Metacodontidae Butler, 1948 by Geolabididae McKenna, 1960 in connection with the synonymy of the type genus is valid, because it was performed before 1961 (ICZN, article 40.2).

Genus *Gobigeolabis* Lopatin, 2004

Gobigeolabis: Lopatin, 2004e, p. 82.

Type species. *Gobigeolabis verigranum* Lopatin, 2004, Upper Paleocene of Mongolia.

Diagnosis. P^3–M^2 short and broad, with considerably projecting lingual lobe. In M^1 and M^2, postcingulum narrow, hypoconal shelf and additional lingual root absent, conules considerably reduced. Stylar shelf of M^2 relatively narrow, parastylar wing small, supplementary stylar cuspules absent, ectoflexus shallow. In P_4, metaconid well-developed; talonid elongated, narrow, unicuspid, lingual talonid basin very small. Trigonid of M_1 and M_2 short, protoconid and metaconid equal in high, entoconid small and low; hypoconulid completely fused with entoconid, entocristid and ectocingulid absent.

Species composition. Type species.

Comparison. *Gobigeolabis* differs from *Centetodon* in all the characters listed in the diagnosis concerning the upper teeth and the talonids of the lower molars, and in the structure of the talonid of P_4. It differs from *Batodon* in the better developed lingual lobe of P^3 and P^4, the absence of a rudimentary metacone on P^4, the narrower stylar shelf of the upper molars, the large metaconid of P_4, in the equal heights of the protoconid and metaconid of M_1 and M_2, and in the reduced hypoconulid of M_1 and M_2. It differs from *Batodonoides* in the better developed lingual lobe of P^3 and P^4, the presence of the metaconule, the reduced paraconule, the narrow stylar shelf, the absence of supplementary stylar cuspules and paraconule crests, the less developed cingula on the upper molars, the small parastylar wing and shallow ectoflexus of M^2, and in the absence of ectocingulid and the shorter trigonids of M_1 and M_2. The distinctions from *Marsholestes* are the reduced entoconid, reduced hypoconulid, and the absence of an entocristid on M_1 and M_2.

Gobigeolabis verigranum Lopatin, 2004

Plate 1, fig. 8

Gobigeolabis verigranum: Lopatin, 2004e, p. 83, text-figs. 1–3.

Holotype. PIN, no. 3104/776, right dentary fragment with P_4–M_2; Mongolia, Tsagan-Khushu locality; Upper Paleocene, Naran-Bulak Formation, Zhigden Member.

Description (Figs. 10, 11). Very small insectivores approaching in size the smallest Soricidae.

P^3 is small, three-rooted. The parastyle is small, low, round. The paracone is relatively high and massive. The postcrista is short and sharp. The metastyle is poorly pronounced. The ectocingulum is hardly discernible and seen only at the level of the postcrista. The protocone lobe projects strongly lingually and is oblique anteriorly. The protocone cusp is low, pointed. The precingulum is absent, the postcingulum is very narrow, extends along the posterior side of the crown from the protocone to the metastyle.

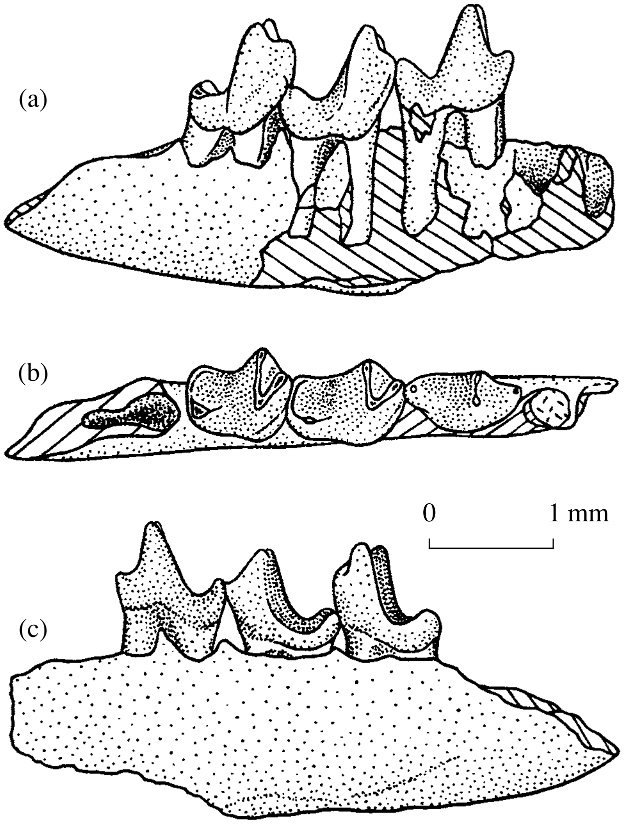


Fig. 10. *Gobigeolabis verigranum* Lopatin, 2004, holotype PIN, no. 3104/776, right dentary fragment with P_4–M_2: (a) labial, (b) occlusal, and (c) lingual views; Tsagan-Khushu locality, Mongolia; Zhigden Member, Naran-Bulak Formation, Upper Paleocene.

P^4 is relatively large, three-rooted. The parastyle is well-developed, conical, projects strongly anteriorly, and has a pointed apex. A short, but distinct parastylar crest connecting the apex of the parastyle to the anterior base of the paracone is present. The paracone is very high, massive at the base and narrow at the apex. The postcrista is very steep, strong, blade-shaped, twice as long as the metacrista of molars (Figs. 11d–11g). The metastyle is small, weakly differentiated. The ectocingulum is poorly pronounced. The protocone is large, broad, relatively short, projects strongly lingually. The apex of the protocone is significantly elevated, the preprotocrista and postprotocrista are positioned at an acute angle. The precingulum is absent. The postcingulum is relatively broad, has a distinct projection (without an eminence) in the hypocone region.

The upper molars are three-rooted. M^1 and M^2 are strongly widened. M^1 is heavily damaged, only the lingual lobe is preserved. The conules are weak. The protocone is larger than that of P^4, while the angle between the preprotocrista and postprotocrista is greater. The cingula anterior and posterior to the protocone are well-developed: the precingulum is narrow, the postcingu-

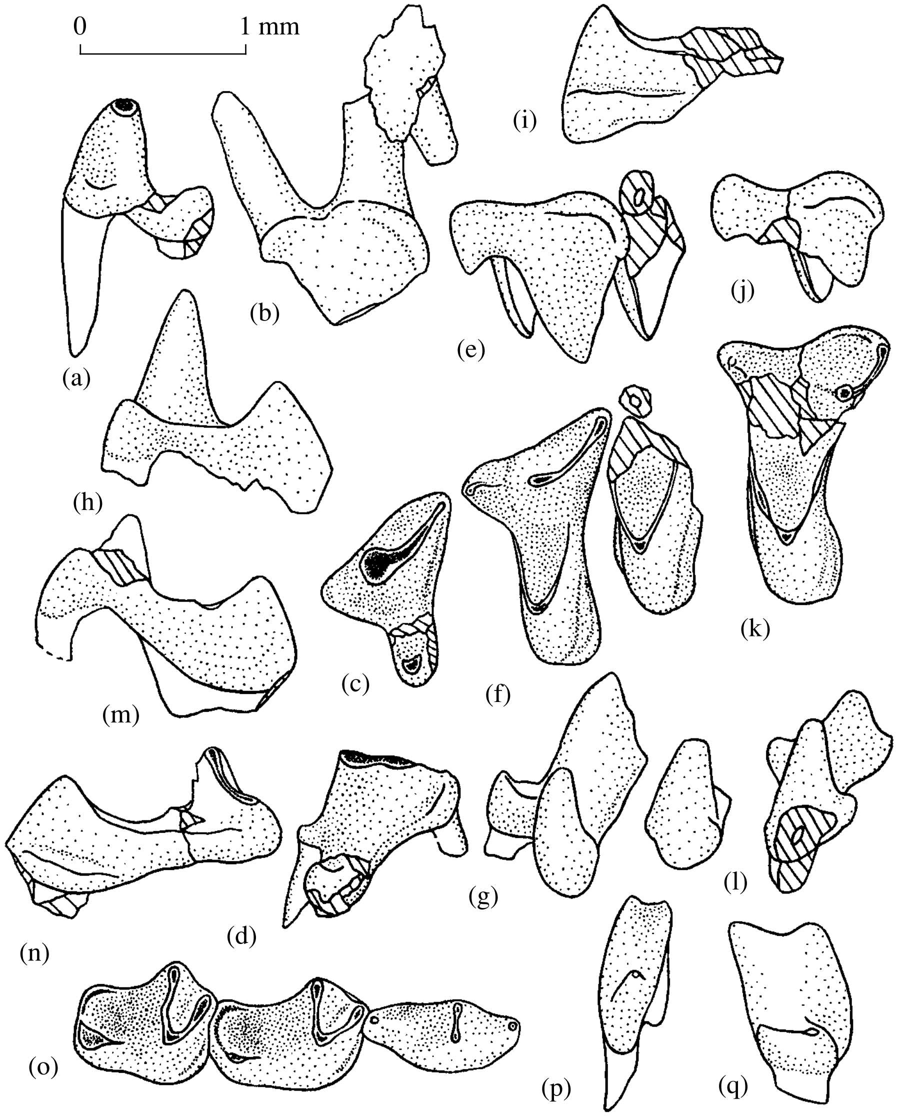


Fig. 11. *Gobigeolabis verigranum* Lopatin, 2004: (a–n) specimen PIN, no. 3104/800, left P^3–M^2: (a–d) P^3, (e–g) P^4 and fragmentary M^1, (h) P^4, (i) fragmentary M^1, and (j–n) M^2; (a, h, m) anterior, (b, e, j) labial, (c, f, k) occlusal, (d, g, l) lingual, and (i, n) posterior views; (o–q) holotype PIN, no. 3104/776, right P_4–M_2: (o) P_4–M_2, occlusal view, (p) P_4, anterior view, and (q) M_2, posterior view; Tsagan-Khushu locality, Mongolia; Zhigden Member, Naran-Bulak Formation, Upper Paleocene.

lum is wider and has a weak eminence in place of the hypocone.

M^2 has a large conical parastyle, which projects significantly anterolabially. The paracrista is short, relatively high. The paracone is damaged. The metacone is relatively high, conical, inclined somewhat posteriorly. The metacrista is high, strong. The metastylar lobe is large, projects posterolabially. The metastyle is small. The ectocingulum is distinct, narrow, particularly well-developed on the metastylar lobe. The paraconule and metaconule are weak, ridgelike. The protocone is more massive than in M^1, the preprotocrista and postprotocrista are more widely spaced, the trigon basin is larger. The precingulum is narrow, but distinct. The postcingulum is slightly weaker than in M^1, but has a distinct expansion and eminence in place of the hypocone. M^3 is not preserved.

The horizontal ramus of the lower jaw is narrow and low, with a gently arched lower edge in the region of P_4–M_2. Judging from the alveoli, P_3 was relatively large and almost as long as P_4.

P_4 is semimolarized, elongated, relatively large and high, slightly higher than the molars. The paraconid is well-pronounced, conical, highly elevated, occupies the central position on the anterior side of the crown. The paracristid is absent. The protoconid and metaconid are approximately equal in height and massiveness, tightly fused almost to the apices. The protocristid

Table 10. Measurements of the upper cheek teeth of *Gobigeolabis verigranum* Lopatin, 2004, specimen PIN, no. 3104/800

Tooth	Length	Protocone length	Width (parastyle–protocone)	Height at paracone	Protocone height
P^3	1.05	0.3	0.9	0.7	0.4
P^4	1.1	0.45	1.35	1.05	0.8
M^1	–	0.55	–	–	0.85
M^2	1.1	0.6	1.65	–	–

is short, transverse. The precingulid is absent. The talonid is relatively long and narrow. The longitudinal crest of the talonid (cristid oblique) is very weak. A very small basin is observed on the lingual side. The labial side of the talonid is slightly concave. The terminal hypoconid cusp is displaced somewhat lingually, elevated to the level of the apex of the paraconid of M_1.

M_1 and M_2 are similar in structure, differing in shape; M_2 is substantially shorter, has a wider trigonid, a short talonid, and more closely positioned paraconid and metaconid. The trigonid of M_1 and M_2 is longitudinally compressed. The paraconid is small, considerably elevated. The protoconid and metaconid are fused at the base, equal in height, turned slightly anterolingually relative to the axis of the tooth row (therefore, the protocristid is subtransverse), and inclined in the same direction. The precingulid is well-developed at the base of the anterolabial wall of the protoconid (it is better developed in M_2 than in M_1). The hypoflexid is shallow. The talonid basin is wide, shallow, open lingually. The cusps of the talonid are low. The hypoconid is located in the posterolabial corner of the talonid. The cristid oblique is low, connected to the posterior wall of the trigonid posterior to the apex of the protoconid. The entoconid is ridgelike, extends along the posterolingual corner of the occlusal surface from the hypoconid to the middle of the lingual side of the talonid. The hypoconulid is indiscernible; apparently, it is completely fused with the entoconid. In M_1, the boundary between the hypoconid and the entoconid–hypoconulid complex is marked by a small posterolabial fold.

Judging from the alveoli preserved, M_3 was slightly shorter than M_2.

Measurements, mm. Tables 10 and 11 show tooth measurements. Length of P_4–M_2, 2.75; alveolar length of P_3, ca. 0.8; lingual depth of the horizontal ramus of the lower jaw under M_2, 1.25 (holotype).

Occurrence. Upper Paleocene (Gashatan) of Mongolia.

Material. In addition to the holotype, specimen PIN, no. 3107/800 from the type locality: P^3, P^4, M^1, and M^2 from a disrupted left maxilla.

SUPERFAMILY SORICOIDEA FISCHER VON WALDHEIM, 1817

Soricini: Fischer von Waldheim, 1817, p. 372.
Soricoidea: Gill, 1872, p. 18.

Diagnosis. Predominantly eudilambdodont soricotan insectivores, varying in size and adaptations. Zygomatic arch present in primitive taxa and absent in advanced taxa. Dental formula, $I^{3-2}/_{3-1}C^{1}/_{1}P^{4-2}/_{4-1}M^{3-2}/_{3-2}$. I^1 ranging from small or slightly increased to excessively developed. I_1 ranging from normal small to excessively developed procumbent or extremely reduced (in this case, I_2 increased). $I^3/_3$ small or absent. $C^1/_1$ small, frequently antemolariform. Upper and lower anterior premolars showing tendency to reduction and antemolariform structure. P^4 submolariform or semimolariform. Molars mostly eudilambdomorph (including ectodilambdomorph) or, infrequently, protodilambdomorph. Upper molars usually with well-developed hypoconal shelf. P_4 submolariform, semimolariform, premolariform, or antemolariform. Lower molars with median or lingual hypoconulid, sometimes transformed into entostylid or completely reduced.

Composition. Three families: Nyctitheriidae Simpson, 1928, Lower Paleocene–Middle Eocene of North America, Upper Paleocene–Lower Oligocene of Europe, Upper Paleocene–uppermost Middle Eocene or basal Upper Eocene of Asia; Plesiosoricidae Winge, 1917, Lower Eocene–Middle Miocene of Asia, Lower Oligocene–Upper Miocene of Europe, Miocene of North America; Soricidae Fischer von Waldheim, 1817, Middle Eocene–Recent of Asia and North America; Lower Oligocene–Recent of Europe; Miocene–Recent of Africa; Pleistocene–Recent of northern South America.

Comparison. The Soricoidea differ from the Micropternodontoidea in the absence of distinct predatory specialization in the structure of the canines and molars, from the Solenodontoidea in the dilambdomorph molars, from the Nesophontoidea in the development of ectodilambdomorphy, large incisors, primary reduction of canines and anterior premolars, and in the structure of P^4, P_4, and molars, and from the Talpoidea in the different specialization of anterior region of the dental system (increased incisors and

Table 11. Measurements of the lower cheek teeth of *Gobigeolabis verigranum* Lopatin, 2004, holotype PIN, no. 3104/776

Tooth	Length	Trigonid width	Talonid width	Height at protoconid
P_4	1.0	0.45	0.35	0.9
M_1	0.95	0.6	0.5	0.85
M_2	0.9	0.65	0.5	0.8

reduced canines and premolars), usually in the more complex structure of P^4 and P_4, and the absence of clearly pronounced high-crowned molars.

FAMILY NYCTITHERIIDAE SIMPSON, 1928

Nyctitheriidae: Simpson, 1928, p. 2.

Ceutholestidae: Rose and Gingerich, 1987, p. 18.

Type genus. *Nyctitherium* Marsh, 1872, Lower–Middle Eocene of North America.

Diagnosis. Small-sized soricoid insectivores with following dental formula: $I^3/_3C^1/_1P^4/_4M^3/_3$. Molars mostly entodilambdomorph (in primitive taxa, protodilambdomorph). P^4 semimolariform, usually with metacone. Labial cusps of upper molars widely spaced, their crests forming characteristic W-shaped pattern in most advanced taxa. Styles large, conules usually well-developed. Hypoconal shelf ranging from weakly developed to broad. I_1 increased, while I_2 and I_3 small. C_1 small, premolariform. P_1 slightly reduced, single-rooted. P_2 and P_3 small, simple in structure. P_4 submolariform or secondarily premolariform to greater or lesser extent. Lower molars usually having moderately high trigonid and elevated paraconid; protoconid and metaconid approximately equal in size, and talonid wide, tricuspid.

Composition. Five subfamilies: Nyctitheriinae Simpson, 1928, Lower Paleocene–Middle Eocene of North America, Upper Paleocene–Lower Oligocene of Europe, Upper Paleocene–uppermost Middle Eocene or basal Upper Eocene of Asia; Asionyctiinae Missiaen et Smith, 2005, Praolestinae subfam nov., Upper Paleocene (Gashatan)–Lower Eocene (Bumbanian) of Asia; Eosoricodontinae Lopatin, 2005, Lower Eocene (Bumbanian) of Mongolia; and Amphidozotheriinae Sigé, 1976, Lower Eocene of North America, Upper Eocene–Lower Oligocene of Europe.

Comparison. The Nyctitheriidae differ from the Soricidae and Plesiosoricidae in the nonreduced antemolar row, structural details of the upper molars (including the absence of clear ectodilambdomorph structure which is characteristic of Soricidae), the structure of P_4, and in the well-developed hypoconulid of M_1–M_3.

Remarks. *Paranyctoides* Fox, 1979, which is represented by teeth and jaws in the Late Cretaceous of North America and Asia, is sometimes referred to the Nyctitheriidae (Fox, 1979, 1984b; Kielan-Jaworowska et al., 2004). However, this genus lacks apomorphic characters in common with Cenozoic nyctitheriids and resembles in the structure of upper and lower cheek teeth the "Zhelestidae," a Late Cretaceous group comprising primitive placentals usually assigned to Ungulatomorpha (see Nessov et al., 1998; Archibald and Averianov, 2001). Among the groups assigned to Lipotyphla, the Adapisoriculidae known from the Paleocene and Lower Eocene of Europe and North Africa (see Gheerbrant, 1988, 1991; Gheerbrant and Russell, 1989, 1991) are most similar in dental structure to *Paranyctoides*. The position of Adapisoriculidae in the insectivore system is uncertain (Lipotyphla indet.: McKenna and Bell, 1997).

Descriptions of species and diagnoses of higher taxa of Asian nyctitheriids are given below in the order corresponding to the evolutionary trends and phylogenetic concept developed in the present study (see Section 5.1.3).

SUBFAMILY NYCTITHERIINAE SIMPSON, 1928

Nyctitheriidae: Simpson, 1928, p. 2.

Nyctitheriinae: Van Valen, 1967, p. 262.

Saturniniinae: Gureev, 1971, p. 64; 1978, p. 315.

Type genus. *Nyctitherium* Marsh, 1872, Lower–Middle Eocene of North America.

Diagnosis. Nyctitheriids with submolariform P_4, having large paraconid, strong protoconid, well-developed metaconid, and differentiated talonid with three cusps and basin. P_2 and P_3 double-rooted. $M_1 \approx M_2 \leq M_3$. M_3 with elongated talonid. Talonid of M_1–M_3 with median hypoconulid. P^4 semimolarized, M^1 and M^2 moderately expanded transversely, usually with strongly concave posterior side of crown, well-developed stylar lobes, and extensive hypoconal shelf.

Generic composition. *Nyctitherium* Marsh, 1872, Lower–Middle Eocene of North America; *Leptacodon* Matthew et Granger, 1921, Lower Paleocene–Lower Eocene of North America, Upper Paleocene–Lower Eocene of Europe; *Remiculus* Russell, 1964, Upper Paleocene of Europe; *Pontifactor* West, 1984, Lower–Middle Eocene of North America; *Saturninia* Stehlin, 1940, Lower Eocene–Lower Oligocene of Europe; *Scraeva* Cray, 1973, Middle–Upper Eocene of Europe; *Euronyctia* Sigé, 1997, Upper Eocene–Lower Oligocene of Europe; *Yuanqulestes* Tong, 1997, uppermost Middle Eocene or basal Upper Eocene of China.

Comparison. The Nyctitheriinae differ from other members of the family in the submolariform P_4. In addition, they differ from the Amphidozotheriinae in the nonreduced, double-rooted P_2 and P_3, different length ratio of the lower molars (in Amphidozotheriinae, $M_2 \gg M_3$), and in the elongated talonid of M_3 with a large hypoconulid; from the Eosoricodontinae in the presence of double-rooted P_2, different size ratio of the lower molars and the talonid structure in M_1–M_3; and from the Asionyctiinae in the presence of the metacone on P^4 and in the shape and structure of the upper molars.

Remarks. The major characters used here for the classification of nyctitheriid subfamilies concern the structure of P_4. Among Asian nyctitheriids, submolariform P_4 is recorded only in *Yuanqulestes*. Accordingly, it is referred to Nyctitheriinae. The Early Paleogene genera *Asionyctia, Oedolius*, and *Voltaia*, with their premolariform P_4, are assigned to the subfamily

Asionyctiinae (see below). In *Bayanulanius* and *Jarveia*, this tooth has not been found; therefore, they are tentatively placed in the Asionyctiinae. The Early Paleogene genera *Praolestes* and *Bumbanius*, which were previously placed in the Nyctitheriinae (Kondrashov et al., 2004a), differ from other nyctitheriids in the semimolariform P_4 and the special structure of molars. These genera are placed below in a separate subfamily, the Praolestinae subfam. nov.

SUBFAMILY PRAOLESTINAE LOPATIN, SUBFAM. NOV.

Type genus. *Praolestes* Matthew, Granger et Simpson, 1929, Upper Paleocene of Mongolia.

Diagnosis. Nyctitheriids with semimolariform P_4, having small paraconid, strong protoconid, moderately developed metaconid, and simplified talonid with transverse terminal crest. P_2 and P_3 double-rooted. $M_1 \approx M_2 \leq M_3$. Trigonid of M_1–M_3 columnar (strongly compressed longitudinally; protoconid and metaconid high, twinned; paraconid small and fused with metaconid), hypoconulid median. M_3 with strongly elongated talonid. M^1 and M^2 strongly expanded transversely, with straight posterior side of tooth crown, small stylar lobes, and narrow hypoconal shelf.

Generic composition. *Praolestes* Matthew, Granger et Simpson, 1929, Upper Paleocene (Gashatan) of Mongolia; *Bumbanius* Russell et Dashzeveg, 1986, Lower Eocene (Bumbanian) of Mongolia.

Comparison. The Praolestinae differ from other subfamilies in the semimolarized P_4, the columnar trigonid of the lower molars, and in the structure of M^1 and M^2. In addition, the Praolestinae differ from the Amphidozotheriinae in the nonreduced, double-rooted P_2 and P_3, the different length ratio of the lower molars, and in the elongated talonid of M_3, which has a large hypoconulid; they differ from the Eosoricodontinae in the presence of double-rooted P_2, the different size ratio of the lower molars, and in the talonid structure in M_1–M_3.

Remarks. Missiaen and Smith (2005) placed the genus *Bumbanius* in the subfamily Asionyctiinae. It is impossible to concur with this point of view because semimolarized P_4 of *Bumbanius* clearly differs it from true Asionyctiinae, which have premolariform P_4, but shows it affinity to *Praolestes.* Additional similarity in the structure of upper and lower molars enables the assignment of *Bumbanius* to Praolestinae.

Genus *Praolestes* Matthew, Granger et Simpson, 1929

Praolestes: Matthew et al., 1929, p. 3; Saban, 1958, p. 875; Szalay and McKenna, 1971, p. 301; Kondrashov et al., 2004a, p. 185.

Type species. *Praolestes nanus* Matthew, Granger et Simpson, 1929, Upper Paleocene of Mongolia.

Diagnosis. M^1–M^3 wide and short, with narrow stylar shelf. Hypoconal shelf of M^1 and M^2 narrow, that of M^3 absent. P_3 with rudimentary metaconid in shape of thickening in posterolingual part of protoconid. P_4 relatively small. Paraconid of P_4 highly elevated, cristid oblique absent. Trigonid of M_1–M_3 very high. $M_2 \ll M_3$. Hypoconulid of M_3 very large, strongly projecting posteriorly and forming posterior lobe.

Species composition. *P. nanus* Matthew, Granger et Simpson, 1929, *P. maximus* Kondrashov, Lopatin et Lucas, 2004, Upper Paleocene of Mongolia.

Comparison. *Praolestes* differs from *Bumbanius* in the presence of a rudimentary metaconid of P_3, relatively smaller P_4, the higher paraconid and the absence of cristid oblique on P_4, the higher trigonid of M_1–M_3, relatively larger M_3 and considerably larger and more strongly projecting hypoconulid of M_3. The upper molars of *Praolestes* are relatively wider and shorter and the hypoconal shelf of M^1 and M^2 is less developed than in *Bumbanius*.

Praolestes nanus Matthew, Granger et Simpson, 1929

Plate 2, figs. 1–3

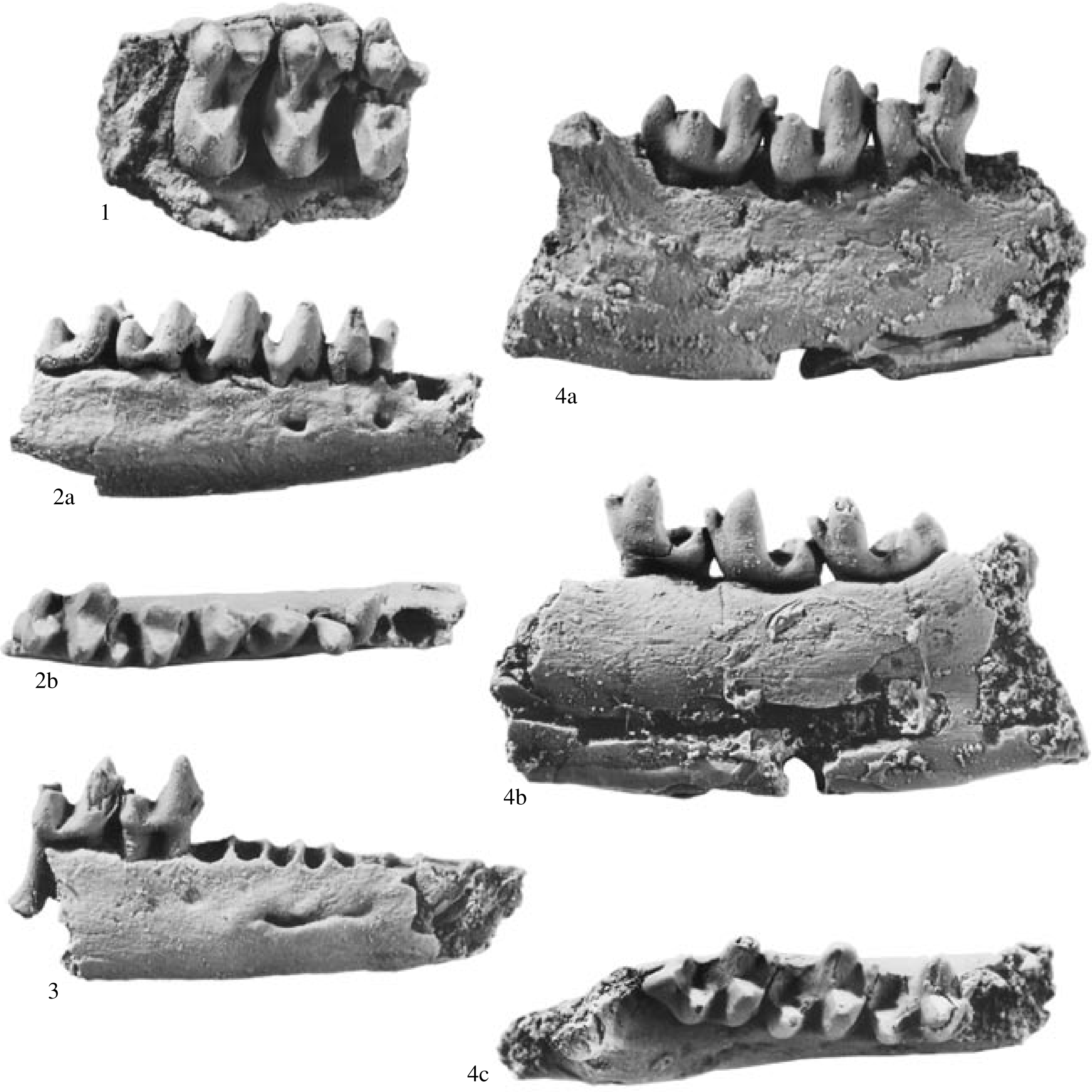
Praolestes nanus: Matthew et al., 1929, p. 3, text-fig. 1; Szalay and McKenna, 1971, p. 301, text-figs. 19–23; Kondrashov et al., 2004a, p. 186, text-figs. 1–4.

Holotype. AMNH, no. 21718, left dentary fragment with P_3–M_1 (the talonid of M_1 is damaged) and alveoli of P_2; Mongolia, Gashato locality; Upper Paleocene, Gashato Formation.

Description (Fig. 12). The upper molars are relatively low-crowned, strongly widened transversely. The crowns of M^1 and M^2 slightly curve anteriorly. In M^1, the paracone is more massive and higher than the metacone. The labial cusps are connected at the base by a weak centrocrista. The posterior slope of the metacone has a weak metacrista extending to the moderately developed metastyle. The ectocingulum is weak, does not form a distinct stylar shelf between the parastylar and metastylar lobes. The parastyle is larger than the metastyle, projects anteriorly. The paracrista is absent. The ectoflexus is poorly pronounced. The protocone is pointed, its apex is located opposite the posterior slope of the paracone. The preprotocrista and postprotocrista are sharp. They connect the apex of the protocone to the paraconule and metaconule and border the relatively large and deep trigon basin. The conules are distinct, approximately equal in size or the paraconule is slightly larger. Each conule has two arms. The preparaconule crest terminates at the anterolingual base of the paracone. The postparaconule crest is indistinct on M^1. The premetaconule crest extends to the anterolingual base of the metacone, the postmetaconule crest reaches the posterolingual base of the metastyle. The precingulum is weak and short, located at the base of the anterior side of the protocone. The hypoconal shelf is much stronger than the precingulum, but lacks a distinct hypocone. Labially, the hypoconal shelf reaches the line of the most labial part of the protocone.

M^2 is slightly wider than M^1; however, they are similar in structure. The metacone slightly deviates posteriorly and is displaced lingually. The ectoflexus is deeper than that of M^1, the parastyle projects anterola-

Plate 2



Explanation of Plate 2

Figs. 1–3. *Praolestes nanus* Matthew, Granger et Simpson, 1929, ×7: (1) specimen PIN, no. 3104/433, left maxillary fragment with M^1–M^3, occlusal view, in a piece of matrix; (2) specimen PIN, no. 3104/427, right dentary fragment with P_1–M_2: (2a) labial and (2b) occlusal views; (3) specimen PIN, no. 3104/360, right dentary fragment with M_1 and M_2 and alveoli of I_1–P_4, labial view; Mongolia, Tsagan-Khushu locality; Upper Paleocene, Naran-Bulak Formation, Zhigden Member.

Fig. 4. *Praolestes maximus* Kondrashov, Lopatin et Lucas, 2004, holotype PIN, no. 3104/363, right dentary fragment with M_1–M_3, ×7: (4a) labial, (4b) lingual, and (4c) occlusal views; Mongolia, Tsagan-Khushu locality; Upper Paleocene, Naran-Bulak Formation, Zhigden Member.

bially and is much better developed than in M^1. The apex of the protocone is located opposite the apex of the paracone. The paraconule is larger than the metaconule. The preparaconule crest terminates at the anterior base of the paracone. The postparaconule crest reaches the lingual base of the paracone. The hypoconal shelf is slightly narrower than in M^1, reaches the posterolingual base of the protocone, and has a distinct hypocone cusp.

M^3 is reduced and compressed longitudinally to a much greater extent than in M^1 or M^2. The parastyle is

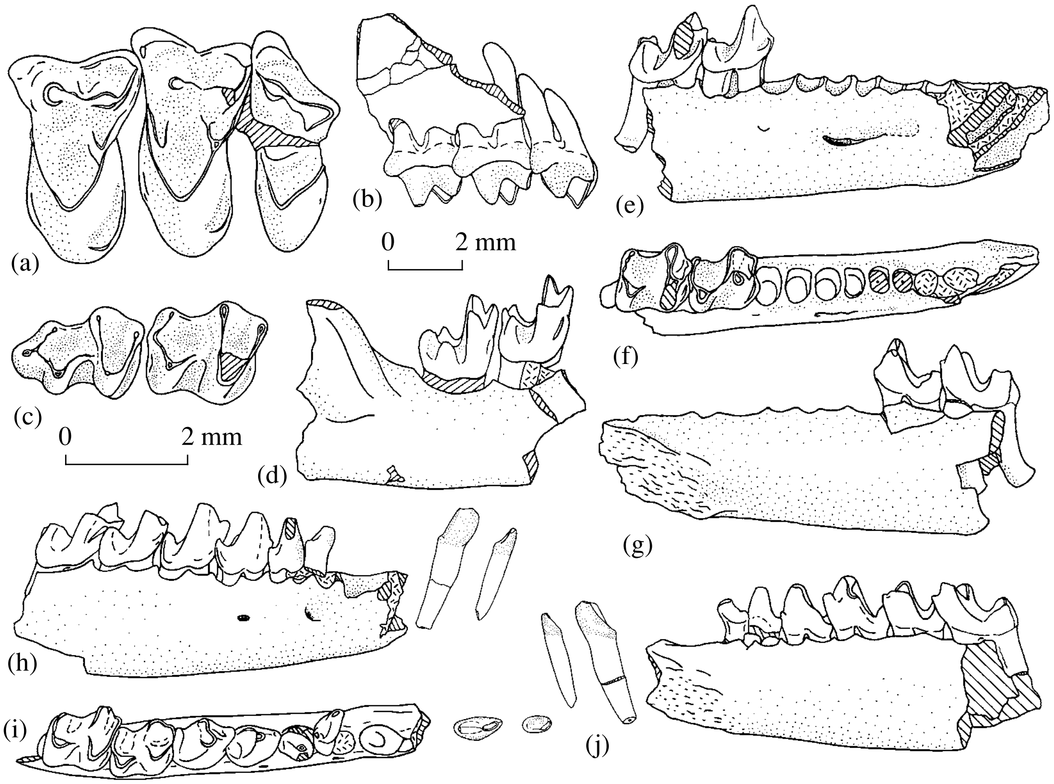


Fig. 12. *Praolestes nanus* Matthew, Granger et Simpson, 1929: (a, b) specimen PIN, no. 3104/433, left maxillary fragment with M^1–M^3: (a) M^1–M^3, occlusal view, (b) general appearance, labial view; (c, d) specimen PIN, no. 3104/362, right dentary fragment with M_2 and M_3 and incomplete coronoid region: (c) M_2 and M_3, occlusal view, (d) general appearance, labial view; (e–g) specimen PIN, no. 3104/360, right dentary fragment with M_1 and M_2 and alveoli of I_1–I_3, C_1, and P_1–P_4: (e) labial, (f) occlusal, and (g) lingual views; (h–j) specimen PIN, no. 3104/427, right dentary fragment with I_3–M_2 (I_3 and C_1 are drawn out of the jaw): (h) labial, (i) occlusal, and (j) lingual views; Tsagan-Khushu locality, Mongolia; Zhigden Member, Naran-Bulak Formation, Upper Paleocene.

large, projects labially. The paracrista is thin but distinct, extends from the apex of the paracone to the anterolingual base of the parastyle. The metacone is considerably reduced, much smaller than the paracone; it is displaced lingually and deviates posteriorly. The metastylar lobe, ectocingulum, precingulum, and hypoconal shelf are absent.

The horizontal ramus of the lower jaw is low, with a straight lower edge. The symphysis is short, reaches the posterior edge of the alveolus of canine. The anterior mental foramen is in line with P_1 or P_2. The posterior mental foramen is in line with the posterior root of P_3 or the anterior root of P_4 in the middle part of the bone. In specimen PIN, no. 3104/360, the posterior mental foramen is slitlike, while the anterior foramen is absent; however, the usual place of the anterior foramen (opposite the middle of P_2) is occupied by a shallow rounded fossa connected to the posterior mental foramen by a small groove. In this specimen, the blood vessel coming through the posterior mental foramen probably extended anteriorly on the bone surface along the groove to the fossa, and only then entered the soft tissue of the lower jaw. A similar structure is frequently observed in various nyctitheriids (Sigé, 1976; Nessov, 1987; Averianov, 1995). However, the shape and position of the mental foramen in the holotype and specimen PIN, no. 3104/427 is typical of these animals (Fig. 12h).

The masseteric crest is strong, the masseteric fossa is relatively deep. The angle between the horizontal ramus and the coronoid process is about 125°.

Judging from the alveoli, all anterior teeth were closely spaced, without substantial gaps. Four anterior alveoli are inclined anteriorly at an angle about 45°. The first three are treated as the alveoli of incisors. The fourth alveolus is larger, circular, with a projecting labial wall; it is regarded as an alveolus of the canine. The alveolus of I_1 is larger than alveoli of subsequent incisors, so that the anterior incisor was probably the largest, almost as large as the canine. The alveolus of single-rooted P_1 is small, circular, closely adjoins the alveolus of the anterior root of P_2. P_2–P_4 are double-rooted. Their alveoli are elongated, oval in shape.

In right dentary of specimen PIN, no. 3104/427 retains P_1–P_4, M_1, and M_2 (Figs. 12h–12j). Two isolated incisiform teeth were found in contact with the anterior

Table 12. Measurements of the lower molars of *Praolestes nanus* Matthew, Granger et Simpson, 1929

Specimen PIN, no.	Tooth	Length	Trigonid width	Talonid width
3104/427	M_1	1.85	1.15	1.1
	M_2	2.0	1.4	1.2
3104/360	M_1	1.85	1.3	1.3
	M_2	1.8	1.45	1.4
3104/361	M_1	1.7	1.3	1.15
	M_2	1.65	1.3	1.15
	M_3	1.8	1.3	–
3104/362	M_2	2.0	1.5	1.3
	M_3	2.25	1.35	1.1

edge of the bone during the preparation of this specimen. Both are right teeth, roots correspond in size to respective alveoli; thus, it is highly probable that they belong to the same individual. Based on the size and structure, the largest of these teeth is determined as a canine, and the smaller is I_3. C_1 (including the root) is approximately 30% higher than I_3. I_3 has a simple, spatulate crown, with a slightly pointed apex. The wear facet is elongated, oval in shape. The crown of C_1 is inclined anteriorly, its root slightly curves anteriorly. The labial side of the crown is rectangular. A small posterior cusp is observed at the crown base. The wear facet is oval, extended longitudinally.

P_1 has the only high cusp and a very weak posterior cingulid. P_2 is larger, the posterior cingulid forms a tiny talonid. P_3 has a small paraconid closely adjoining the base of the protoconid. The metaconid is in the shape of a thickening on the posterolingual wall of the protoconid. The talonid is small, but well-pronounced, with a longitudinal median crest. P_4 is semimolarized. The trigonid is composed of a large protoconid, a small paraconid, and a moderately developed metaconid. The paraconid is positioned more anterolingually than the protoconid. The paracristid is relatively weak. The metaconid is positioned just lingual to the protoconid. The protocristid is well-pronounced. The talonid has the only terminal cusp, which is relatively high, highly elevated, compressed longitudinally, ridgelike. A longitudinal talonid crest is absent. The premolar wear facet descends along the posterior slope of the protoconid (in the case of P_4, along the protoconid and metaconid).

The lower molars are inclined slightly lingually. M_1 and M_2 are almost identical in shape. The talonid is somewhat wider than the trigonid because of its labially projecting hypoconid. The trigonid is twice as high as the talonid. The lingual walls of lower molars are almost straight, whereas the labial walls are convex, with a distinct narrowing between the trigonid and talonid. M_1 is substantially narrower than M_2. The paraconid projects anteriorly and is located more lingually than in M_2. The paraconid is fused at the base with the metaconid; in worn teeth, this is evident from the fusion of wear facets of these cusps. The paracristid is weak. The precingulid is well-developed, extends from the anterolabial end of the crown to the middle of the labial side. The precingulid is separated anteriorly from the paraconid by a well-pronounced anterior groove. The protoconid and metaconid are connected at the base for three-fourths of their height and form together the columnar structure of the trigonid. The protocristid is weak. The metaconid is slightly higher than the protoconid (in worn teeth, just the opposite is observed). The trigonid basin of unworn teeth is small, open lingually; in slightly worn teeth, it disappears. The talonid is compressed slightly longitudinally. The cristid oblique is connected to the middle of the posterior wall of the trigonid. The talonid basin is broad and almost closed lingually by a weak entocristid, which closely approaches the metaconid. The entoconid is much smaller than the hypoconid and displaced posteriorly with reference to it. The hypoconulid is weak and becomes indiscernible in worn teeth. The hypoconid and entoconid are connected by a slightly curving, narrow, and low postcristid. The postcingulid is relatively weak.

M_2 is similar in structure to M_1, differing in only minor features. The trigonid and talonid are slightly wider, the paraconid is displaced lingually to a lesser extent. The talonid basin is almost closed by the lingually low and narrow entocristid, which is weaker than that of M_1. The entoconid is larger and displaced posteriorly to a lesser extent, the postcristid is better developed and curved posteriorly to a greater extent. The hypoconulid is developed better than in M_1.

M_3 is similar in structure and trigonid shape to M_2, but paraconid is more reduced. The talonid is significantly narrower than the trigonid, the hypoconulid is distinct, large, forms a posterior lobe strongly projecting posteriorly.

Measurements, mm. Length of M^1–M^3, 5.45; upper molars (length × width): M^1, 2.2 × 3.4; M^2, 2.0 × 3.75; M^3, 1.45 × 3.55 (specimen PIN, no. 3104/433).

Length of I_3, 0.8; width, 0.5; height of the crown, 0.7; height with the root, 2.7; length of C_1, 1.2; width, 0.65; height of the crown, 1.2; height with the root, 3.6; premolars (length × width): P_1, 0.75 × 0.55; P_2, 0.95 × 0.7; P_3, 1.55 × 0.75; P_4, 1.75 × 0.9 (specimen PIN, no. 3104/427).

Depth of the horizontal ramus of the lower jaw: under P_2, 2.4; under P_3, 2.6; under P_4, 2.7; under M_1–M_2, 2.95 (specimen PIN, no. 3104/360); under P_2, 2.3; under P_3, 2.7; under P_4, 2.75; under M_1–M_2, 2.6 (specimen PIN, no. 3104/427).

Measurements of the lower molars are given in Table 12.

Comparison. *Praolestes nanus* is approximately 30% smaller than *P. maximus* and differs from it in the different size ratio of I_1 and I_2 ($I_1 > I_2$ versus $I_1 \leq I_2$ in *P. maximus*), the better developed entocristid of M_1 and M_2, and in the absence of a postcingulid on M_3.

Occurrence. Upper Paleocene (Gashatan) of Mongolia.

Material. Five specimens stored in PIN from the Zhigden Member of the Naran-Bulak Formation of the Tsagan-Khushu locality: a fragment of the left maxilla with M^1–M^3 (PIN, no. 3104/433); right dentary fragment with I_3–M_2 (PIN, no. 3104/427); right dentary fragment with M_1 and M_2 and alveoli of I_1–I_3, C_1, and P_1–P_4 (PIN, no. 3104/360); right dentary fragment with M_1–M_3 (PIN, no. 3104/361); right dentary fragment with M_2 and M_3 and a part of the coronoid region (PIN, no. 3104/362).

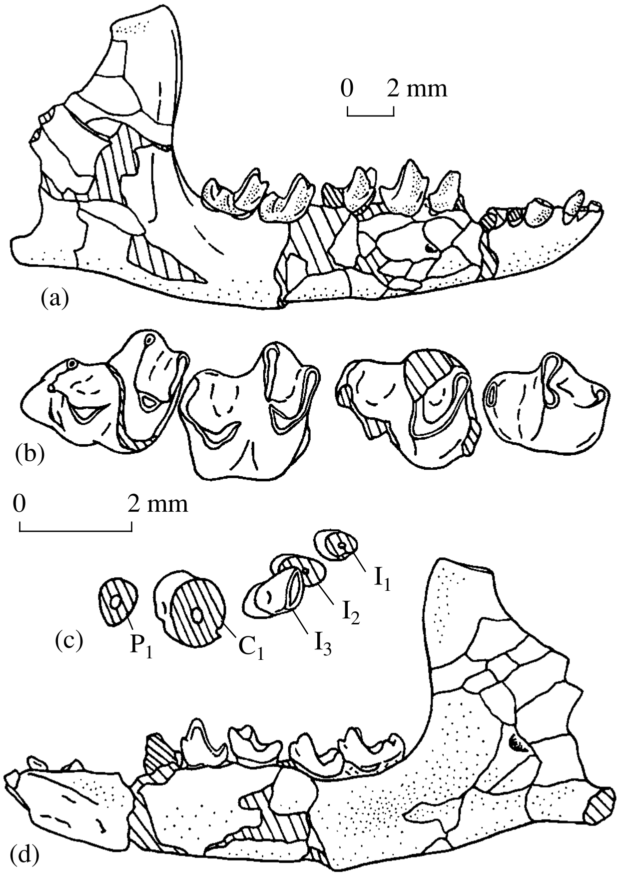


Fig. 13. *Praolestes maximus* Kondrashov, Lopatin et Lucas, 2004, specimen PIN, no. 3102/75, right dentary fragment with I_3, P_3–M_3, and roots of I_1, I_2, C_1, P_1, and P_2: (a) general appearance, labial view; (b) P_3–M_3, occlusal view; (c) I_3 and roots of I_1, I_2, C_1, and P_1, occlusal view; and (d) general appearance, lingual view; Naran-Bulak locality, Mongolia; Zhigden Member, Naran-Bulak Formation, Upper Paleocene.

Praolestes maximus Kondrashov, Lopatin et Lucas, 2004

Plate 2, fig. 4; Plate 3, fig. 1

Praolestes maximus: Kondrashov et al., 2004a, p. 188, text-figs. 5 and 6.

Holotype. PIN, no. 3104/363, right dentary fragment with M_1–M_3; Mongolia, Tsagan-Khushu locality; Upper Paleocene, Naran-Bulak Formation, Zhigden Member.

Description (Fig. 13). The lower jaw is massive, high, its lower edge curves slightly ventrally. The symphysis is short, extends posteriorly to the line of P_1. The posterior mental foramen is located at the posterior root of P_3. The ascending ramus is perpendicular to the horizontal ramus. The height of the ascending ramus is approximately half of the length of the horizontal ramus. The coronoid process is vertical, relatively high, narrow, with a flattened apex inclined posteriorly. The masseteric crest is rather strong, the masseteric fossa is relatively deep. The mandibular foramen is located below the posterior slope of the coronoid process at the level of the tooth row. This foramen is circular, faces posteriorly. The base of the articular process is positioned relatively highly, at the level twice as high as the horizontal ramus. The angular process is thin at the base.

The lower incisors are inclined anteriorly. Judging from the preserved roots of I_1 and I_2 and the crown base of I_3, I_2 was the largest incisor, while I_1 was the smallest; however, the differences in size were not great. I_3 is spatulate, its cutting surface is nonparallel to the axis of the tooth row. Judging from the preserved base of the canine crown, this tooth was twice as large as I_3. P_1 is approximately equal in size to I_3 (Fig. 13c). P_4 has a relatively small paraconid, which is highly elevated at the base both and projects anteriorly, and a relatively large metaconid distinctly separated from the protoconid. The talonid is relatively long, with a well-developed transverse crest.

The lower molars are inclined slightly lingually. The trigonids are high, the talonids are half as high as the trigonids. The lingual walls are almost straight, the labial walls are convex, with a deep fold between the trigonid and talonid. M_1 and M_2 are approximately equal in length (or M_1 is slightly shorter), M_3 is much longer. The cusps are relatively massive. The paraconid is low, relatively large, projects anterolingually, and closely adjoins the metaconid. The metaconid is slightly higher than the protoconid. The cristid oblique is relatively weak, connected to the posterior wall of the protoconid. The talonid is tricuspid, the talonid basin is open lingually because the entocristid is very weak or absent. The hypoconid, hypoconulid, and entoconid are connected by strong crests. The hypoconulid is larger than the entoconid. M_3 has a narrow talonid and a well-developed hypoconulid. The entocristid is better developed than in M_1 or M_2. A distinct postcingulid is located ventrolabial to the hypoconulid.

Measurements, mm. For measurements of lower molars, see Table 13. Length of M_1–M_3, 7.1; depth of the horizontal ramus of the lower jaw under M_1, 4.4; under M_3, 4.1 (holotype).

Length of I_3–M_3, about 17.4; antemolars (length × width): I_3, 0.75 × 0.7; C_1, 1.1 × 1.2; P_4, 2.05 × 1.4; depth of the horizontal ramus of the lower jaw under C_1,

Table 13. Measurements of the lower molars of *Praolestes maximus* Kondrashov, Lopatin et Lucas, 2004

Specimen PIN, no.	Tooth	Length	Trigonid width	Talonid width
3104/365	M_1	2.25	1.5	1.5
3104/366	M_2	2.1	1.65	1.55
3104/367	M_2	2.1	1.55	1.45
3104/429	M_2	2.3	1.6	1.45
3102/75	M_1	~2.05	1.8	–
	M_2	2.45	2.0	1.75
	M_3	2.75	1.85	1.35
3104/363 (holotype)	M_1	2.4	1.75	1.55
	M_2	2.4	1.95	1.65
	M_3	2.95	1.8	1.45
3104/364	M_3	2.85	1.8	1.5
3104/430	M_3	2.7	1.8	1.5

2.0; under P_1, 2.2; under P_3, 3.2; under P_4–M_2, 3.5; under M_3, 3.9; height of the jaw at the coronoid process, 12.0 (specimen PIN, no. 3102/75).

Comparison. *Praolestes maximus* is 30% larger than the type species, has different size ratio of I_1 and I_2 ($I_1 \le I_2$ versus $I_1 > I_2$ in *P. nanus*), a less developed entocristid of M_1 and M_2, and a clear postcingulid on M_3.

Occurrence. Upper Paleocene (Gashatan) of Mongolia.

Material. In addition to the holotype, the type locality yielded seven specimens stored in PIN: a left dentary fragment with alveoli of P_4–M_3 (PIN, no. 3104/368); a right dentary fragment with M_1 (PIN, no. 3104/429), right dentary fragments with M_3 (PIN, nos. 3104/364 and 430); and isolated teeth: left M_1 (PIN, no. 3104/365), right M_2 (PIN, no. 3104/366), and left M_2 (PIN, no. 3104/367). In addition, the Zhigden Member of the Naran-Bulak Formation of the Naran-Bulak locality yielded a right dentary fragment with I_3, P_3–M_3, and roots of I_1, I_2, C_1, P_1 and P_2 (specimen PIN, no. 3102/75).

Genus *Bumbanius* Russell et Dashzeveg, 1986

Bumbanius: Russell and Dashzeveg, 1986, p. 269.

Type species. *Bumbanius rarus* Russell et Dashzeveg, 1986, Lower Eocene of Mongolia.

Diagnosis. M^1 and M^2 relatively long, slightly widened, with large stylar shelf. Hypoconal shelf on M^1 and M^2 well-developed. P_3 without metaconid. P_4 relatively large. Paraconid of P_4 basal, cristid oblique present. Trigonid of M_1–M_3 moderately high. $M_2 \approx M_3$. Hypoconulid of M_3 moderately large, not forming posterior lobe.

Species composition. Type species.

Comparison. *Bumbanius* differs from *Praolestes* in the absence of a rudimentary metaconid of P_3, relatively larger P_4, basal paraconid, the presence of a cristid oblique on P_4, lower trigonids of M_1–M_3, different length ratio of M_2 and M_3, considerably smaller and less projecting hypoconulid of M_3, and in the relatively narrower and longer M^1 and M^2 with a better developed hypoconal shelf.

Bumbanius rarus Russell et Dashzeveg, 1986

Plate 3, figs. 2 and 3

Bumbanius rarus: Russell and Dashzeveg, 1986, p. 270, text-figs. 3 and 4.

Holotype. PSS (Paleontology and Stratigraphy Section of the Institute of Geology of the Mongolian Academy of Sciences, Ulan Bator), no. 20-96, right dentary fragment with M_1–M_3; Mongolia, Tsagan-Khushu locality; Lower Eocene, Naran-Bulak Formation, Bumban Member.

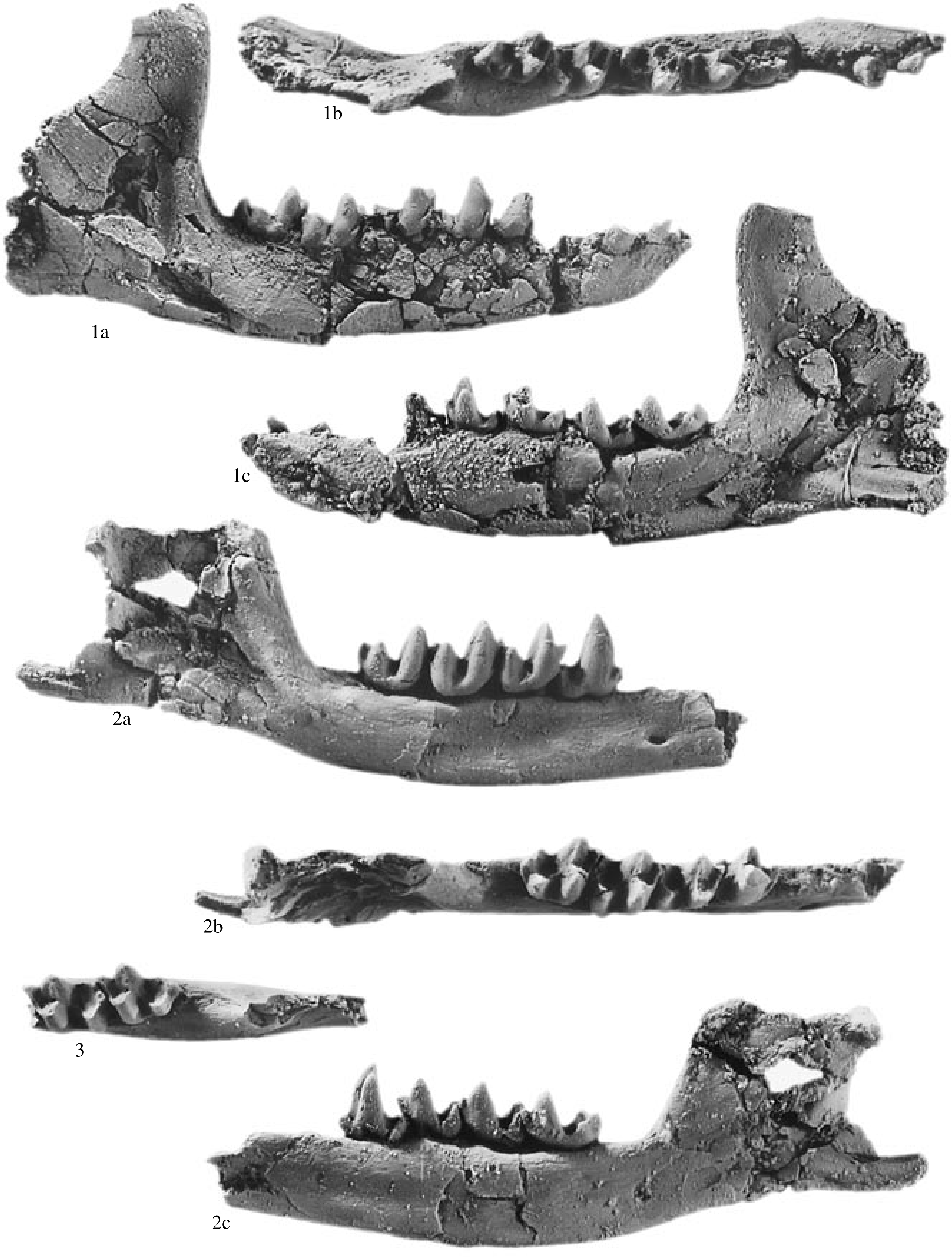
Description (Figs. 14, 15). M^2 is strongly expanded transversely. The ectoflexus is superficial; the parastyle is directed anterolabially; the metastylar lobe is relatively large, projects posterolabially. The ectocingulum is narrow. The paracone and metacone are widely spaced, their bases are completely separated. The paracone is slightly higher and more massive than the metacone. The paracrista is weak, crests of the centrocrista are distinct; the metacrista is sharp, strong. The conules are well-developed, large; the paraconule is larger and higher than the metaconule. The preparaconule crest is connected to the anterolingual corner of the parastyle, the postparaconule crest closely approaches the lingual base of the paracone, the premetaconule crest extends to the anterolingual corner of the base of the metacone, the postmetaconule crest terminates at the base of the lingual side of the metastyle. The trigon basin is deep. The protocone is as high as the paracone and has a steep lingual slope. The hypocone cusp is small hardly discernible within the well-developed hypoconal shelf. The precingulum is short, but distinct.

Explanation of Plate 3 →

Fig. 1. *Praolestes maximus* Kondrashov, Lopatin et Lucas, 2004, specimen PIN, no. 3102/75, right dentary fragment with I_3 and P_3–M_3 and roots of I_1, I_2, and C_1–P_2, ×5: (1a) labial, (1b) occlusal, and (1c) lingual views; Mongolia, Naran-Bulak locality; Upper Paleocene, Naran-Bulak Formation, Zhigden Member.

Figs. 2 and 3. *Bumbanius rarus* Russell et Dashzeveg, 1986, ×7: (2) specimen PIN, no. 3104/864, right dentary fragment with P_4–M_3, alveoli of P_3, and partially preserved ascending ramus: (2a) labial, (2b) occlusal, and (2c) lingual views; (3) specimen PIN, no. 3104/868, left dentary fragment with M_2–M_3, occlusal view; Mongolia, Tsagan-Khushu locality; Lower Eocene, Naran-Bulak Formation, Bumban Member.

Plate 3



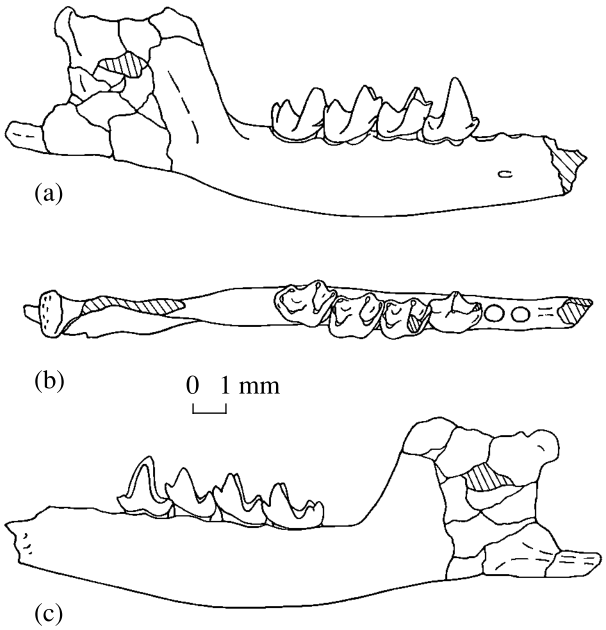


Fig. 14. *Bumbanius rarus* Russell et Dashzeveg, 1986, specimen PIN, no. 3104/864, right dentary fragment with P_4–M_3, alveoli of P_3, and partially preserved ascending ramus: (a) labial, (b) occlusal, and (c) lingual views; Tsagan-Khushu locality, Mongolia; Bumban Member, Naran-Bulak Formation, Lower Eocene.

The horizontal ramus of the lower jaw is long and low, with a convex lower edge. The mental foramen is under the middle or posterior root of P_3. Under M_1 and M_2, the surface of the labial side is usually substantially concave. The symphysis reaches posteriorly P_2. The angle between the ascending and horizontal rami is about 120°. The coronoid process is high and slender. The masseteric crest is strong, the masseteric fossa is deep. The articular process is located at the level 2.5 times higher than the depth of the horizontal ramus. The condyle is relatively narrow, approximately equal in width to M_2 or M_3. The incisure between the articular and angular processes is broad and deep. The angular process is long and narrow, with a well-pronounced muscular area on the dorsomedial surface.

The structure of incisors, canine, and P_1–P_2 is not known. Alveoli of P_2 and P_3 are separated by a small diastema, which is as long as the alveolus of a root of these premolars. The crown of P_3 is relatively low, rather massive, with a protoconid and small and low terminal cusps of the paraconid and talonid. The crowns of P_4 and M_1 are inclined slightly lingually relative to the bone body (in fact, these teeth are parallel to the vertical plane of the symphysis, whereas the horizontal ramus deviates labially).

P_4 is relatively large, its trigonid is at least as long and as wide as those of M_1. The paraconid is low, ridgelike, directed anterolingually. A short precingulid is present. The protoconid and metaconid are positioned opposite to each other. The protoconid is very high, pointed. The metaconid is almost as high as the protoconid, but is less massive. The protocristid notch is deep. The anterior edge of the protoconid forms a long vertical crest (preprotocristid), which descending to the base of the paraconid. The talonid is short, with a very shallow lingual basin, a sharp, longitudinally directed cristid oblique, and a relatively low, expanded transversely, ridgelike terminal cusp, which gives rise to a thin posterolingual crest.

The trigonids of M_1–M_3 are moderately high, have a well-developed, relatively small basin, which is completely or partially closed lingually (in M_1, to a lesser extent, in M_3, to a greatest extent). The paraconid is high, ridgelike, projects anterolingually. The wear facet of the lingual (metaconid) portion of the protocristid is turned posterodorsally and directed subvertically (Fig. 15k). In addition, clear traces of occlusion are seen on the enamel of the posterior wall of the metaconid ventral to the protocristid. This is two oblique facets connected in the protocristid region, the first is under the protocristid notch, while the second extends downward the medial side of the inflated posterolingual part of the metaconid and closely approaches the anterior end of the cristid oblique (Fig. 15k, facets are designated as dotted areas). The talonid is broad, with a large and deep basin. The cristid oblique is strong, connected to the trigonid at the level of the protocristid notch and usually slightly ascends onto the posterior wall of the trigonid. The hypoconid is larger and higher than the other cusps of the talonid, the hypoconulid is larger than the entoconid. The cusps are connected by crests of the postcristid, so that its lingual portion (between the hypoconulid and entoconid) is higher than the labial portion (between the hypoconid and hypoconulid). The precingulid is relatively strong, the postcingulid ranges from distinct to very weak, frequently absent in M_3. Occasionally, a greater or lesser developed, narrow anterolingual cingulid is observed at the level of the paraconid and the anterior part of the metaconid; anteriorly, it is fused with the base of the paraconid (specimens PIN, nos. 3104/872 and 873; Figs. 15p, 15r, 15s). In M_3, the talonid is longer than in M_1 and M_2 and has a large projecting hypoconulid.

Measurements, mm. M^2 (length × width), 2.0 × 3.0 (specimen PIN, no. 3104/882).

Length of P_4–M_3, 6.9; M_1–M_3, 5.3; depth of the horizontal ramus of the lower jaw under P_4, 2.2; under M_1, 2.45; under M_2, 2.25; and under M_3, 2.15; length of the coronoid region, 6.4; width of the head the condyle, 1.5; thickness, 1.1; length, 0.8 (specimen PIN, no. 3104/864).

For measurements of the lower teeth, see Table 14.

Remarks. The structural characters of the ascending ramus of the lower jaw and P_3 of *Bumbanius rarus* are presented for the first time.

Occurrence. Lower Eocene (Bumbanian) of Mongolia.

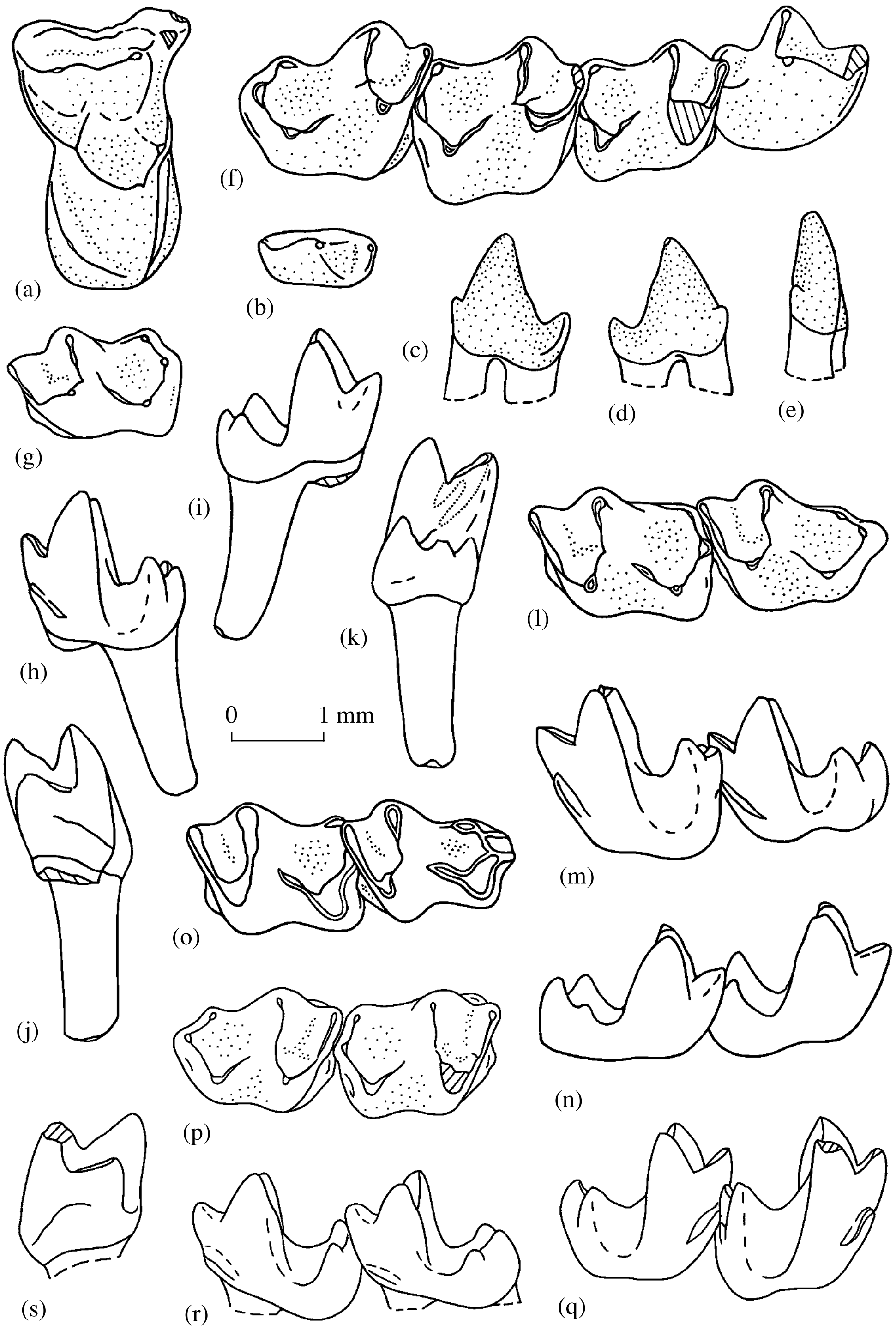


Fig. 15. *Bumbanius rarus* Russell et Dashzeveg, 1986: (a) specimen PIN, no. 3104/883, right M^2, occlusal view; (b–e) specimen PIN, no. 3104/865, left P_3: (b) occlusal, (c) labial, (d) lingual, and (e) anterior views; (f) specimen PIN, no. 3104/864, right P_4–M_3, occlusal view; (g–k) specimen PIN, no. 3104/885, left M_1: (g) occlusal, (h) labial, (i) lingual, (j) anterior, and (k) posterior views; (l–n) specimen PIN, no. 3104/868, left M_2–M_3: (l) occlusal, (m) labial, and (n) lingual views; (o) specimen PIN, no. 3104/869, left M_2–M_3, occlusal view; (p–s) specimen PIN, no. 3104/870, right M_2–M_3: (p) occlusal, (q) labial, (r) lingual views, and (s) M_2, anterior view; Tsagan-Khushu locality, Mongolia; Bumban Member, Naran-Bulak Formation, Lower Eocene.

Table 14. Measurements of the lower cheek teeth of *Bumbanius rarus* Russell et Dashzeveg, 1986

Specimen PIN, no.	Tooth	Length	Trigonid width	Talonid width
3104/865	P_3	1.3	0.55	0.65
3104/884	P_3	~1.3	0.6	0.6
3104/885	P_4	–	1.0	0.8
3104/864	P_4	1.75	1.35	1.15
	M_1	1.75	1.2	1.25
	M_2	2.0	1.5	1.5
	M_3	2.1	1.5	1.2
3104/866	M_1	1.85	1.15	1.1
3104/881	M_1	1.9	1.2	1.15
3104/867	M_1	1.9	1.35	1.25
	M_2	2.0	1.4	1.3
3104/873	M_2	1.9	1.35	1.3
3104/874	M_2	1.95	1.35	1.25
3104/875	M_2	2.0	1.35	1.3
3104/868	M_2	2.1	1.4	1.3
	M_3	2.05	1.25	1.0
3104/869	M_2	2.05	1.35	1.35
	M_3	2.0	1.2	1.0
3104/870	M_2	1.9	1.35	1.3
	M_3	1.9	1.25	0.95
3104/871	M_2	1.8	1.4	1.3
	M_3	1.9	1.35	1.05
3104/872	M_2	2.0	1.35	1.3
	M_3	2.0	1.25	1.0
3104/878	M_3	1.95	1.3	1.0

Material. The type locality yielded 18 dentary fragments stored in PIN: (PIN, no. 3104/864) with P_4–M_3, alveoli of P_3, and partially preserved ascending ramus; (PIN, no. 3104/865) with P_3, fragmentary P_4 and M_1, and posterior alveolus of P_2; (PIN, no. 3104/866) with M_1, fragmentary P_4 and alveoli of P_2 and P_3; (PIN, no. 3104/867) with M_1 and M_2; seven specimens (PIN, nos. 3104/868–873 and 886) with M_2 and M_3; four specimens (PIN, nos. 3104/874–877) with M_2; (PIN, no. 3104/878) with M_3; and two specimens (PIN, nos. 3104/879 and 880) without teeth, with alveoli of M_2 and M_3; in addition, five isolated teeth: (PIN, no. 3104/882) M^2, (PIN, no. 3104/883) fragmentary M^2, (PIN, no. 3104/884) P_3, (PIN, no. 3104/885) P_4, and (PIN, no. 3104/881) M_1.

SUBFAMILY ASIONYCTIINAE MISSIAEN ET SMITH, 2005

Type genus. *Asionyctia* Missiaen et Smith, 2005, Upper Paleocene of China.

Diagnosis. Nyctitheriids with premolariform or partially molarized P_4. Metaconid of P_4 considerably reduced or absent; paraconid small, frequently located basally; talonid simplified, with longitudinal shearing crest and large terminal cusp. P_2 and P_3 double-rooted. $M_1 \approx M_2 \leq M_3$. Talonid of M_3 narrow, long, with large, posteriorly projecting hypoconulid. P^4 partially molarized, without metacone, M^1 and M^2 expanded strongly transversely, with straight posterior side of crown, large stylar lobes, and narrow hypoconal shelf.

Generic composition. *Asionyctia* Missiaen et Smith, 2005, *Bayanulanius* Meng, Zhai et Wyss, 1998, Upper Paleocene (Gashatan) of China; *Voltaia* Nessov, 1987, Upper Paleocene (Gashatan) of Kazakhstan; *Jarveia* Nessov, 1987, Upper Paleocene (Gashatan) of Kazakhstan and Mongolia; *Oedolius* Russell et Dashzeveg, 1986, *Edzenius* gen. nov., Lower Eocene (Bumbanian) of Mongolia.

Comparison. The Asionyctiinae differ from the Nyctitheriinae, Praolestinae, and Amphidozotheriinae in the premolariform P_4; in addition, they differ from the Amphidozotheriinae in the nonreduced, double-rooted P_2 and P_3, different length ratio of the lower molars, and in the elongated talonid of M_3 with a large hypoconulid. The differences from the Eosoricodontinae include the double-rooted P_2, more reduced metaconid (down to complete loss of this cusp), the presence of a large terminal cusp on the talonid of P_4, and different length ratio of the lower molars, the structure of the paraconid and talonid of M_1–M_3 (in the Eosoricodontinae, $M_1 > M_2 > M_3$, the paraconid is long, the hypoconulid is small, and the talonid of M_3 is reduced, see below). Regarding the structure of the upper teeth, the Asionyctiinae clearly differ from the Nyctitheriinae in the less molarized P^4 (without metacone); from the Nyctitheriinae and Eosoricodontinae, in the wider molars with a straightened posterior wall of the crown and a narrow hypoconal shelf; and from the Praolestinae, in the better developed stylar lobes.

Remarks. The structure of P_4 in *Jarveia* is not known, but the assignment of this genus to the Asionyctiinae is supported by the presence of partially molarized P^4 without metacone in *J. erronea* (Kondrashov et al., 2004a). *Bayanulanius* is tentatively placed in the Asionyctiinae based on the similarity to *Asionyctia* in the structure of M^2 (see Meng et al., 1998, text-fig. 4; Missiaen and Smith, 2005, text-fig. 2).

Genus *Oedolius* Russell et Dashzeveg, 1986

Oedolius: Russell and Dashzeveg, 1986, p. 275.

Type species. *Oedolius perexiguus* Russell et Dashzeveg, 1986, Lower Eocene of Mongolia.

Diagnosis. P_4 lacking metaconid; paraconid basal, talonid unicuspid, without basin. Trigonid of M_1–M_3 very high, talonid narrow and short, talonid basin small, entoconid and entocristid weak; hypoconulid of M_1 and M_2 fused with entoconid.

Species composition. Type species.

Comparison. *Oedolius* differs from *Voltaia* in the absence of a rudimentary basin and a supplementary cusp on the talonid of P_4, and in the higher trigonid, narrow talonid, and less developed entocristid of the lower molars. *Oedolius* differs from *Asionyctia* in the low paraconid of P_4, in the height of the trigonid, and the structure of the talonid of lower molars. The differences from *Jarveia* include the narrower talonid of M_1–M_3 (as regards M_2, this is true for the differences from *Bayanulanius*) and the separate entoconid and hypoconulid of M_3.

Oedolius perexiguus Russell et Dashzeveg, 1986

Plate 4, figs. 1–3

Oedolius perexiguus: Russell and Dashzeveg, 1986, p. 275, text-fig. 5.

Holotype. PSS, no. 20-103, left dentary fragment with M_1 and M_2 and talonid of P_4; Mongolia, Tsagan-Khushu locality; Lower Eocene, Naran-Bulak Formation, Bumban Member.

Description (Fig. 16). The horizontal ramus of the lower jaw is low. The symphysis reaches posteriorly the line of P_1/P_2. The mental foramina are under P_1 or interval P_1/P_2 and under the posterior part of P_3. The posterior mental foramen is much smaller than the anterior foramen. The masseteric fossa is deep. The mandibular foramen is large, located below the tooth row, at the mid-depth of the horizontal ramus.

Judging from the alveoli, C_1 and P_1 are single-rooted and relatively large. P_2 and P_3 are double-rooted, substantially smaller than P_4 and approximately equal in size to one another or P_3 is slightly smaller than P_2. P_2 is not available. P_3 is simple in structure, with a tiny basal paraconid, an anteriorly inclined protoconid, and a small unicuspid talonid.

P_4 is high and relatively large. The paraconid is small, positioned low, slightly displaced lingually from the middle of the anterior wall of the tooth. The paracristid is absent. The precingulid is rudimentary or absent. The apex of the protoconid is inclined slightly posteriorly. The sharp posterolingual edge of the protoconid descends to the talonid. The talonid is unicuspid, usual lacks a basin and cristid oblique. The lingual margin of the talonid has a relatively sharp longitudinal crest connecting the base of the posterolingual edge of the protoconid with the terminal talonid cusp. Only one specimen (PIN, no. 3104/924) has a rudimentary cristid oblique, which is located labial to the longitudinal talonid crest and borders a superficial depression between them, which seems to be a rudimentary talonid basin (Figs. 16l, 16m). In the P_4–M_2 row, the terminal cusp (hypoconulid in the case of molars) of a preceding tooth enters the fold between the paraconid and precingulid of a posteriorly adjoining tooth.

M_1–M_3 are approximately equal in size or M_3 is slightly longer due to the projecting hypoconulid lobe. The trigonid is relatively high. The paraconid is small, ridgelike, highly elevated (substantially above the level of the talonid). The precingulid is narrow, but well-developed, long; less frequently, the precingulid is reduced to a small prominence. The trigonid basin is open, narrow and shallow. The protoconid and metaconid are approximately equal in size, the protocristid notch is deep. The apex of the metaconid is displaced slightly posteriorly in relation to the apex of the protoconid. The talonid is slightly narrower than the trigonid. The cristid oblique ascends high onto the metaconid, terminating close to the midheight of this cusp in an unworn condition. The hypoconid is the largest and highest cusp of the talonid, the hypoconulid is slightly lower, occupies a central position; the entoconid is the smallest of three cusps, located in the posterolingual corner of the occlusal surface, close to the hypoconulid and, in a worn tooth, fuses with to form a single element. The entocristid is very narrow and low, rapidly disappears as the tooth is worn. The talonid basin is deep, narrow, widely open lingually. The postcingulid is absent. In M_3, the talonid is narrow and long; its hypoconulid projects strongly posteriorly, forming the posterior lobe.

Measurements, mm. For measurements of cheek teeth, see Table 15; for the depth of the horizontal ramus of the lower jaw, see Table 16.

Labial height of unworn teeth at the protoconid: P_4 (specimen PIN, no. 3104/941), 1.45; M_1 (PIN, no. 3104/942), 1.3; M_2 (PIN, no. 3104/943), 1.45.

Length of premolar alveoli: P_1, 0.55 (PIN, no. 3104/923); P_2, 0.85 (PIN, nos. 3104/922, 937) and 1.0 (PIN, nos. 3104/923, 925); P_3, 0.75 (PIN, no. 3104/923) and 0.9 (PIN, nos. 3104/925, 937).

Occurrence. Lower Eocene (Bumbanian) of Mongolia.

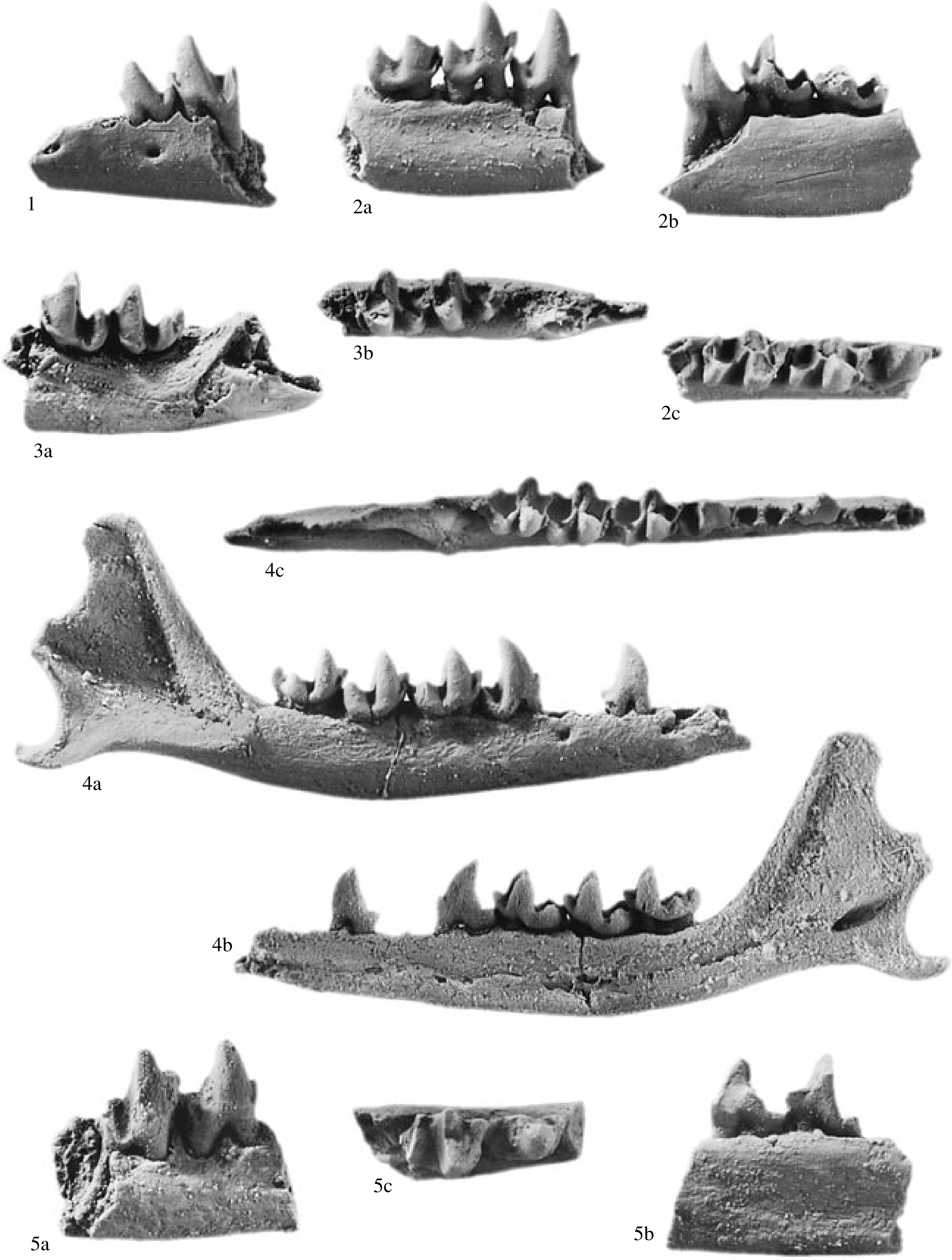
Material. The collection of PIN contains 23 specimens, including 20 dentary fragments, from the type locality: with P_3 and P_4 (PIN, no. 3104/922), with P_4–M_2 and alveoli of C_1–P_3 (PIN, no. 3104/923), with P_4–M_2 (PIN, no. 3104/924), with P_4, M_1, and alveoli of P_1–P_3 (PIN, no. 3104/925), with fragmentary M_1–M_3 (PIN, no. 3104/926), with M_1 and M_2 (PIN, no. 3104/927), with M_2 and M_3 (PIN, no. 3104/929), with P_4 and M_3 in the state of eruption and fragmentary M_1 (PIN, no. 3104/928), four specimens with M_1 (PIN, nos. 3104/930–932, 937), five with M_2 (PIN, nos. 3104/933–936 and 944), one with M_3 (PIN, no. 3104/938), and two with M_3 and incomplete ascending ramus (PIN, nos. 3104/939, 940); in addition, three isolated lower teeth: P_4 (PIN, no. 3104/941), M_1 (PIN, no. 3104/942), and M_2 (PIN, no. 3104/943).

Genus *Voltaia* Nessov, 1987

Voltaia: Nessov, 1987, p. 207.

Type species. *Voltaia minuta* Nessov, 1987, Upper Paleocene of Kazakhstan.

Plate 4



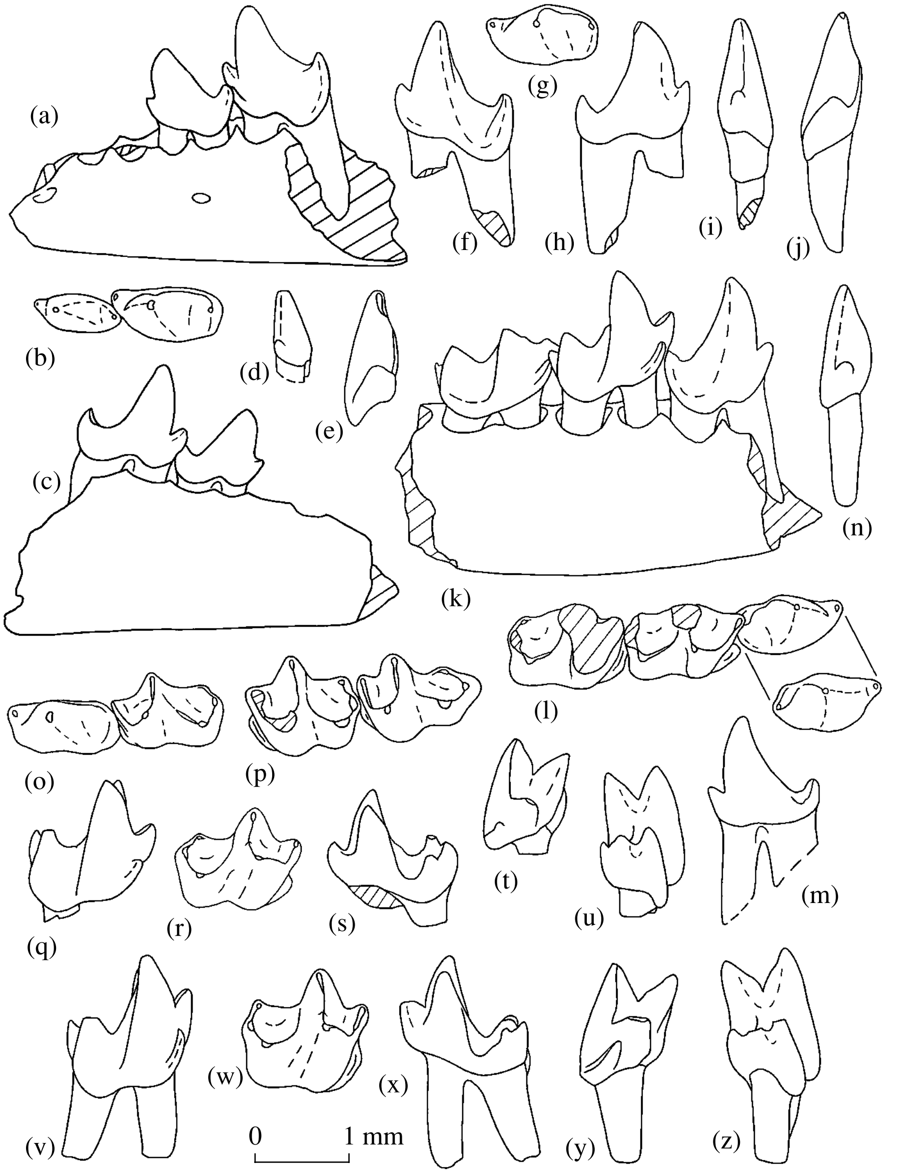


Fig. 16. *Oedolius perexiguus* Russell et Dashzeveg, 1986: (a–e) specimen PIN, no. 3104/922, left dentary fragment with P_3–P_4: (a) labial view, (b) P_3–P_4, occlusal view, (c) lingual view, (d) P_3, anterior view, and (e) P_4, posterior view; (f–j) specimen PIN, no. 3104/941, left P_4: (f) labial, (g) occlusal, (h) lingual, (i) anterior, and (j) posterior views; (k–n) specimen PIN, no. 3104/924, right dentary fragment with P_4–M_2: (k) labial view, (l) P_4–M_2, occlusal view (in addition, P_4 is shown separately, inclined slightly posteriorly, which opens the posterior region of the talonid), (m) P_4, lingual view, and (n) P_4 anterior view; (o) specimen PIN, no. 3104/927, left P_4–M_1, occlusal view; (p) specimen PIN, no. 3104/929, left M_2–M_3, occlusal view; (q–u) specimen PIN, no. 3104/942, right M_1: (q) labial, (r) occlusal, (s) lingual, (t) anterior, and (u) posterior views; (v–z) specimen PIN, no. 3104/943, right M_2: (v) labial, (w) occlusal, (x) lingual, (y) anterior, and (z) posterior views; Tsagan-Khushu locality, Mongolia; Bumban Member, Naran-Bulak Formation, Lower Eocene.

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Explanation of Plate 4

Figs. 1–3. *Oedolius perexiguus* Russell et Dashzeveg, 1986, ×10: (1) specimen PIN, no. 3104/922, left dentary fragment with P_3–P_4, labial view; (2) specimen PIN, no. 3104/924, right dentary fragment with P_4–M_2: (2a) labial, (2b) lingual, and (2c) occlusal views; (3) specimen PIN, no. 3104/929, left dentary fragment with M_2–M_3: (3a) labial and (3b) occlusal views; Mongolia, Tsagan-Khushu locality; Lower Eocene, Naran-Bulak Formation, Bumban Member.

Fig. 4. *Voltaia minuta* Nessov, 1987, holotype TsNIGR Museum, no. 11/12455, right dentary fragment with P_2, P_4–M_3, and alveoli of C_1–P_1 and P_3, ×7: (4a) labial, (4b) lingual, and (4c) occlusal views; Kazakhstan, Dzhilga 1a locality; Upper Paleocene.

Fig. 5. *Edzenius lus* sp. nov., holotype PIN, no. 3104/949, right dentary fragment with P_4–M_1, ×10: (5a) labial, (5b) occlusal, (5c) and lingual views; Mongolia, Tsagan-Khushu locality; Lower Eocene, Naran-Bulak Formation, Bumban Member.

Table 15. Measurements of the lower cheek teeth of *Oedolius perexiguus* Russell et Dashzeveg, 1986

Specimen PIN, no.	Tooth	Length	Trigonid width	Talonid width
3104/922	P_3	0.95	0.4	0.3
	P_4	1.2	0.6	0.5
3104/941	P_4	1.25	0.55	0.5
3104/923	P_4	1.3	0.6	0.55
	M_1	1.35	0.9	0.85
	M_2	1.3	1.0	0.85
3104/924	P_4	1.2	0.6	0.45
	M_1	1.3	0.8	0.7
	M_2	1.35	0.9	0.75
3104/925	P_4	1.2	0.6	0.5
	M_1	1.25	0.75	0.6
3104/930	M_1	1.35	0.8	0.75
3104/932	M_1	1.45	0.9	0.85
3104/942	M_1	1.4	0.85	0.7
3104/927	M_1	1.35	0.85	0.85
	M_2	1.45	0.9	0.85
3104/933	M_2	1.35	1.0	0.8
3104/934	M_2	1.35	0.95	0.8
3104/935	M_2	1.35	0.9	0.75
3104/936	M_2	1.3	0.85	0.75
3104/943	M_2	1.4	1.0	0.8
3104/929	M_2	1.3	0.9	0.7
	M_3	1.35	0.8	0.6
3104/938	M_3	1.35	0.85	0.65

Table 16. Depth of the horizontal ramus of the lower jaw of *Oedolius perexiguus* Russell et Dashzeveg, 1986 (collection of PIN)

Level	*N*	Limits	Δ
under P_3	4	1.2–1.6	1.4
under P_4	6	1.4–1.9	1.6
under M_1	7	1.55–2.25	1.85
under M_2	10	1.6–2.25	1.75
under M_3	4	1.4–1.6	1.5

Diagnosis. P_4 without metaconid; paraconid basal; talonid bicuspid, with small basin. Trigonid of M_1–M_3 relatively low, talonid broad, entoconid and entocristid well-developed, hypoconulid and entoconid separate.

Species composition. Type species.

Comparison. *Voltaia* differs from *Oedolius* and *Jarveia* in the relatively lower trigonid and different structure of the talonid of M_1–M_3. In addition, *Voltaia* differs from *Oedolius* in the presence of a rudimentary basin and entoconid on the talonid of P_4. *Voltaia* differs from *Asionyctia* in the structure of P_4 (in *Asionyctia*, this tooth has a highly positioned paraconid and an unicuspid talonid: Missiaen and Smith, 2005, text-figs. 1, 2).

Voltaia minuta Nessov, 1987

Plate 4, fig. 4

Voltaia minuta: Nessov, 1987, p. 208, pl. I, fig. 11.

Holotype. TsNIGR Museum, no. 11/12455, right dentary fragment with P_2, P_4–M_3, and alveoli of C_1, P_1, and P_3; southern Kazakhstan, Tashkentskie Chuli Area, Dzhilga 1a locality (outcrop TDA-2); Upper Paleocene.

Description (Fig. 17). The horizontal ramus of the lower jaw is low, particularly, in the anterior region. The lower edge of the horizontal ramus curves slightly ventrally in the middle region. The symphysial area is weak, reaches posteriorly the line of P_1. The anterior mental foramen is small, located under the interval between P_1 and P_2. The posterior mental foramen is relatively large, circular, located under the posterior part of P_3. The ascending ramus is moderately high, the angle between the anterior edge of the coronoid process and the horizontal ramus is about 130°. At the ventral edge of the dentary, the transition from the horizontal ramus to the ascending ramus is marked by a substantial dorsal curvature. The apex of the coronoid process is smoothly rounded, the incisure between the coronoid and articular processes is moderately deep. The masseteric fossa is deep, clearly bordered by crests ventrally and anterodorsally. The medial side of the coronoid process has a relatively large, shallow, but well outlined internal temporal fossa (for the musculus temporalis pars profundus). It extends along the anterior side of the coronoid process (from the base to two-thirds of its heights) and is separated from the anterior border by a sharp crest. The ventral and posterior borders of the temporal fossa are outlined less distinctly by a depression in the bone surface. The mandibular foramen is slightly ventral to the alveolar margin of the jaw, positioned close to the base of the angular process. The articular process is short, located slightly dorsal to the level of the apices of protoconids of molars; the condylar neck is narrow; the condylar head is not preserved. The incisure between the articular and angular processes is relatively deep. The angular process is long, curved, and relatively massive; it has three well-pronounced muscular areas: two relatively deep areas are on the lateral and medial sides, and a flat area is on the ventral side; the lateral and ventral areas were insertions for the posterior portion of the masseter, and the medial area was for the posterior end of pterygoideus internus muscle.

Judging from the alveoli, the canine is relatively small, P_1 is much smaller than the canine, inclined anteriorly. P_2 is relatively large, high, transversely flattened, simple in structure. The paraconid is absent; the talonid

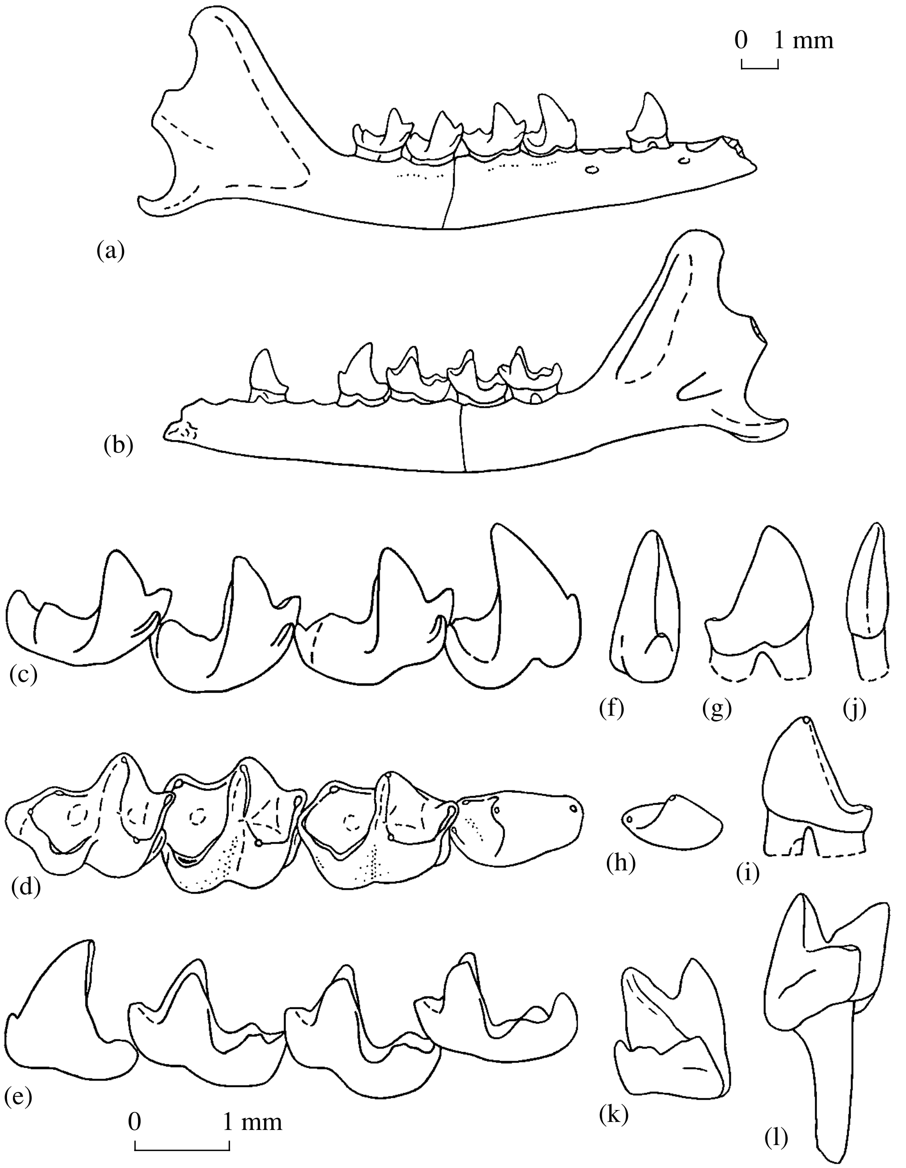

Fig. 17. *Voltaia minuta* Nessov, 1987, holotype TsNIGR Museum, no. 11/12455, right dentary fragment with P_2 and P_4–M_3 and alveoli of C_1–P_1 and P_3: (a, b) general appearance: (a) labial and (b) lingual views; (c–e) P_4–M_3: (c) labial, (d) occlusal, and (e) lingual views; (f) P_4, anterior view; (g–j) P_2: (g) labial, (h) occlusal, (i) lingual, and (j) anterior views; (k) M_1, posterior view; (l) M_2 anterior view; Dzhilga 1a locality, southern Kazakhstan, Upper Paleocene.

is very small, without a basin; the protoconid apex curves posteriorly. The anterior wall of the protoconid is convex, the posterior wall is slightly concave, with a poorly pronounced posterolabial edge. Judging from the length of alveoli, P_3 was a little larger than P_2.

P_4 is the highest tooth in the cheek row. The paraconid is small, located basally, slightly displaced lingually from the middle of the anterior wall of the crown. The precingulid is absent. The protoconid apex is inclined strongly posteriorly, the posterolabial edge is sharp. In addition, the tooth has a posterolingual edge, which is fused posteroventrally with a low and narrow entocristid to close lingually the small talonid basin. The entocristid (longitudinal lingual talonid crest) terminates posteriorly in a small, but distinct entoconid cuspule. The talonid is widely open labially; the cristid oblique is absent; the hypoconid is separated from the protoconid by a large fold and occupies a posterolabial position on the talonid, entering the fold between the projections of the paraconid and precingulid of M_1.

Molars are approximately equal in size. The trigonid is moderately high, compressed longitudinally in M_2 and M_3. The paraconid is elevated; the paracristid is

Table 17. Measurements of the lower cheek teeth of *Voltaia minuta* Nessov, 1987, holotype TsNIGR Museum, no. 11/12455

Tooth	Length	Trigonid width	Talonid width	Height at protoconid
P_2	1.15	0.5	–	1.2
P_4	1.45	0.8	0.75	1.5
M_1	1.75	1.3	1.35	1.35
M_2	1.65	1.3	1.25	1.25
M_3	1.75	1.3	0.9	1.25

sharp; in M_2 and M_3, it is much longer than in M_1. The precingulid is well-developed, inflated, and projecting strongly anteriorly. The protoconid and metaconid are approximately equal in size, positioned opposite to each other, widely spaced at the level of the upper third of the height of the posterior side of the trigonid. The hypoflexid is deep and narrow. The talonid is slightly wider than the trigonid in M_1, slightly narrower in M_2, and much narrower in M_3. The talonid basin is very deep and relatively large, closed lingually by the long and high entocristid. The hypoconid is relatively large, massive, projects strongly posterolabially. The hypoconulid and entoconid are smaller, but well-developed and distinctly differentiated. The hypoconulid occupies the central position on the posterior side of the occlusal surface; in M_1 and M_2, it enters the fold between anterior projections of the precingulid and paraconid of the subsequent molar, while in M_3, it forms the increased posterior lobe. The cristid oblique is connected to the base of the posterior wall of the trigonid at the level of the protocristid notch, and its anterior end is fused with a weak subvertical crest, which obliquely ascends onto the posterior wall of the metaconid and closely approaches the apex of this cusp.

Measurements, mm. Holotype: length of P_2–M_3, 8.6; length of P_4–M_3, 6.4; alveolar length of P_1, 0.6; P_3, 1.2; depth of the horizontal ramus of the lower jaw under P_2, 1.45; under P_4 and M_3, 1.8; under M_1 and M_2, 1.9; height of the ascending ramus at the coronoid process, 5.4.

For measurements of cheek teeth, see Table 17.

Remarks. The holotype (stored in TsNIGR Museum) was broken into two parts approximately at the middle of the horizontal ramus, between M_1 and M_2 (Figs. 17a, 17b). A.O. Averianov (personal communication) informed that the photograph of the holotype as an integral specimen in the original description (Nessov, 1987, pl. 1, fig. 11) was mounted using the two parts. As the posterior side of M_1 and the anterior side of M_2, with the anterior root seen in the break, were drawn (Figs. 17k, 17l) the two parts of the holotype were glued together; this enabled the tooth row length to be measured accurately.

Occurrence. Upper Paleocene (Gashatan) of Kazakhstan.

Material. Holotype (found by L.A. Nessov in 1984).

Genus *Edzenius* Lopatin, gen. nov.

Etymology. From the mythological Mongolian *edzen* (host, spirit of a locality).

Type species. *Edzenius lus* sp. nov.

Diagnosis. P_4 with rudimentary metaconid; paraconid basal; talonid unicuspid, without basin. Trigonid of M_1–M_3 relatively low, talonid broad, entoconid and entocristid well-developed, hypoconulid and entoconid separate.

Species composition. Type species, Lower Eocene of Mongolia.

Comparison. The new genus differs from *Asionyctia*, *Oedolius*, and *Voltaia* in the presence of a rudimentary metaconid of P_4; it differs from *Asionyctia* in the basal paraconid of P_4, from *Voltaia* in the unicuspid talonid of P_4, and from *Oedolius* and *Jarveia* in the structure of the trigonid and talonid of M_1–M_3.

Edzenius lus Lopatin, sp. nov.

Plate 4, fig. 5

Etymology. From the mythological Mongolian *lus* (spirit of nature, locality).

Holotype. PIN, no. 3104/949, right dentary fragment with P_4 and M_1; Mongolia, Tsagan-Khushu locality; Lower Eocene, Naran-Bulak Formation, Bumban Member.

Description (Fig. 18). The horizontal ramus of the lower jaw is relatively low. The mental foramen is located under the middle of P_3. Judging from the alveoli, P_2 and P_3 are double-rooted, substantially smaller than P_4 and approximately equal in length to one another.

P_4 has a small basal paraconid (sometimes, it is hardly discernible, looking like a tiny prominence), which is displaced to the lingual edge of the anterior wall of the tooth. The precingulid is absent. The protoconid is massive, with an inclined posterior wall and a flat lingual side. The metaconid is extremely small, in the shape a subordinate rudimentary cuspule at the base of the protoconid, incorporated in the posterolingual edge of the protoconid. In an unworn condition, the metaconid has its own apex; in a worn tooth, it looks like a prominence at the base of the ventrolingual region of the protocristid (Figs. 18j, 18l, 18m). The talonid is relatively long and wide at the base, without a basin; the terminal cusp is large, relatively high, enters a fold between the precingulid and paraconid of M_1. The longitudinal shearing crest is not sharp, extends along the lingual margin of the talonid.

In molars, the trigonid is moderately high, compressed longitudinally. The paraconid is lowly posi-

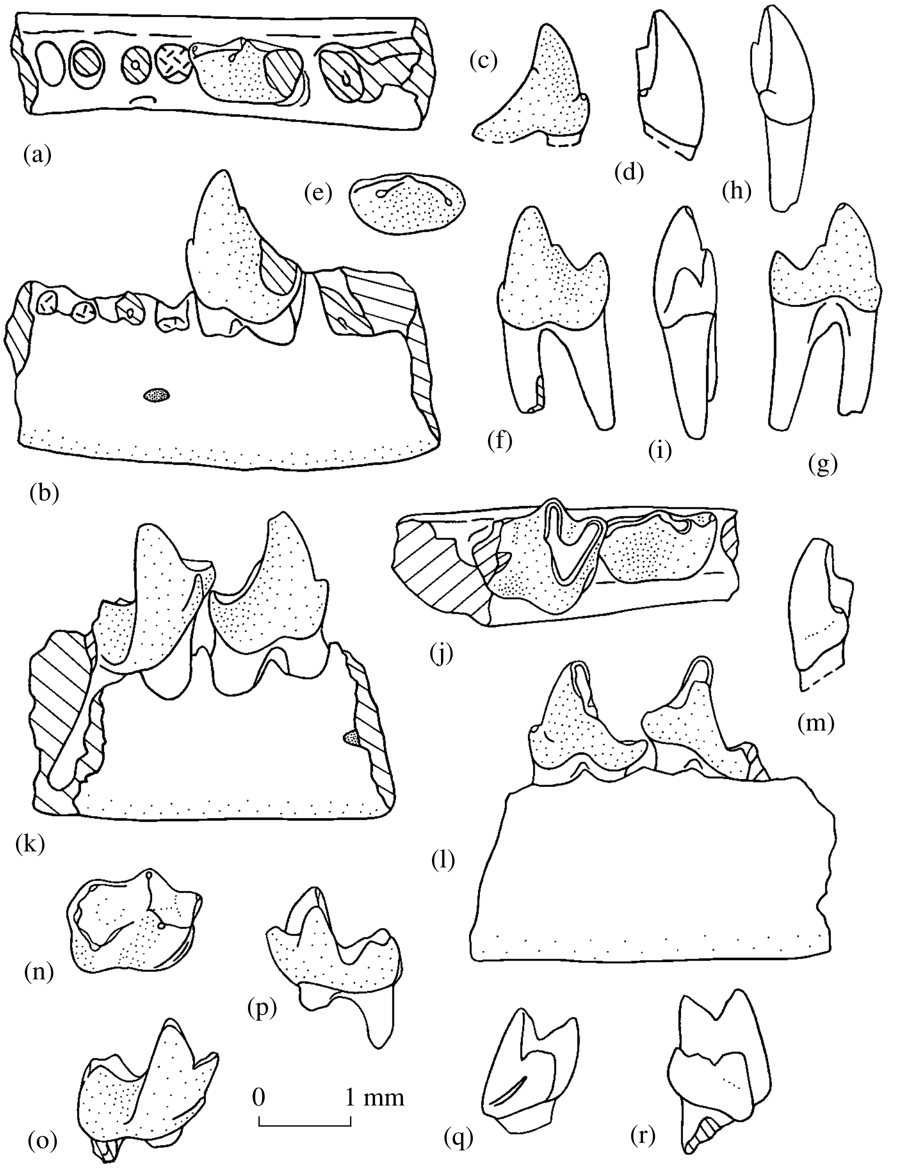

Fig. 18. *Edzenius lus* sp. nov.: (a–d) specimen PIN, no. 3104/947, left dentary fragment with P_4 and alveoli of P_2, P_3, and M_1: (a) occlusal, (b) labial, and (c) lingual views and (d) P_4, anterior view; (e–i) specimen PIN, no. 3104/950, left P_4: (e) occlusal, (f) labial, (g) lingual, (h) anterior, and (i) posterior views; (j–m) holotype PIN, no. 3104/949, right dentary fragment with P_4–M_1: (j) occlusal, (k) labial, and (l) lingual views and (m) P_4, anterior view; (n–r) specimen PIN, no. 3104/951, right M_1: (n) occlusal, (o) labial, (p) lingual, (q) anterior, and (r) posterior views; Tsagan-Khushu locality, Mongolia; Bumban Member, Naran-Bulak Formation, Lower Eocene.

tioned, clearly detached, relatively short. The paracristid is sharp, with a distinct notch. The precingulid is narrow. The trigonid basin is widely open. The metaconid and protoconid are positioned opposite to each other, approximately equal in height, although the protoconid is somewhat more massive. In a heavily worn tooth, the metaconid becomes much lower than the protoconid. The protocristid notch is deep. The talonid is slightly narrower than the trigonid. The hypoflexid is deep and wide. The cristid oblique ascends a little onto the posterior wall of the trigonid in its middle part, just under the protocristid notch. The hypoconid is large and relatively high. The hypoconulid is wide, low, and flat, occupies the central position in the posterior margin of the talonid. The entoconid is smaller than the other talonid cusps; however, it is distinct and clearly differentiated. The entocristid is well developed, but relatively short; anteriorly, it reaches only the middle of the talonid; therefore, the talonid basin is incompletely closed. The postcingulid is absent.

Measurements, mm. For tooth measurements, see Table 18.

Table 18. Measurements of the lower cheek teeth of *Edzenius lus* sp. nov.

Specimen PIN, no.	Tooth	Length	Trigonid width	Talonid width	Height at protoconid
3104/950	P_4	1.25	0.65	0.55	1.35
3104/947	P_4	1.25	0.75	0.65	1.6
3104/948	P_4	1.25	0.65	0.55	–
	M_1	1.3	0.85	0.6	–
3104/949 (holotype)	P_4	1.3	0.8	0.65	–
	M_1	–	1.15	–	–
3104/951	M_1	1.45	1.05	1.0	1.3

Table 19. Depth of the horizontal ramus of the lower jaw of *Edzenius lus* sp. nov. (collection of PIN)

Level	no. 3104/947	no. 3104/948	no. 3104/949 (holotype)
under P_3	1.7	1.65	–
under P_4	1.7	1.7	1.85
under M_1	1.7	–	1.85

Height of P_4 at the protoconid, including the posterior root, 2.55 (specimen PIN, no. 3104/950).

Alveolar length of premolars: P_2, 0.85 (specimen PIN, no. 3104/947); P_3, 0.8 (PIN, nos. 3104/947 and 948), 0.9 (PIN, no. 3104/948).

For depth of the horizontal ramus of the lower jaw, see Table 19.

Material. In addition to the holotype, the type locality yielded five specimens (collection of PIN), including two isolated P_4 (PIN, nos. 3104/946, 950), well-preserved M_1 (PIN, no. 3104/951), and dentary fragments with P_4 and M_1 (PIN, no. 3104/948) and with P_4 and alveoli of P_2, P_3, and M_1 (PIN, no. 3104/947).

Genus *Jarveia* Nessov, 1987

Jarveia: Nessov, 1987, p. 208; Averianov, 1995, p. 216; Kondrashov et al., 2004a, p. 190.

Type species. *Jarveia minuscula* Nessov, 1987, Upper Paleocene of Kazakhstan.

Diagnosis. Trigonid of M_1–M_3 relatively high; talonid wide and long; entoconid small, fused with hypoconulid; entocristid weak. Stylar shelf of M^1–M^3 relatively narrow; hypoconal shelf of M^2 weak; in M^3 hypoconal shelf absent.

Species composition. *J. minuscula* Nessov, 1987, Upper Paleocene of Kazakhstan; *J. erronea* Kondrashov, Lopatin et Lucas, 2004, Upper Paleocene of Mongolia.

Comparison. *Jarveia* differs from *Oedolius* in the wide and long talonid of M_1 and M_2 and in the fused entoconid and hypoconulid of M_3; it differs from *Voltaia, Asionyctia, Edzenius*, and *Bayanulanius* in the high trigonid, weak entocristid, and fused entoconid and hypoconulid of lower molars. In addition, *Jarveia* differs from *Asionyctia* in the narrow stylar shelf of M^1–M^3, weak hypoconal shelf of M^2, and in the absence of hypoconal shelf on M^3.

Jarveia minuscula Nessov, 1987

Plate 5, figs. 1 and 2

Jarveia minuscula: Nessov, 1987, p. 209, pl. II, fig. 1; Averianov, 1995, p. 216, text-fig. 1.

Jarveia sp.: Averianov, 1995, p. 217, text-fig. 2.

Holotype. TsNIGR Museum, no. 13/12455, left dentary fragment with M_1–M_3 and alveoli of P_1–P_4;

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Explanation of Plate 5

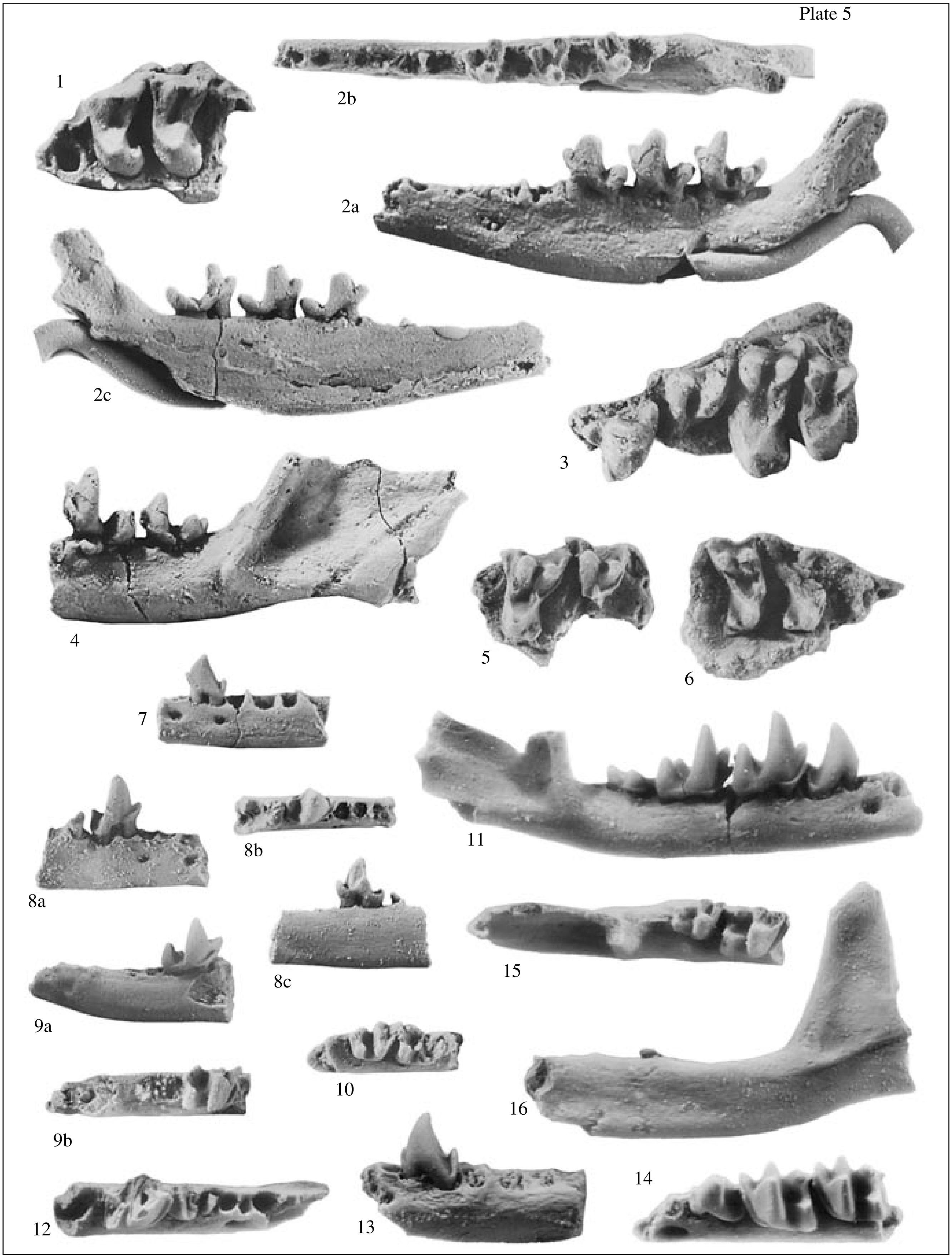
Figs. 1 and 2. *Jarveia minuscula* Nessov, 1987, ×10: (1) specimen ZIN, no. 79206, left maxillary fragment with M^1 and M^2 and alveoli of P^4 and M^3, occlusal view; (2) holotype TsNIGR Museum, no. 13/12455, left dentary fragment with M_1–M_3 and alveoli of P_1–P_4: (2a) labial, (2b) occlusal, and (2c) lingual views; Kazakhstan, Dzhilga 1a locality; Upper Paleocene.

Figs. 3 and 4. *Jarveia erronea* Kondrashov, Lopatin et Lucas, 2004, ×10: (3) holotype PIN, no. 3104/434, left maxillary fragment with P^4–M^3, occlusal view (zygomatic process is broken off); (4) specimen PIN, no. 3104/428, left dentary fragment with partially preserved M_2 and complete M_3, labial view; Mongolia, Tsagan-Khushu locality; Upper Paleocene, Naran-Bulak Formation, Zhigden Member.

Figs. 5–10. *Eosoricodon terrigena* Lopatin, 2005, ×10: (5) specimen PIN, no. 3104/901, left maxillary fragment with M^1 and M^2 and alveoli of M^3, occlusal view; (6) specimen PIN, no. 3104/902, right maxillary fragment with M^1 and M^2 and fragmentary M^3, occlusal view; (7) specimen PIN, no. 3104/890, left dentary fragment with P_3 and alveoli of P_1–P_2 and P_4–M_1, labial view; (8) specimen PIN, no. 3104/891, right dentary fragment with P_4 and alveoli of P_2, P_3, and M_1: (8a) labial, (8b) occlusal, and (8c) lingual views; (9) holotype PIN, no. 3104/900, right dentary fragment with M_2 and alveoli of M_3: (9a) labial and (9b) occlusal views; (10) specimen PIN, no. 3104/481, right dentary fragment with M_2 and M_3, occlusal view; Mongolia, Tsagan-Khushu locality; Lower Eocene, Naran-Bulak Formation, Bumban Member.

Figs. 11–16. *Soricolestes soricavus* Lopatin, 2002, ×10: (11) holotype PIN, no. 3107/405, right dentary fragment with P_4–M_3, labial view; (12) specimen PIN, no. 3107/409, right dentary fragment with damaged P_4–M_1 and alveoli of I_1–P_3, occlusal view; (13) specimen PIN, no. 3107/407, left dentary fragment with P_4, labial view; (14) specimen PIN, no. 3107/406, left dentary fragment with P_4–M_2, occlusal view; (15) specimen PIN, no. 3107/408, right dentary fragment with M_2 and M_3, occlusal view; (16) specimen PIN, no. 3107/410, right dentary fragment with the coronoid process, lingual view; Mongolia, Khaychin-Ula 2 locality; Middle Eocene, Khaychin Formation.

Plate 5



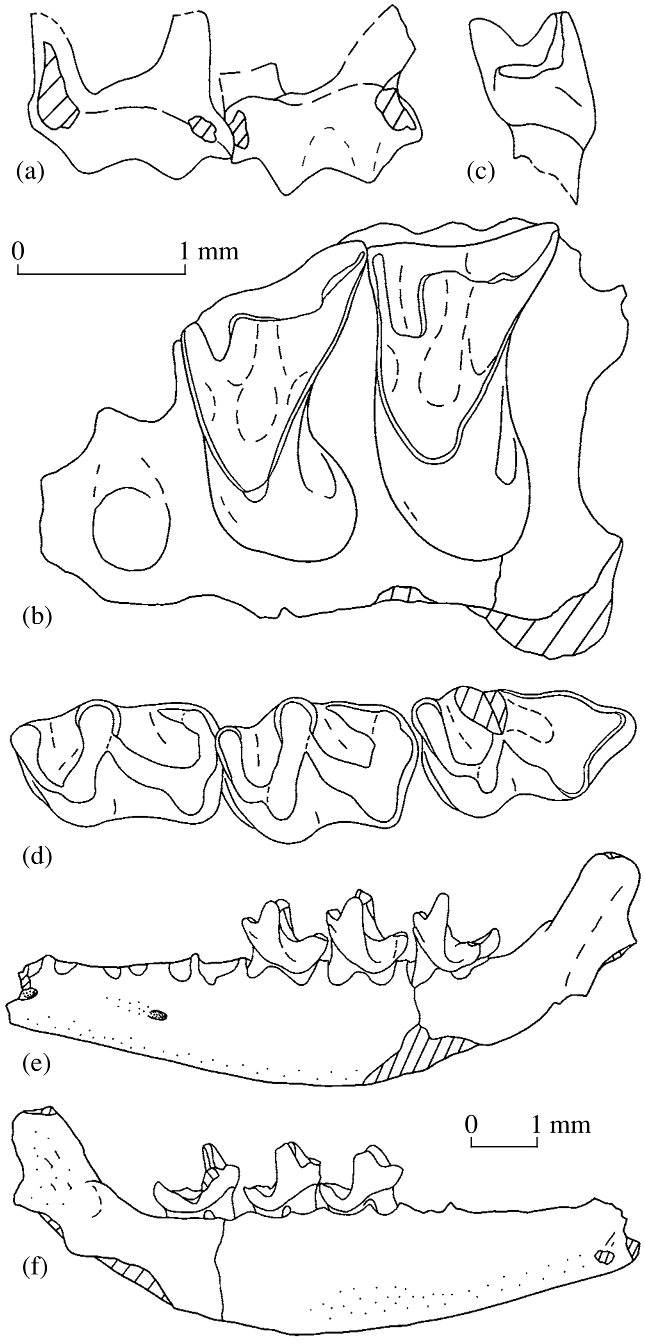


Fig. 19. *Jarveia minuscula* Nessov, 1987: (a, b) specimen ZIN, no. 79206, left maxillary fragment with M^1 and M^2 and alveoli of P^4 and M^3: (a) M^1 and M^2, labial view, and (b) general appearance, occlusal view; (c–f) holotype TsNIGR Museum, no. 13/12455, left dentary fragment with M_1–M_3 and alveoli of P_1–P_4: (c) M_1, anterior view, (d) M_1–M_3, occlusal view, (e) general appearance, labial view, and (f) general appearance, lingual view; Dzhilga 1a locality, southern Kazakhstan, Upper Paleocene.

southern Kazakhstan, Tashkentskie Chuli Area, Dzhilga 1a locality (outcrop TDA-2); Upper Paleocene.

Description (Fig. 19). Judging from the alveoli, P^4 is three-rooted, relatively narrow, and M^3 is somewhat smaller than M^2. M^1 and M^2 are widened strongly transversely, the crowns curve substantially anteriorly in the middle part. The stylar shelf is absent, the external walls of the paracone and metacone are positioned close to the labial edge of the crown, the ectocingulum is absent, the ectoflexus is poorly pronounced. The parastyle is small, directed anteriorly. The metastylar lobe is relatively large, projects substantially posterolabially. The paracone and metacone are approximately equal in size, with elongated lingual slopes projecting deep into the trigon basin. The metacrista is well-developed, particularly in M^2. The protocone is large, its apex is opposed to the notch of the centrocrista. Most of the occlusal surface lingual to the apices of the paracone and metacone and labial to the apex of the protocone is heavily worn; however, it is incompletely evened by wear; therefore, individual structural elements in the central part of the crown are recognizable. Conules are absent, they are probably lost as a result of wear (the fact that they are present in an intact tooth is supported by the presence of leveled sites in respective places of the worn occlusal surface). The preprotocrista and postprotocrista are sharp, border a relatively deep trigon basin and reach respective styles. The hypoconal shelf is flattened, with a distinct low crest, but without a clear cusp. The precingulum is short and narrow, but clearly pronounced.

The lower jaw has a low horizontal ramus and a gently sloping anterior edge of the coronoid process. The masseteric fossa is deep. The internal temporal fossa is superficial; a small rounded tubercle is located at the base of the coronoid process anterior to this fossa. The symphysis reaches posteriorly the line of P_1/P_2. The mental foramina are located in line with P_1/P_2 and P_3/P_4, the posterior foramen is larger. Judging from the alveoli, P_1 is single-rooted, relatively large; P_2 and P_3 are double-rooted, P_3 is longitudinally much shorter than P_2 and is separated from it by a small space. P_4 is approximately equal in length to M_1.

The trigonid of M_1–M_3 is high, with a small subtransverse paraconid raised much above of the talonid. The precingulid thin. The trigonid basin narrow and shallow, open. The protoconid and metaconid approximately equal in size, with subvertical posterior walls. The apex of the metaconid is substantially displaced posteriorly in relation to the apex of the protoconid. The talonid of M_1 and M_2 is approximately equal in length to the trigonid; in M_3, it is much longer. The talonid basin is relatively small and shallow. The cristid oblique ascends to the upper part of the metaconid. The hypoconid is large; the hypoconulid is wide, low, and flat, occupies the central position on the posterior margin of the talonid; in M_3, it projects strongly posteriorly and forms the posterior lobe. The entoconid is small, but distinct, fused with the hypoconulid in M_1 and M_2 and remains mostly separate in M_3. The entocristid is weak, rapidly disappears as a tooth is worn; the talonid basin is open lingually. The postcingulid is undeveloped. In M_3, the talonid is worn to a greater extent than in M_1 and M_2.

Measurements, mm. Length of M^1, 1.25; width, 1.9; length of M^2, 1.2; width, 2.0 (specimen ZIN, no. 79206).

Length of M_1–M_3, 3.75; length of M_1, 1.25; trigonid width, 0.8; talonid width, 0.7; length of M_2, 1.25; trigonid width, 0.9; talonid width, 0.85; length of M_3, 1.3; trigonid width, ca. 0.8; talonid width, 0.65; alveolar length of P_2, ca. 0.9; P_3, 0.6; P_4, 1.1; depth of the horizontal ramus of the lower jaw under P_3, 1.2; under P_3, 1.7; under M_1 and M_2, 1.75 (holotype).

Comparison. *Jarveia minuscula* is substantially smaller than *J. erronea* and differs from this species in the absence of postcingulid on M_2, the greater anterior curvature of M^2, and in certain structural details of this tooth: the less developed parastyle, ectoflexus, and hypoconal shelf and the better pronounced precingulum.

Remarks. Averianov (1995) redescribed the holotype of *J. minuscula* (dentary fragment with M_1–M_3). He also described a maxillary fragment with M^1 and M^2 from the type locality, which he determined as *Jarveia* sp., and indicated that this specimen could have belonged to a species other than *J. minuscula*, because it is somewhat larger in size. However, the same size ratio of the upper and lower molars is observed in *J. erronea*, *Praolestes* (Kondrashov et al., 2004a), and *Bayanulanius* (Meng et al., 1998); thus, the maxillary fragment of *Jarveia* sp. possibly belongs to *J. minuscula.*

Occurrence. Upper Paleocene (Gashatan) of Kazakhstan.

Material. In addition to the holotype (found by L.A. Nessov in 1984), the type locality yielded a left maxillary fragment with M^1 and M^2 and alveoli of P^4 and M^3 (specimen ZIN, no. 79206; collected by Nessov in 1985).

***Jarveia erronea* Kondrashov, Lopatin et Lucas, 2004**

Plate 5, figs. 3 and 4

Jarveia erronea: Kondrashov et al., 2004a, p. 190, text-figs. 7–9.

Holotype. PIN, no. 3104/434, left maxillary fragment with P^4–M^3; Mongolia, Tsagan-Khushu locality; Upper Paleocene, Naran-Bulak Formation, Zhigden Member.

Description (Fig. 20). The base of the zygomatic process of the maxilla is in line with the middle of M^2. The angle between the process and the bone body is about 15°. The anterior side of the process has a distinct depression.

P^4 is displaced lingually in relation to the molar row. The paracone is large, occupies the central part of the crown. The metacone is absent. The stylar shelf is absent; the parastyle is well-developed, projects anteriorly. The metastyle is relatively large, the metastylar crest is connected to the paracone. Judging from the preserved base, the protocone is relatively large. Conules are absent.

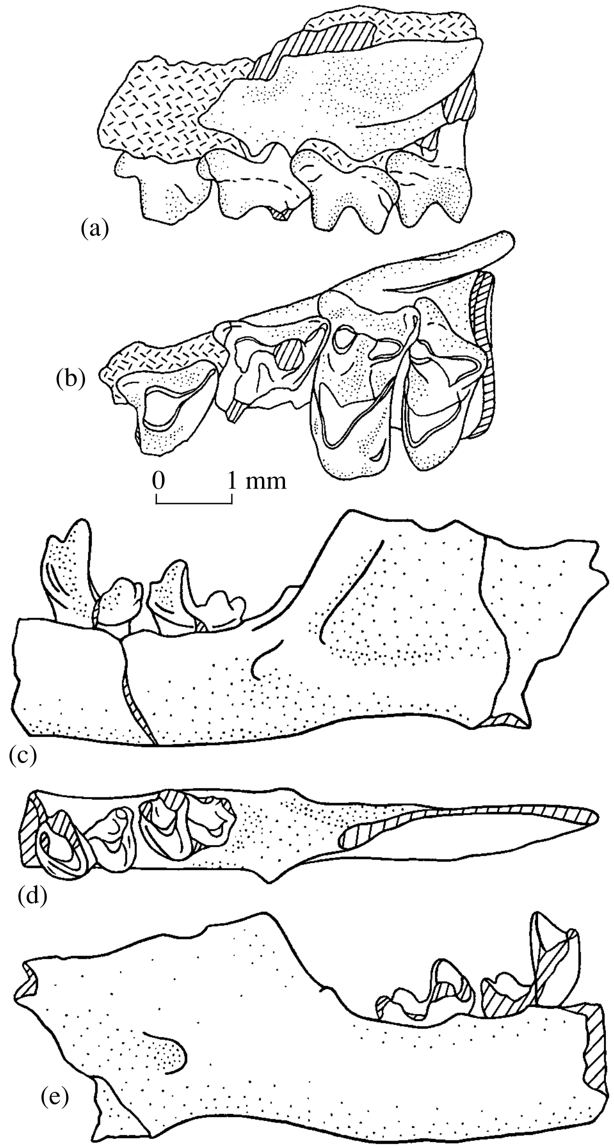


Fig. 20. *Jarveia erronea* Kondrashov, Lopatin et Lucas, 2004: (a, b) holotype PIN, no. 3104/434, left maxillary fragment with P^4–M^3: (a) labial and (b) occlusal views; (c–e) specimen PIN, no. 3104/428, left dentary fragment with partially preserved M_2 and complete M_3: (c) labial, (d) occlusal, and (e) lingual views; Tsagan-Khushu locality, Mongolia; Zhigden Member, Naran-Bulak Formation, Upper Paleocene.

In M^1, the paracone is larger than the metacone. The metacrista is short. The stylar shelf is absent, the parastyle and metastyle are of the same structure, as in P^4. The anterior wall of the crown is almost straight. The tooth has a narrow postmetaconule crest extending along the posterior wall of the metacone to the base of the metastyle.

In M^2, the paracone and metacone are widely spaced and smaller than those of M^1. The lingual slopes of these cusps project deep into the trigon basin. The metacrista is very short. The well-developed parastyle projects anterolabially, and the large metastyle projects posterolabially; the labial side of the crown is slightly concave (a distinct ectoflexus is present). The protocone is massive, its apex is opposed to the apex of the paracone. The preprotocrista reaches the anterior base of the paracone. The postprotocrista extends to a weak metaconule, which is low and poorly pronounced. The paraconule is absent. The narrow postmetaconule crest connects the metaconule to the metastyle. The precingulum is short and weak. The hypoconal shelf has a distinct low crest and a small, lingually located cusp.

M^3 is smaller than M^2. The metacone is somewhat reduced and displaced slightly lingually. The parastylar lobe projects anterolabially. The paracrista is strong, but does not reach the parastyle. The metastylar lobe is absent. The protocone is pointed. The preprotocrista extends to the anterior base of the paracone. The postprotocrista extends to a small metaconule. A short and weak postmetaconule crest is present between the metaconule and the posterior base of the metacone. The precingulum and hypocone shelf are absent.

The horizontal ramus is low and curved slightly lingually. The angle between the horizontal and ascending rami of the lower jaw is about 130°. The masseteric fossa is relatively deep, the masseteric crest is strong. A distinct tubercle is observed at the base of the masseteric crest. The mandibular foramen is large, oval in shape, faces posteriorly, is located slightly below the level of the tooth row, under the middle of the coronoid process. A circular, dorsally pointed medial tubercle is present at the base of the coronoid process just posterior to M_3.

The crowns of M_2 and M_3 curve labially, have a deep hypoflexid. The paraconid is positioned highly, displaced slightly lingually. The precingulid is short, but relatively strong. M_2 has a weak postcingulid, which extends dorsolingually from the posterior base of the hypoconid to the posterolabial base of the hypoconulid. The cristid oblique is connected to the base of the posterior wall of the trigonid. The talonid is wide, has a large hypoconid. The hypoconulid is relatively large, distinctly separated from the hypoconid, and projects posteriorly. The entoconid is fused at the base with the hypoconulid (most of the entoconid is not preserved).

In M_3, the talonid is substantially narrower than the trigonid. The trigonid is compressed slightly longitudinally. The talonid basin is open lingually. The cristid oblique is connected to the posterior wall of the trigonid close to the protoconid. The hypoconid is large, projects labially. The hypoconulid is almost as large as the hypoconid, projects posteriorly. The entoconid is fused at the base with the hypoconulid and is considerably reduced.

Measurements, mm. Length of P^4, 1.4; length of M^1, 1.6; length of M^2, 1.5; width of M^2, 2.5; length of M^3, 1.1; width of M^3, 2.3 (holotype).

Depth of the horizontal ramus of the lower jaw under M_2, 1.7; under M_3, 1.6; length of M_2, ca. 1.45; length of M_3, more than 1.35; width of trigonid of M_3, ca. 0.95; width of the talonid of M_3, ca. 0.7 (specimen PIN, no. 3104/428).

Comparison. *Jarveia erronea* is substantially larger than the type species and differs from it in the well-developed postcingulid of M_2, M^2 which is curved anteriorly to a lesser extent, and in certain structural details of this tooth: better developed parastyle, ectoflexus, and hypoconal shelf and a less developed precingulum.

Occurrence. Upper Paleocene (Gashatan) of Mongolia.

Material. In addition to the holotype, the type locality yielded a left dentary fragment with partially preserved M_2 and almost complete M_3 (specimen PIN, no. 3104/428).

SUBFAMILY EOSORICODONTINAE LOPATIN, 2005

Eosoricodontinae: Lopatin, 2005b, p. 842.

Type genus. *Eosoricodon* Lopatin, 2005, Lower Eocene of Mongolia.

Diagnosis. Small nyctitheriids with partially molarized P_4 with low paraconid, high protoconid, rudimentary metaconid, and unicuspid cingulid-like talonid. P_1 and P_2 single-rooted. P_3 double-rooted. $M_1 > M_2 > M_3$. Paraconid of M_1–M_3 substantially elongated, projecting strongly anteriorly; trigonid low; talonid short. Hypoconulid relatively small, displaced lingually, located directly posterolabial to entoconid, separated from entoconid by distinct fold and connected to hypoconid by postcristid. Talonid of M_3 short. Upper molars widened moderately transversely, with concave posterior side of crown, well-developed stylar lobes, and moderately developed hypoconal shelf.

Generic composition. Type genus.

Comparison. The Eosoricodontinae differ from the Nyctitheriinae, Praolestinae, Asionyctiinae, and Amphidozotheriinae in the structure of P_4 and the paraconid and talonid of M_1–M_3. In addition, they differ from the Nyctitheriinae, Praolestinae, and Asionyctiinae in the reduced P_2 and other length ratio of the lower molars, and they differ from the Amphidozotheriinae in the double-rooted P_3. The structure of the upper molars of Eosoricodontinae clearly differs from that of Asionyctiinae and Praolestinae in the narrower crowns with a concave posterior side and better developed hypoconal shelf, and from Praolestinae, in the larger stylar lobes.

Remarks. The Eosoricodontinae are similar to the Soricolestinae (Soricidae) in the structure of P_4 and M_3 and differ in the presence of P_1, less reduced P_2 and P_3, and in the presence of a distinct hypoconulid, which is not transformed into the entostylid, on M_1–M_3. Hence, they are regarded as Nyctitheriidae with a peculiar specialization pattern and are not included in Soricidae (see Lopatin, 2005b).

Genus *Eosoricodon* Lopatin, 2005

Eosoricodon: Lopatin, 2005b, p. 843.

Type species. *Eosoricodon terrigena* Lopatin, 2005, Lower Eocene of Mongolia.

Diagnosis. The same as the diagnosis of the subfamily.

Species composition. Type species.

Eosoricodon terrigena Lopatin, 2005

Plate 5, figs. 5–10

Eosoricodon terrigena: Lopatin, 2005b, p. 843, text-figs. 1 and 2.

Holotype. PIN, no. 3104/900, right dentary fragment with M_2 and alveoli of M_3; Mongolia, Tsagan-Khushu locality; Lower Eocene, Naran-Bulak Formation, Bumban Member.

Description (Fig. 21). The zygomatic process of the maxilla is rudimentary. M^1 and M^2 are similar in shape and structure, M^2 is somewhat shorter and wider than M^1, with a deeper ectoflexus and shorter metastylar wing. The stylar lobes are large, the stylar cusps are relatively small. The ectocingulum is narrow. The paracrista, centrocrista, and, particularly, the metacrista are well-developed. The labial cusps are closely positioned. The paracone is higher and more massive than the metacone. The paraconule is large, massive; the metaconule is ridgelike. The protocone is compressed longitudinally, the preprotocrista and postprotocrista are sharp; on the anterior side of the crown between the protocone and paraconule, there is a distinct depression. The precingulum is short, but distinct. The hypocone is clearly pronounced, the hypoconal shelf is small. The postcingulum is narrow and weak. M^3 is three-rooted, short and wide, with a projecting parastylar wing.

The horizontal ramus of the lower jaw is low, it is approximately as high as the crown of M_2. The lower edge of the jaw is straight over most of its extent and slightly curves under M_2 and M_3. The anterior mental foramen is large, located under P_2; the posterior mental foramen is smaller, located under the posterior root of P_3. The symphysis reaches posteriorly the line of P_1/P_2. The masseteric fossa is deep, bordered anteriorly by a well-developed crest. The anteroventral corner of the masseteric fossa has a small, deep pit. The medial crest is weak.

Judging from the preserved alveoli, incisors are small, the canine is larger than I_3 or P_1; the size ratios of premolars are $P_4 > P_3 \gg P_2 > P_1$. P_1 is single-rooted. The single root of P_2 is composed of two fused roots. P_3 and P_4 are large, with separate, widely spaced roots. P_3 has a low protoconid, very small paraconid, well-pronounced posterior cingular cuspule, posterolabial postcingulid, and weak entocingulid, which reaches anteriorly the middle of the crown.

P_4 is substantially larger than P_3, has a well-developed paraconid, well-pronounced paracristid, weak precingulid, high massive protoconid with a flat, steep posterior wall. The shearing lingual crest of the protoconid descends to the considerably reduced metaconid, which is fused at the base with the protoconid but has its own small apex. The talonid is short, with a high, longitudinal shearing crest, which extends along the lingual margin from the posterior base of the metaconid to the well-pronounced terminal cuspule. Labial to the longitudinal crest, the talonid is deepened down to the base by a large fold, which is bordered posteriorly by a distinct postcingulid, which descends ventrolabially from the terminal cuspule.

M_1 and M_2 are similar in structure. The trigonid is slightly longer and wider than the talonid. The paraconid is elongated; the paracristid is sharp, directed anterolingually; the paracristid notch is well developed. The precingulid is weak, extends from the anterolabial edge of the paraconid to the level of the protoconid apex. The protoconid and metaconid are inclined strongly lingually, compressed longitudinally, are separated by a deep protocristid notch; the protoconid is much higher and more massive than the metaconid. The posterior wall of the trigonid is vertical. The hypoflexid is relatively small. The ectocingulid and entocingulid are absent. The cristid oblique is connected to the middle of the base of the posterior wall of the protoconid; sometimes, it has a poorly pronounced branch ascending almost to the apex of the metaconid. The hypoconid is relatively large and high. The entoconid is small, longitudinal extended. The entocristid is high, closes a deep talonid basin. The postcristid terminates in the hypoconulid. The hypoconulid is displaced lingually, positioned close to the entoconid, but is separated from it by a small postentoconid fold. The postcingulid is very weak, extends from the base of the posterior wall of the hypoconid to the base of the hypoconulid.

M_3 is narrow, its talonid is reduced. The precingulid is weak, the paraconid is long, projects strongly anterolingually. The protoconid and metaconid are approximately equal in size. The hypoflexid is small. The cristid oblique is very short, connected to the middle of the base of the posterior wall of the protoconid. The entoconid is substantially smaller than the other talonid cusps, fused with the high entocristid. The hypoconulid projects slightly posteriorly. The postcristid structure is the same as in M_1 and M_2. The postentoconid fold is distinct. The postcingulid is absent.

Measurements, mm. For tooth measurements, see Table 20. Length of M^1 and M^2, 2.35 (specimen PIN, no. 3104/901).

Depth of the horizontal ramus of the lower jaw on the lingual side: under P_2, 0.8; under P_3, 0.95; under P_4, 1.05; under M_1, 1.1 (PIN, no. 3104/484); under M_2, 1.2 (PIN, no. 3104/480); 1.15 (PIN, no. 3104/482); 1.1 (PIN, no. 3104/481); and 1.0 (PIN, no. 3104/483); and under M_3, 1.1 (PIN, no. 3104/481) and 1.0 (PIN, no. 3104/482).

Occurrence. Lower Eocene (Bumbanian) of Mongolia.

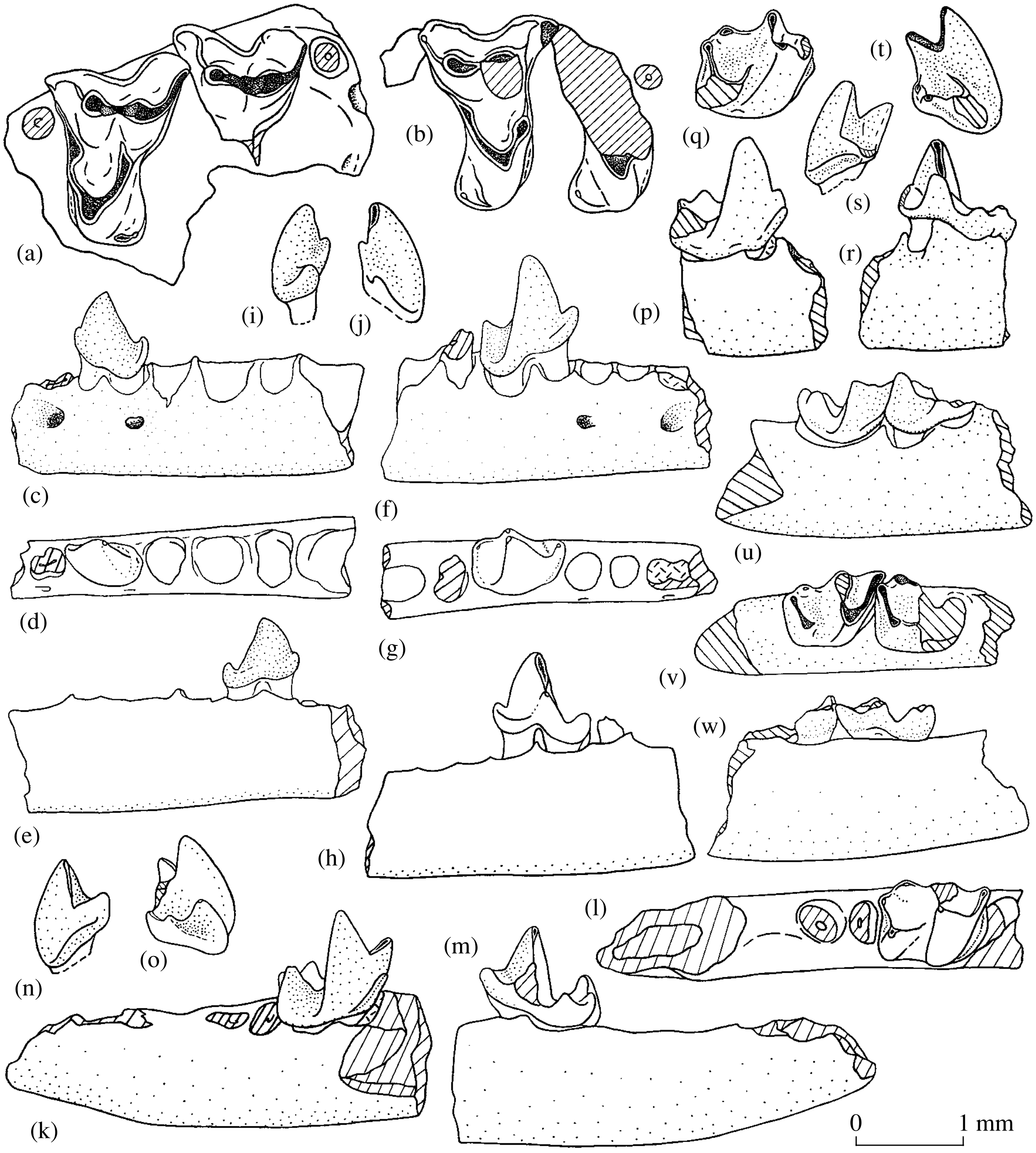


Fig. 21. *Eosoricodon terrigena* Lopatin, 2005: (a) specimen PIN, no. 3104/901, left maxillary fragment with M^1 and M^2 and alveoli of M^3, occlusal view; (b) specimen PIN, no. 3104/902, right M^1 and M^2 and fragmentary M^3, occlusal view; (c–e) specimen PIN, no. 3104/890, left dentary fragment with P_3 and alveoli of P_1, P_2, P_4–M_1: (c) labial, (d) occlusal, and (e) lingual views; (f–j) specimen PIN, no. 3104/891, right dentary fragment with P_4 and alveoli of P_2, P_3, and M_1: (f) labial, (g) occlusal, and (h) lingual views, (i) P_4, anterior view, and (j) P_4, posterior view; (k–o) holotype PIN, no. 3104/900, right dentary fragment with M_2 and alveoli of M_3: (k) labial, (l) occlusal, and (m) lingual views, (n) M_2, anterior view, and (o) M_2, posterior view; (p–t) specimen PIN, no. 3104/480, right dentary fragment with M_2: (p) labial view, (q) M_2, occlusal view, (r) lingual view, (s) M_2, anterior view, and (t) M_2, posterior view; (u–w) specimen PIN, no. 3104/481, right dentary fragment with M_2 and M_3: (u) labial, (v) occlusal, and (w) lingual views; Tsagan-Khushu locality, Mongolia; Bumban Member, Naran-Bulak Formation, Lower Eocene.

Material. In addition to the holotype, the collection of PIN contains 21 specimens from the type locality: a maxillary fragment with M^1–M^3 and alveoli of P^4 (PIN, no. 3104/902); a maxillary fragment with M^1 and M^2 and alveoli of M^3 (PIN, no. 3104/901); 19 dentary fragments: with P_3 and alveoli of P_1, P_2, P_4, and M_1 (PIN, no. 3104/890); with P_3 and alveoli of C_1–P_2, and P_4 (PIN, no. 3104/889); with P_4 and alveoli of P_2, P_3, and M_1 (PIN, no. 3104/891); two specimens with M_2, the talonid of M_1, and alveoli of M_3 (PIN, nos. 3104/893 and 894); one specimen with the talonid of M_1, roots of M_2, and M_3 (PIN, no. 3104/895); with M_2 and M_3 (PIN, no. 3104/481); two specimens with M_2 (PIN, nos. 3104/480 and 896); 10 specimens without teeth: one with alveoli of I_3–P_4 (PIN, no. 3104/892), one with alveoli of C_1–M_1 (PIN, no. 3104/484), one with alveoli of M_1–M_3 (PIN, no. 3104/903), and seven with alveoli of M_2 and M_3 (PIN, nos. 3104/482, 483, 897–899, 904, 905), three of which (PIN, nos. 3104/897–899) have a partially preserved ascending ramus.

FAMILY SORICIDAE FISCHER VON WALDHEIM, 1817

Soricini: Fischer von Waldheim, 1817, p. 372.

Soricidae: Gray, 1821, p. 300.

Type genus. *Sorex* Linnaeus, 1758; Upper Miocene–Recent of Eurasia and North America.

Diagnosis. Small ectodilambdodont soricoid insectivores with dental formula ranging from $I^3/_3C^1/_1P^3/_3M^3/_3$ to $I1A^{5-2}/_{4-1}P4M^{3-2}/_{3-2}$ (where I1 and P4 are the anterior incisor and posterior premolar, which are always present, M is molars, A is antemolars, including I2–I3, C1, and P2–P3 that are not differentiated in structure; another variant of formulation is 1.1–4.1.3–2). Molars ectodilambdomorph. P^4 semimolariform, with metacone. Upper molars with widely spaced labial cusps, labial crests forming characteristic W-shaped pattern. Styles large, conules absent. Hypoconal shelf wide, hypocone well developed. I^1 and I_1 increased, I_1 procumbent. P_1 absent. I_2, I_3, C_1, P_2, and P_3 (antemolars, or intermediate teeth) single-rooted, with trends towards reduction of each antemolar and compacting and uniformity of the entire tooth row. P_4 double-rooted, semimolariform (partially molarized) or antemolariform, with cingulid-like talonid. $M_1 > M_2 \gg M_3$. Paraconid of M_1–M_3 substantially elongated, projecting anteriorly; trigonid relatively low; talonid short, entocristid usually well developed; hypoconulid displaced to lingual edge and transformed into entostylid or completely reduced. Talonid of M_3 short and narrow.

Composition. Seven subfamilies: Soricolestinae Lopatin, 2002, Middle Eocene of Mongolia; Heterosoricinae Viret et Zapfe, 1951, Middle Eocene–Upper Miocene of North America, Upper Eocene–Upper Miocene of Europe, Lower Oligocene–Lower Pliocene of Asia; Crocidosoricinae Reumer, 1987, Lower Oligocene–Upper Miocene of Europe, Upper Oligocene–Lower Miocene of Asia; Limnoecinae Repenning, 1967, Lower Miocene–Pliocene of North America, Upper Miocene of Europe; Allosoricinae Fejfar, 1966, Lower Miocene–Upper Pliocene of Europe, Upper Miocene–Lower Pliocene of Asia; Soricinae Fischer von Waldheim, 1817, Lower Miocene–Recent of Eurasia, Africa, and North America; Crocidurinae Milne-Edwards, 1868, Middle Miocene–Recent of Eurasia and Africa.

Table 20. Measurements of the cheek teeth of *Eosoricodon terrigena* Lopatin, 2005

Specimen PIN, no.	Tooth	Length	Width
3104/901	M^1	1.35	1.7
3104/902	M^2	1.25	1.75
3104/889	P_3	0.7	0.4
3104/890	P_3	0.7	0.4
3104/891	P_4	0.9	0.6
3104/894	M_1	~1.1	–
3104/893	M_1	~1.15	–
	M_2	1.1	–
3104/900 (holotype)	M_2	1.05	–
3104/480	M_2	~1.1	0.8
3104/481	M_3	0.95	0.65

Comparison. The Soricidae differ from the other Soricoidea in the ectodilambdomorph structure of molars, primarily in the hypoconulid transformed into the entostylid (or completely reduced) on lower molars, and in the characteristic structure of $I^1/_1$, intermediate antemolars, and P_4.

SUBFAMILY SORICOLESTINAE LOPATIN, 2002

Soricolestinae: Lopatin, 2002c, p. 79.

Type genus. *Soricolestes* Lopatin, 2002, Middle Eocene of Mongolia.

Diagnosis. Small primitive shrews with differentiated lower antemolars and dental formula $I_3C_1P_3M_3$ (1.5.1.3). P_4 large, partially molarized: with low paraconid, high protoconid, rudimentary metaconid, and well-developed unicuspid talonid. $M_1 \geq M_2 > M_3$. Entostylid of M_1 and M_2 large, well-developed. M_3 having hypoconulid, its postcristid separated from entoconid. Horizontal ramus of lower jaw long and low. Mental foramen under P_3. Ascending ramus of lower jaw long, masseteric fossa large and deep, external temporal fossa absent, internal temporal fossa superficial, without pocketlike depression.

Generic composition. Type genus.

Comparison. The Soricolestinae differ from the Heterosoricinae, Crocidosoricinae, Soricinae, Crocidurinae, Limnoecinae, and Allosoricinae in the presence of clearly differentiated antemolars, the structure of P_4 and M_3, and in the long ascending ramus of the lower jaw with a poorly pronounced internal temporal fossa. In addition, in contrast all the subfamilies listed, except for Heterosoricinae, soricolestines have a masseteric fossa and lack a pocketlike depression of the internal temporal fossa. The dental formula is more complete, at least, includes an additional antemolar compared to the other Soricidae (except for *Srinitium* Hugueney, 1976), the entostylid of M_1 and M_2 is better developed, the mental foramen is positioned more anteriorly.

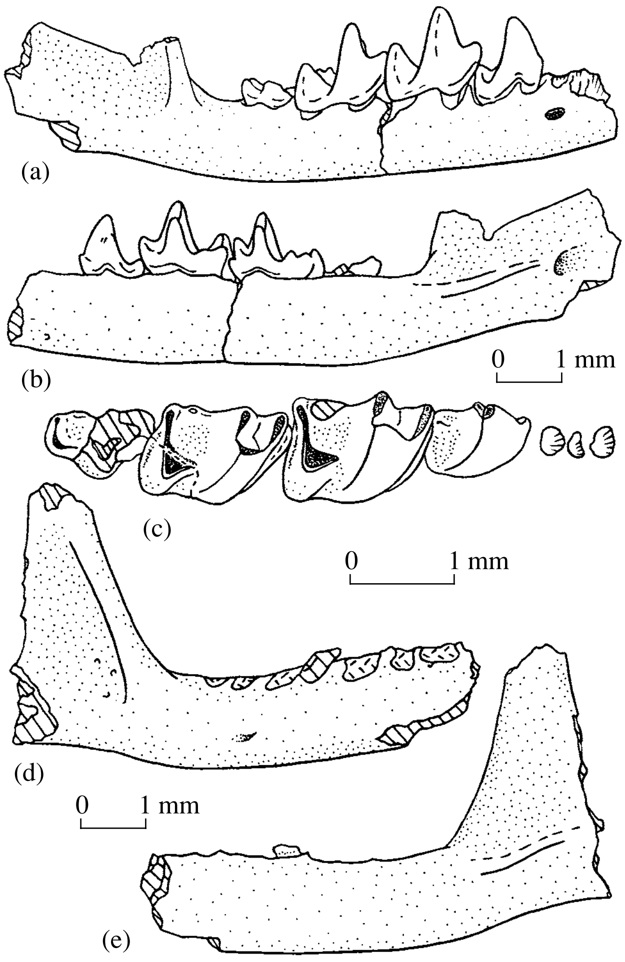


Fig. 22. *Soricolestes soricavus* Lopatin, 2002: (a–c) holotype PIN, no. 3107/405, right dentary fragment with P_4–M_3 and alveoli for C_1–P_3: (a) labial and (b) lingual views, and (c) occlusal view of alveoli and teeth; (d, e) specimen PIN, no. 3107/410, right dentary fragment with incomplete ascending ramus: (d) labial and (e) lingual views; Khaychin-Ula 2 locality, Mongolia; Khaychin Formation, Middle Eocene.

Genus *Soricolestes* Lopatin, 2002

Soricolestes: Lopatin, 2002c, p. 79.

Type species. *Soricolestes soricavus* Lopatin, 2002, Middle Eocene of Mongolia.

Diagnosis. The same as the diagnosis of the subfamily.

Species composition. Type species.

Soricolestes soricavus Lopatin, 2002

Plate 5, figs. 11–16

Soricolestes soricavus: Lopatin, 2002c, p. 79, text-figs. 1–3.

Holotype. PIN, no. 3107/405, right dentary fragment with P_4–M_3 and alveoli of C_1–P_3; Mongolia, Khaychin-Ula 2 locality; Middle Eocene, Khaychin Formation.

Description (Figs. 22, 23). The horizontal ramus of the lower jaw is elongated, very low, lower than M_1 or M_2 and only slightly higher than M_3. The lower edge of the bone slightly curves. The lower part of the labial surface is frequently flattened at the level of molars. The mental foramen is large, located under P_3. Sometimes, the labial side of the jaw has a very small additional foramen under the space between M_2 and M_3 (Fig. 22d); it faces posteriorly and coincides with a short and narrow groove. The symphysis is long, weak, reaches posteriorly the line of the anterior root of P_4. At P_2, the lower part of a symphysial region has a small postsymphysial foramen, which is open anteromedially.

The distance between M_3 and the base of the coronoid process is approximately equal to the length of M_3. The angle between the coronoid process and the horizontal ramus is approximately 110–115°. The length of the ascending ramus at the incisure between the articular and angular processes (lower sigmoid incisure) is equal to the distance from the anterior edge of M_2 to the base of the coronoid process. The coronoid process is high, more than 2.5 times as high as the horizontal ramus. The dorsal part of the coronoid process is very short, acute-angled, with an almost vertical posterior side. The masseteric fossa is deep, bordered anteriorly by a strong crest, which ascends along the coronoid process, closely approaching its apex. In the anteroventral corner of the masseteric fossa, the bone surface is rough, with one or several tiny pits. The internal temporal fossa is superficial, the crest at its base is sharp, well-pronounced, ascends dorsally in the posterior part. The mandibular foramen is large, located at the level of the alveolar margin of the horizontal ramus and displaced far posteriorly close to the lower sigmoid incisure. This incisure is broad, its height suggests that the condyle was located above the apices of the cusps of molars. The lower edge of the ascending ramus is curved strong dorsally, the base of the angular process is directed posteroventrally.

Judging from the alveoli (Figs. 23a, 23b), I_1 is relatively large, elongated, directed anteriorly, while I_2 and, particularly, I_3 are considerably reduced. The inclinations of alveoli of I_1, I_2, and I_3 with reference to the horizontal ramus are 10°, 20°, and 30°, respectively. The alveolus of I_3 is displaced labially. The alveolus of the canine is relatively large, circular; the inclination is about 40°. Two small alveoli, presumably for single-rooted P_2 and P_3, are present between alveolus of C_1 and P_4. The alveolus of P_2 is substantially smaller than the alveolus of P_3. Thus, the size ratios of alveoli of the single-rooted antemolars between I_1 and P_4 are $C_1 > P_3 > P_2 > I_2 > I_3$ (i.e., $A_3 > A_5 > A_4 > A_1 > A_2$).

P_4 is double-rooted, large, high. The paraconid is small, basal, positioned anterolingually; sometimes, it is considerably reduced and almost invisible in labial view. The precingulid is very short and weak or absent.

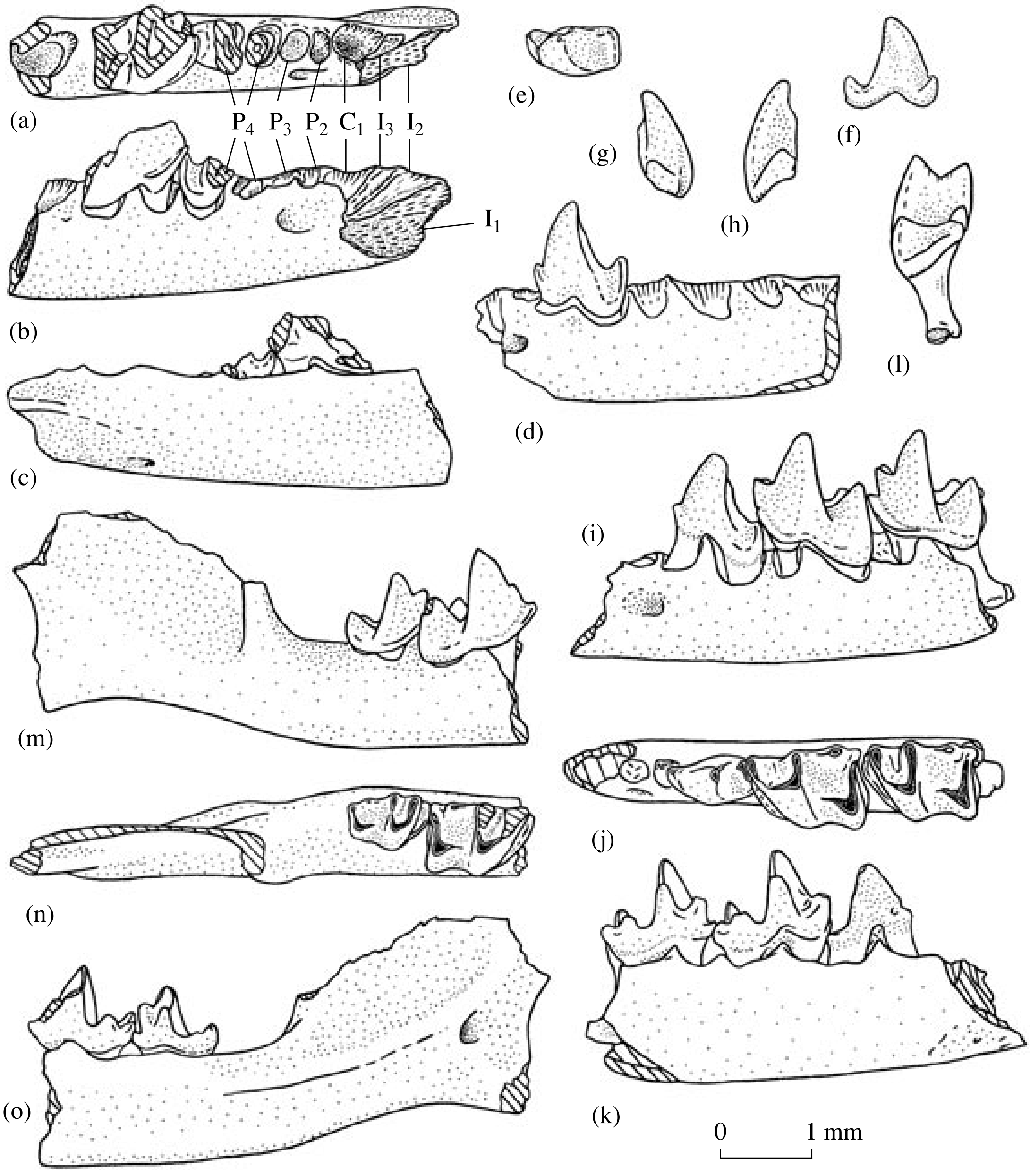


Fig. 23. *Soricolestes soricavus* Lopatin, 2002: (a–c) specimen PIN, no. 3107/409, right dentary fragment with damaged P_4–M_1 and alveoli of I_1–P_3: (a) occlusal, (b) labial, and (c) lingual views; (d–h) specimen PIN, no. 3107/408, left dentary fragment with P_4: (d) labial view, (e) P_4, occlusal view, (f) P_4, lingual view, (g) P_4, anterior view, and (h) P_4, posterior view; (i–l) specimen PIN, no. 3107/406, left dentary fragment with P_4–M_2: (i) labial, (j) occlusal, and (k) lingual views and (l) M_2, posterior view; (m–o) specimen PIN, no. 3107/407, right dentary fragment with M_2 and M_3: (m) labial, (n) occlusal, and (o) lingual views; Khaychin-Ula 2 locality, Mongolia; Khaychin Formation, Middle Eocene.

The protoconid is high, conical–pyramidal, with a flat posterior wall. Its posterolingual and posterolabial corners form sharp ribs; the posterolingual edge has a rudimentary metaconid in the shape of a small thickening, which is located much lower than the apex of the protoconid. The talonid is short, lacks a posterior groove (sulcus posterior); the lingual corner projects strongly posteriorly. A relatively high posterolingual cusp is present. The posterolabial margin has a distinct postcingulid.

The shape of M_1–M_3 is typical of shrews: the trigonid is elevated, the cusps are inclined lingually; in M_1 and M_2, the trigonid is only slightly longer and wider than the talonid.

Table 21. Measurements of the lower cheek teeth of *Soricolestes soricavus* Lopatin, 2002

Specimen PIN, no.	Tooth	Total length	Talonid length	Trigonid width	Talonid width
3107/408	P_4	1.05	0.3	0.6	0.55
3107/405 (holotype)	P_4	1.05	0.3	0.6	0.55
	M_1	1.35	0.65	1.0	1.0
	M_2	1.3	0.6	0.95	0.9
	M_3	~0.9	0.4	–	0.5
3107/406	P_4	1.0	0.25	0.6	0.55
	M_1	1.38	0.6	0.9	0.95
	M_2	1.33	0.6	0.85	0.85
3107/407	M_2	1.3	0.6	0.95	0.9
	M_3	0.95	0.45	0.87	0.52

M_1 is slightly larger than M_2. The precingulid is well-developed, extends on the anterolabial side of the crown from the line of the paracristid notch to the line of the apex of the protoconid. The paraconid is relatively low. The paracristid curves abruptly anterolabially, has a distinct notch. The trigonid basin is relatively broad and deep. The entocingulid is very weak, looks like a small elevation at the level of the space between the paraconid and metaconid. The protoconid and metaconid are compressed strongly longitudinally, positioned close to one another; the protoconid is much more massive and higher than the metaconid. The posterior wall of the trigonid is vertical. The hypoflexid is relatively shallow. The ectocingulid is very narrow and weak. The hypoconid is relatively large, projects strongly posterolabially. The cristid oblique reaches the middle of the base of the posterior wall of the protoconid. The entoconid is small, conical. The entocristid is distinct, relatively high, closes the talonid basin lingually. The postcristid is free, terminates in the entostylid. The entostylid is relatively large (slightly smaller than the entoconid), but low, separated from the entoconid by a small postentoconid fold, projects substantially posterolingually. The postcingulid is well developed, extends from the base of the posterior wall of the hypoconid to the entostylid.

M_2 is similar in structure to M_1, but differs in the smaller size and some minor features. Its precingulid is better developed and originates from the level of the apex of the paraconid. The paraconid is smaller, the paracristid curves more gently. The trigonid basin is narrow because the paraconid and metaconid are positioned closely. The entocingulid is indiscernible. The protocristid is longer because the protoconid and metaconid are more widely spaced. The hypoflexid is deeper, all cusps are less massive than in M_1.

M_3 is substantially smaller than M_2. The trigonid structure is similar to that of M_2. The hypoflexid is deep, the ectocingulid is weak. The talonid is narrow, but is subequal in length to the trigonid. The hypoconid is well developed, the cristid oblique is weak. The entoconid is considerably reduced and fused with a relatively high entocristid, which closes the talonid basin lingually. The hypoconulid is larger than the entoconid, separated from it by a distinct postentoconid fold, and connected to the hypoconid by a short postcristid. The postcingulid is absent.

Measurements, mm. For tooth measurements, see Table 21. Length of tooth rows in the holotype: P_4–M_3, 4.6; P_4–M_2, 3.7; P_4–M_1, 2.35; M_1–M_3, 3.7; M_1–M_2, 2.8; M_2–M_3, 2.35; specimen PIN, no. 3107/406: P_4–M_2, 3.6; P_4–M_1, 2.3; M_1–M_2, 2.7; specimen PIN, no. 3107/407: M_2–M_3, 2.37.

Alveoli of antemolars (length × width): C_1, 0.55 × 0.4; P_2, 0.2 × 0.35; P_3, 0.33 × 0.35 (specimen PIN, no. 3107/409), 0.35 × 0.3 (holotype and specimen PIN, no. 3107/406), 0.3 × 0.3 (PIN, no. 3107/408).

Height of the coronoid process (specimen PIN, no. 3107/410), ca. 4.0. For depth of the horizontal ramus of the lower jaw, see Table 22.

Occurrence. Middle Eocene (Irdinmanhan) of Mongolia.

Material. In addition to the holotype, the collection of PIN contains five dentary fragments from the type locality: with P_4–M_2 and alveolus of P_3 (PIN, no. 3107/406); with M_2 and M_3 and partially preserved ascending ramus (PIN, no. 3107/407); with P_4 and alveoli of P_3, M_1, and M_2 (PIN, no. 3107/408); with par-

Table 22. Depth of the horizontal ramus of the lower jaw of *Soricolestes soricavus* Lopatin, 2002 on the lingual side (collection of PIN)

Level	Holotype	no. 3107/406	no. 3107/407	no. 3107/408	no. 3107/409	no. 3107/410
under P_2	1.15	–	–	–	1.25	–
under P_3	1.2	1.2	–	–	1.25	–
under P_4	1.25	1.25	–	1.25	1.25	–
under M_1	1.3	1.35	–	1.35	1.35	1.5
under M_2	1.25	1.4	1.30	1.3	1.4	1.45
under M_3	1.25	–	1.25	–	–	1.35
behind M_3	1.2	–	1.15	–	–	1.35

tially broken P_4 and M_1 and alveoli of I_1–P_3 (PIN, no. 3107/409); and with the base of the trigonid of M_2, alveoli of P_4–M_3, and almost complete coronoid process (PIN, no. 3107/410).

FAMILY PLESIOSORICIDAE WINGE, 1917

Plesiosoricini: Winge, 1917, p. 124.

Plesiosoricidae: Romer, 1966, p. 381; Van Valen, 1967, p. 264.

Type genus. *Plesiosorex* Pomel, 1848; Upper Oligocene–Miocene of Eurasia and North America.

Diagnosis. Entodilambdodont soricoid insectivores with dental formula $I^3/_3C^1/_1P^4/_{4-3}M^3/_3$. Molars entodilambdomorph, superficially similar in structure to teeth of erinaceomorph insectivores. P^4 semimolariform. Upper molars with strong hypocone, well-developed stylar lobes, stylocone and conules, long and strong paracrista and metacrista, and deep ectoflexus. I^2 and I_2 increased, I_2 procumbent. I_3, C_1, P_1–P_3 antemolariform. P_4 semimolariform, with paraconid, metaconid, and talonid. $M_1 \geqslant M_2 \geqslant M_3$. M_1 with carnassial notch and strongly elongated paraconid. Trigonid of M_1 and M_2 high; talonid short and wide; entocristid usually well-developed; hypoconulid median, considerably reduced.

Composition. Two subfamilies: Plesiosoricinae Winge, 1917, Middle Eocene–Middle Miocene of Asia, Upper Oligocene–Upper Miocene of Europe, Lower Miocene–Upper Miocene of North America; Butseliinae Quinet et Misonne, 1965, Lower–Middle Eocene of Asia, Lower Oligocene of Europe.

Comparison. The Plesiosoricidae differ from the Nyctitheriidae and Soricidae in the increased I^2 and I_2, the structure of P^4 and P_4, and in the erinaceomorph-like and carnassial features in the structure of the upper and lower molars; in addition, they differ from the Nyctitheriidae in the reduced and antemolariform intermediate teeth, i.e., I_3–P_3.

Remarks. Butler (1948) combined the plesiosoricid genera *Plesiosorex* Pomel, 1848 and *Meterix* Hall, 1929 and the geolabidid genus *Metacodon* Clark, 1936 (which was subsequently shown to be a junior synonym of *Centetodon* Marsh, 1872, see above) in the family Metacodontidae Butler, 1948, which was subsequently recognized by other researchers (Thenius, 1949; Saban, 1954, 1958; etc.). Later, the family name Metacodontidae was replaced by Geolabididae McKenna, 1960 (see McKenna, 1960; McKenna and Bell, 1997) because of synonymy of the type genus; however, the plesiosoricid family (Plesiosoricidae Winge, 1917: Romer, 1966; Van Valen, 1967) was for a long time incorrectly named Metacodontidae by some researchers (see Ziegler, 1990; Rzebik-Kowalska, 1993; Bernor et al., 2004).

SUBFAMILY BUTSELIINAE QUINET ET MISONNE, 1965

Butselidae: Quinet and Misonne, 1965, p. 6.

Butseliidae: McKenna and Bell, 1997, p. 286.

Type genus. *Butselia* Quinet et Misonne, 1965, Lower Oligocene of Europe.

Diagnosis. Plesiosoricids with relatively broad upper molars. Hypocone moderately large, precingulum well-developed. Metaconid of P_4 high and clearly detached. Entoconid of M_1–M_3 reduced, ridgelike.

Generic composition. *Butselia* Quinet et Misonne, 1965, Lower Oligocene of Europe; *Pakilestes* Russell et Gingerich, 1981, basal Middle Eocene of Pakistan; *Ordolestes* gen. nov., Lower Eocene (Bumbanian) of Mongolia.

Comparison. The Butseliinae differ from the Plesiosoricinae in the wider upper molars with a less massive and less detached hypocone and better developed precingulum, in the high and clearly detached metaconid of P_4 and reduced entoconid of M_1–M_3.

Genus *Ordolestes* Lopatin, gen. nov.

Etymology. From the Mongolian *orda* (command post of khan) and the Greek *lestes* (robber).

Type species. *Ordolestes ordinatus* sp. nov.

Diagnosis. Lower molars with considerably reduced metaconid and well-developed cingulid at base of hypoconid. Talonid of M_2 and M_3 narrow, entoconid rudimentary, entocristid long.

Species composition. Type species, Lower Eocene of Mongolia.

Comparison. *Ordolestes* differs from *Butselia* and *Pakilestes* in the presence of a relatively small metaconid and well-developed cingulid at the base of the hypoconid of M_1–M_3, the narrow talonid of M_2 and M_3, greater reduction of the entoconid, and in the relatively longer entocristid.

Ordolestes ordinatus Lopatin, sp. nov.

Plate 6, figs. 1–3

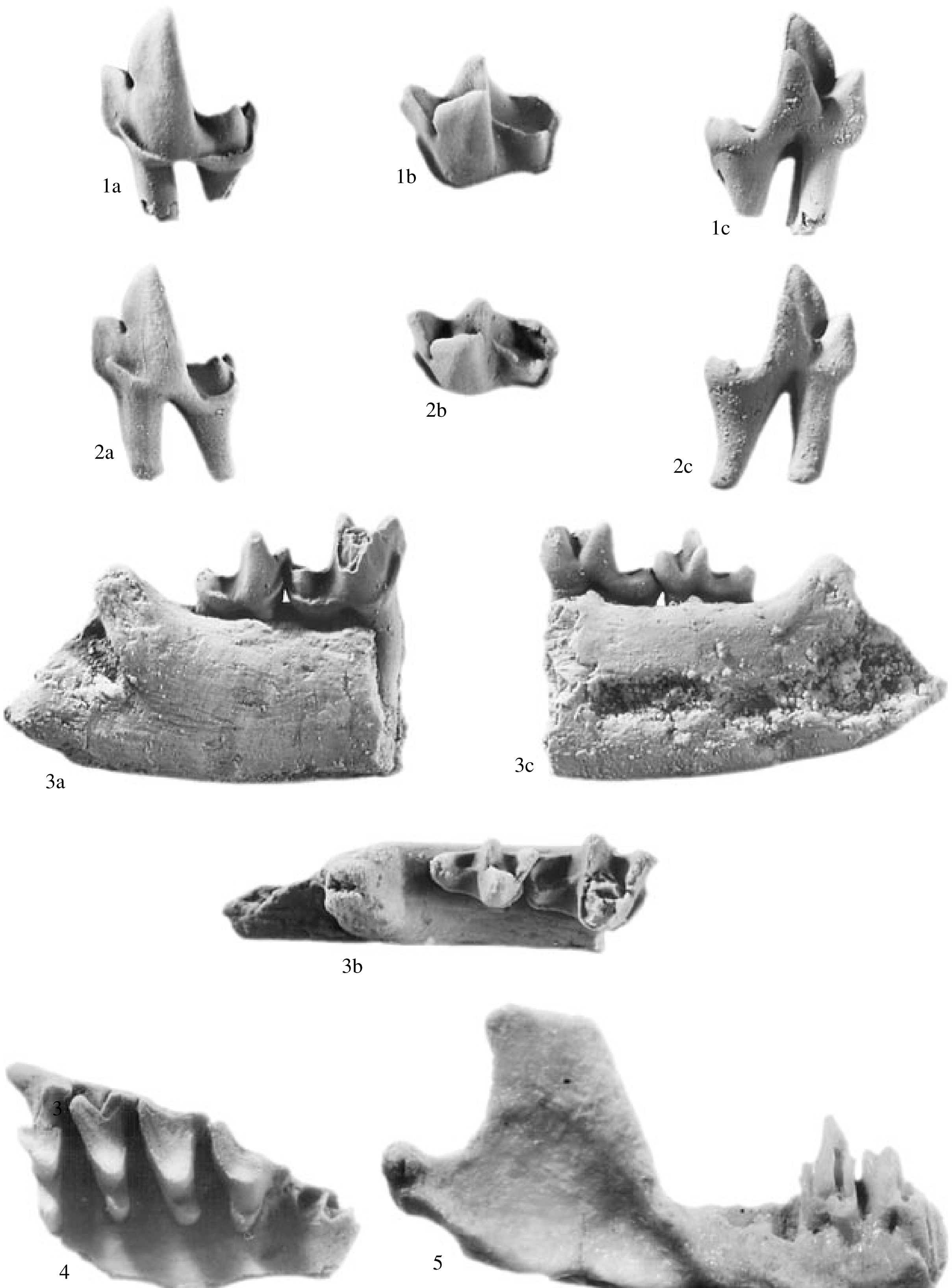
cf. *Hyracolestes* sp.: Russell and Dashzeveg, 1986, p. 289, text-figs. 9d and 9e.

Etymology. From the Latin *ordinatus* (put in order).

Holotype. PIN, no. 3104/952, isolated left M_1; Mongolia, Tsagan-Khushu locality; Lower Eocene, Naran-Bulak Formation, Bumban Member.

Description (Figs. 24, 25). The horizontal ramus of the lower jaw is relatively high and massive. The lower molars have a high and broad trigonid and a reduced, short and narrow talonid. The trigonid basin is small, open. The paraconid is well developed; the paracristid is strong, shearing, with a wide and deep carnassial notch. The anterior side of the paraconid has a distinct, ventrally convex vertical keel, which provides close contact between neighboring cheek teeth. The precingulid is strong. The wear facet on the labial walls of the paraconid and protoconid is of a carnassial type (see Figs. 24k, 24l). The protoconid is massive, high (much higher than the metaconid), with an abrupt anterior wall and a subvertical posterior wall. The protoconid and metaconid are widely spaced (beginning

Plate 6



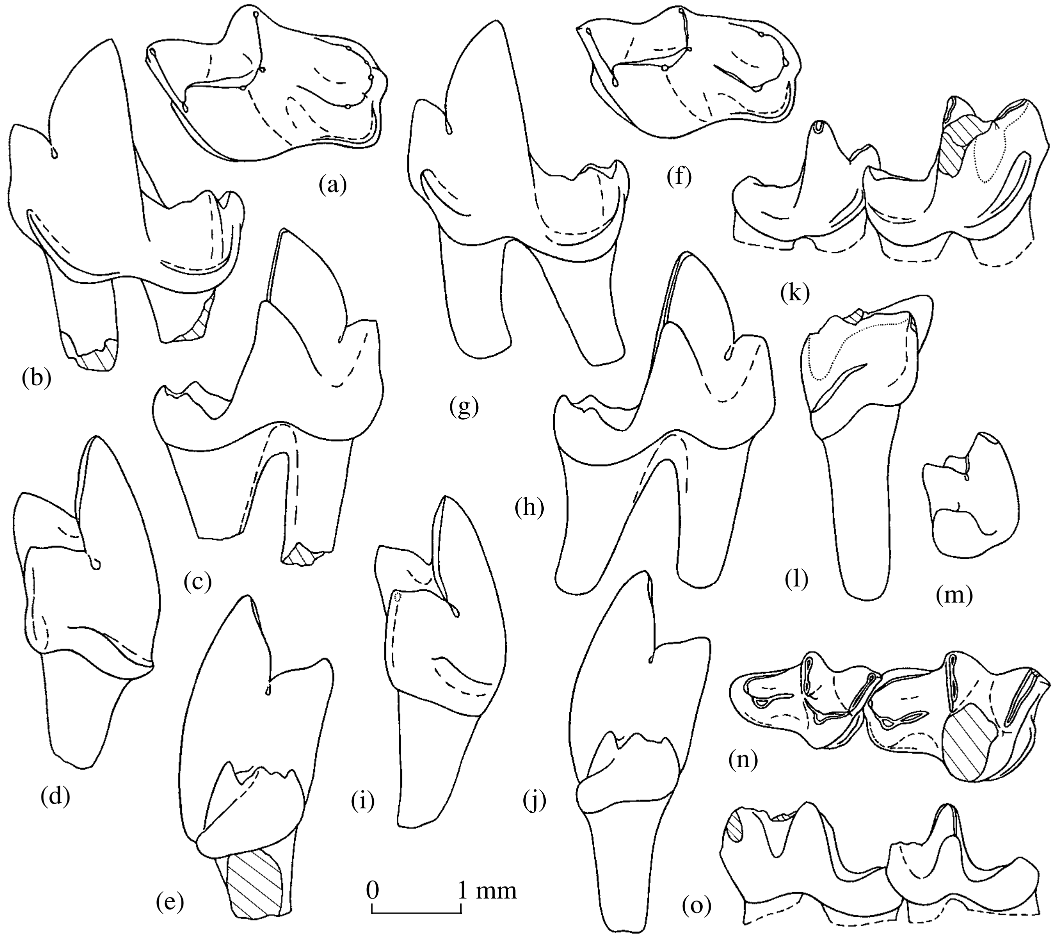


Fig. 24. *Ordolestes ordinatus* sp. nov.: (a–e) holotype PIN, no. 3104/952, left M_1: (a) occlusal, (b) labial, (c) lingual, (d) anterior, and (e) posterior views; (f–j) specimen PIN, no. 3104/954, left M_1: (f) occlusal, (g) labial, (h) lingual, (i) anterior, and (j) posterior views; (k–o) specimen PIN, no. 3104/956, right M_2 and M_3: (k) labial view, (l) M_2, anterior view, (m) M_3, posterior view, (n) M_2 and M_3, occlusal view, (o) M_2 and M_3, lingual view; Tsagan-Khushu locality, Mongolia; Bumban Member, Naran-Bulak Formation, Lower Eocene.

from the midheight of the posterior wall of the trigonid), because the metaconid deviates strongly lingually. Accordingly, the protocristid is divided into two portions; the subvertical protoconid portion is in the shape of a rib on the lingual side of this cusp, while the subhorizontal metaconid portion is represented by a relatively long, transverse cutting crest. The hypoflexid is deep. The talonid is narrow, with a shallow closed basin. The cristid oblique is distinct, relatively low, connected to the base of the posterior wall of the trigonid at the level of the protocristid notch. The hypoconid is relatively large; the hypoconulid is small, but distinct. The entoconid is rudimentary; in M_1, it looks like a small ridgelike cuspule; in M_2 and M_3, it lacks an apex and is completely included in the long and narrow entocristid, which closes the talonid basin. The base of the hypoconid is bordered labially and posteriorly by a cingulid (composed of ectocingulid and postcingulid), which is very strong in M_1, somewhat narrow in M_2, and very short and weak in M_3. M_1 is distinguished by

Explanation of Plate 6

Figs. 1–3. *Ordolestes ordinatus* sp. nov., ×10: (1) holotype PIN, no. 3104/952, left M_1: (1a) labial, (1b) occlusal, and (1c) lingual views; (2) specimen PIN, no. 3104/954, left M_1: (2a) labial, (2b) occlusal, and (2c) lingual views; (3) specimen PIN, no. 3104/956, right dentary fragment with M_2 and M_3: (3a) labial, (3b) occlusal, and (3c) lingual views; Mongolia, Tsagan-Khushu locality; Lower Eocene, Naran-Bulak Formation, Bumban Member.

Figs. 4 and 5. *Asiapternodus mackennai* Lopatin, 2003, ×7: (4) holotype PIN, no. 3107/400, right maxillary fragment with P^4–M^3, occlusal view; (5) specimen PIN, no. 3107/399, right dentary fragment with M_1 and M_2, labial view; Mongolia, Khaychin-Ula 2 locality; Middle Eocene, Khaychin Formation.

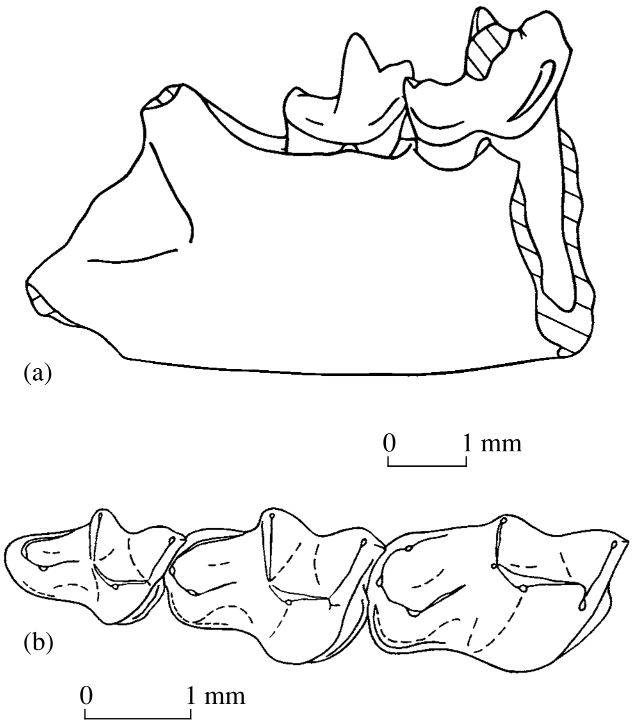


Fig. 25. *Ordolestes ordinatus* sp. nov. (a) specimen PIN, no. 3104/956, right dentary fragment with M_2 and M_3, labial view; (b) reconstruction of right molar row based on specimens PIN, nos. 3104/956 and 954 (left M_1, image reversed laterally), occlusal view; Tsagan-Khushu locality, Mongolia; Bumban Member, Naran-Bulak Formation, Lower Eocene.

its elongated trigonid, which is much higher than in M_2 and M_3. M_3 differs from M_1 and M_2 in the considerably smaller size, relatively longer and narrower talonid, and more poorly pronounced hypoconulid. The roots of molars are relatively short.

Measurements, mm. For tooth measurements, see Table 23. Depth of the horizontal ramus of the lower jaw under M_2, 2.7 (specimen PIN, no. 3104/956).

Remarks. The lower molar (PSS, no. 20-124) from the Bumban Member of the Naran-Bulak Formation of the Tsagan-Khushu locality described by Russell and Dashzeveg (1986, p. 289, text-figs. 9d, 9e) and identified as M_1 or M_2 cf. *Hyracolestes* sp., corresponds in size (2.6 × 1.5) and structure to M_1 of *Ordolestes ordinatus* sp. nov. and undoubtedly belongs to this species.

Table 23. Measurements of the lower molars of *Ordolestes ordinatus* sp. nov.

Specimen PIN, no.	Tooth	Length	Trigonid width	Talonid width	Height at protoconid
3104/952 (holotype)	M_1	2.7	1.6	1.2	2.75
3104/953	M_1	2.55	1.5	1.2	2.75
3104/954	M_1	2.5	1.5	1.15	2.5
3104/955	M_1	–	–	1.15	–
3104/956	M_2	2.1	1.5	0.9	–
	M_3	1.7	1.0	0.65	–

Russell and Dashzeveg (1986) noted a general carnivorous pattern of the molar considered and indicated that it resembled somewhat M_1 of *Hyracolestes* (which was then regarded as ordo et fam. indet.) from the Paleocene of Asia and *Simpsonictis* (Miacidae) from the Paleocene of North America. However, the assignment of *Ordolestes* to Butseliinae is supported by every structural character of its lower molars, including the much higher labial side of the tooth crown compared to the lingual side, the distinctive orientation of the paracristid and protocristid, the presence of vertical paraconid keel, strong precingulid and ectocingulid, and reduced talonid with a long entocristid and a reduced entoconid (see M_1 and M_2 of *Butselia biveri* Quinet et Misonne, 1965: Butler, 1976, p. 256, text-figs. 1D–1H). The reduced metaconid and narrower talonid of *Ordolestes* suggest a more profound predatory specialization of its molars. The same structural characters of the lower molars (the considerable labial rise of the trigonid and reduction of the metaconid and talonid) were developed in parallel in other insectivore groups that presumably adapted to predation, for example, in the short-faced hedgehogs of the subfamily Brachyericinae (see Lopatin and Zazhigin, 2003).

Material. In addition to the holotype, the collection of PIN contains three isolated M_1 (PIN, nos. 3104/953–955) and a dentary fragment with M_2 and M_3 (PIN, no. 3104/956) from the type locality.

SUPERFAMILY SOLENODONTOIDEA GILL, 1872

Solenodontinae: Gill, 1872, p. 19.

Solenodontidae: Dobson, 1882, p. 87.

Solenodontoidea: Paula Couto, 1979, p. 128.

Diagnosis. Zalambdodont soricotan insectivores. Zygomatic arches absent. Antorbital and sagittal crests usually present. Deciduous tooth generation reduced. Molars parazalambdomorph.

Composition. Two families: Apternodontidae Matthew, 1910, Lower Eocene–Lower Oligocene of North America, Middle Eocene of Asia; Solenodontidae Gill, 1872, Pleistocene–Recent, Antilles.

Comparison. The Solenodontoidea differ from the other Soricota in the zalambdomorph molar structure and, usually, in the presence of the antorbital (bordering posteriorly the area where the nasolabialis muscle originates) and sagittal crests.

FAMILY APTERNODONTIDAE MATTHEW, 1910

Apternodontinae: Matthew, 1910, p. 35.

Apternodontidae: Osborn, 1910, p. 519; Asher et al., 2002, p. 17.

Oligoryctidae: Asher et al., 2002, p. 58.

Parapternodontidae: Asher et al., 2002, p. 68.

Type genus. *Apternodus* Matthew, 1903, Middle Eocene–Lower Oligocene of North America.

Diagnosis. Medium-sized and large solenodontoid insectivores. Zygomatic process of maxilla rudimentary. Dental formula: $I^2/_3C^1/_1P^3/_3M^3/_3$. $I_1 > I_2$. P_2 single-rooted. M^1–M^3 without metacone; hypocone reduced; protocone developed to varying degree. Talonid of M_1–M_3 considerably reduced, unicuspid, and lacking basin.

Composition. Four subfamilies: Parapternodontinae Asher et al., 2002, Lower Eocene (Wasatchian) of Wyoming; Oligoryctinae Asher et al., 2002, uppermost Lower Eocene–Lower Oligocene (Bridgerian–Orellan) of western North America; Apternodontinae Matthew, 1910, uppermost Middle Eocene–Lower Oligocene (Duchesnean–Lower Orellan) of western North America; Asiapternodontinae subfam. nov., Middle Eocene (Irdinmanhan) of Mongolia.

Comparison. The Apternodontidae differ from the Solenodontidae in the reduced hypocone of M^1–M^3 and the other ratio of I_1 and I_2 (in the Solenodontidae, $I_1 \ll I_2$), single-rooted P_2, and in the more reduced zygomatic process of the maxillary arch.

Remarks. Asher et al. (2002) rank the Parapternodontinae, Oligoryctinae, and Apternodontidae as distinct families of uncertain taxonomic position. This question is discussed in Chapter 5 (section 5.1.6).

SUBFAMILY ASIAPTERNODONTINAE LOPATIN, SUBFAM. NOV.

Type genus. *Asiapternodus* Lopatin, 2003, Middle Eocene of Mongolia.

Diagnosis. Small-sized apternodontids. Zygomatic process of maxilla relatively long, directed posterolaterally, projecting posteriorly beyond M^3. P^3 small. P^4 slightly molarized: narrow, with small lingual projection, without trigon basin. Molars very broad, in width $M^3 > M^2 > M^1$. Protocone of M^1–M^3 well-developed, large, expanded considerably transversely; hypocone absent; precingulum and postcingulum weak. M^3 nonreduced. Coronoid process of lower jaw located far posterior to tooth row. Condyle moderately widened. Lower molars without precingulid. Talonid of M_1 unicuspid, narrow. Talonid of M_2 expanded transversely and strongly projecting ventrolabially. M_3 large, with long talonid and well-developed talonid cusp.

Generic composition. Type genus.

Comparison. The Asiapternodontinae differ from the Parapternodontinae in the large M_3 with a long talonid and well-developed talonid cusp. The new subfamily differs from Apternodontinae and Oligoryctinae in the larger, posterolaterally directed zygomatic process of maxilla, which projects posteriorly to a greater extent (i.e., less reduced); in its only slightly molarized P^4; wider M^1–M^3; different width ratios of molars (in the Apternodontinae, $M^1 > M^2 > M^3$ or $M^1 < M^2 > M^3$, while in the Oligoryctinae, $M^1 > M^2 > M^3$); better developed protocone of M^1–M^3; large M^3; and in the structure of the talonid of M_2. In addition, the Asiapternodontinae differ from the Apternodontinae in the weakly developed cingula and complete absence of hypocones of M^1 and M^2, the more posterior position of the coronoid process of the lower jaw in relation to the tooth row (in the Apternodontinae, the anterior edge of the coronoid process is located lateral to M_3), the narrower condyle of the lower jaw, and the elongated talonid of M_3; they differ from the Oligoryctinae in the considerably smaller P^3 and the absence of medial depression on the coronoid process of the lower jaw.

Genus *Asiapternodus* Lopatin, 2003

Asiapternodus: Lopatin, 2003b, p. 83.

Type species. *Asiapternodus mackennai* Lopatin, 2003, Middle Eocene of Mongolia.

Diagnosis. The same as the diagnosis of the subfamily.

Species composition. Type species.

Asiapternodus mackennai Lopatin, 2003

Plate 6, figs. 4 and 5

Asiapternodus mackennai: Lopatin, 2003b, p. 84, text-figs. 1–4.

Holotype. PIN, no. 3107/400, right maxillary fragment with P^4–M^3; Mongolia, Khaychin-Ula 2 locality; Middle Eocene, Khaychin Formation.

Description (Figs. 26–28). The infraorbital canal is short, large, narrowed transversely. The anterior foramen of the infraorbital canal is oval, its height is almost three times as great as the width (in the holotype, 2.0 × 0.7 mm); it is located in line with the middle of P^4. Anterior to the infraorbital foramen, the lateral side of the maxilla has a small, posterolaterally open foramen conducting in the nasal cavity. The posterior foramen of the infraorbital canal is semicircular, located above the central part of M^1, has a straight medial wall. The inner surface of the medial wall of the infraorbital canal has a relatively small ridge that marks the division of the canal into two unequal parts: the larger ventral and smaller dorsal parts (this suggests that the infraorbital nerve and vessels passing through this canal were located one above the other). The canal extends in the space between the labial and lingual roots of P^4 and M^1; in the ventral part, its lateral walls are pierced by small foramina, which were probably connected to the root canals of cheek teeth. The largest of these foramina opens in the medial wall of the canal at the level of the apex of the lingual root of M^1, it faces posteriorly and coincides with a distinct groove extending on the floor of the canal to its posterior opening. Just posterior to the infraorbital canal, the orbital floor has a large depression; short grooves extend laterally and medially from this depression and terminate in very small foramina, which are probably connected to the roots of M^2. The orbital floor is short, with a rough, pitted surface; in the posterior part, it is pierced by the roots of M^3. A thick lateral wall of the infraorbital canal

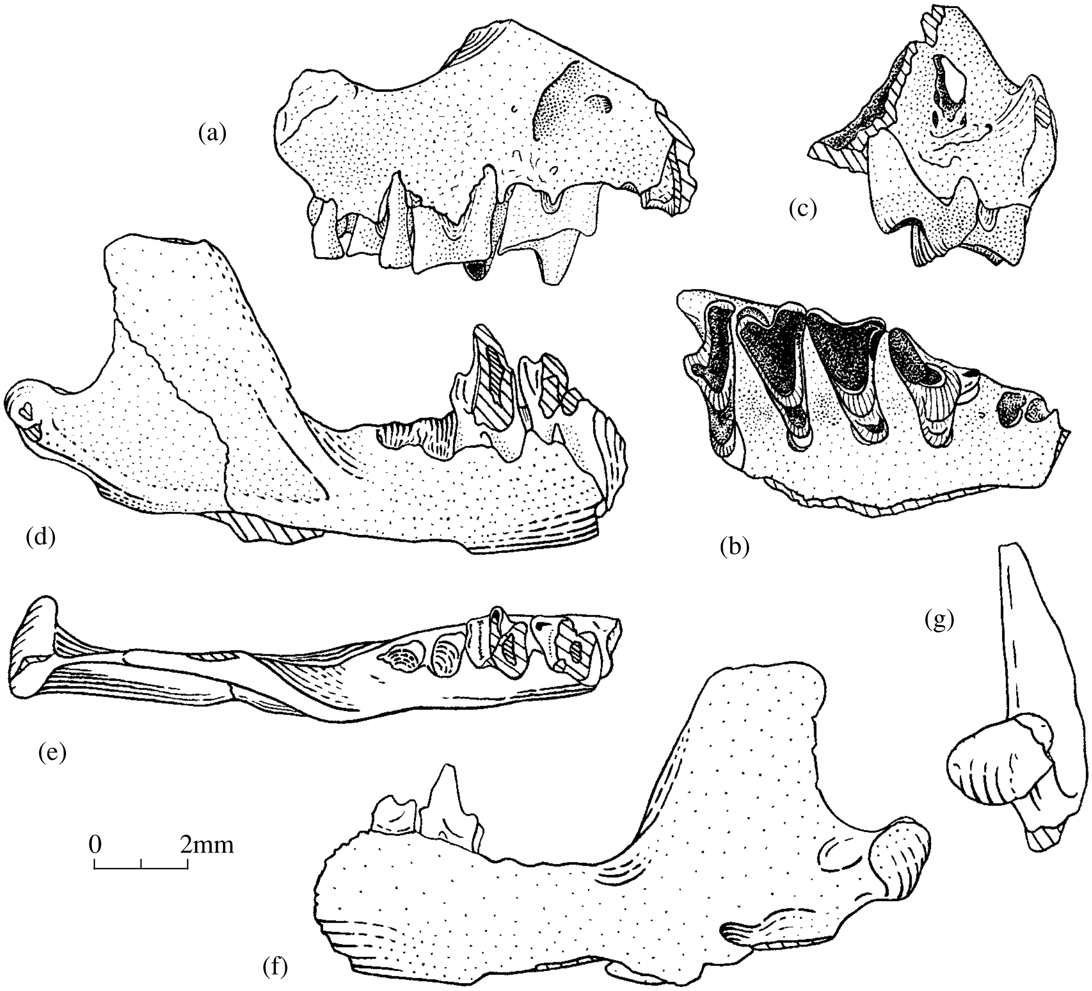


Fig. 26. *Asiapternodus mackennai* Lopatin, 2003: (a–c) holotype PIN, no. 3107/400, right maxillary fragment with P^4–M^3: (a) labial, (b) occlusal, and (c) posterior views; (d–g) specimen PIN, no. 3107/399, right dentary fragment with M_1 and M_2: (d) labial, (e) occlusal, (f) lingual, and (g) posterior views; Khaychin-Ula 2 locality, Mongolia; Khaychin Formation, Middle Eocene.

passes posteriorly into a massive zygomatic process of maxilla.

The zygomatic arch is reduced. The zygomatic process of the maxilla is relatively well developed, directed posteriorly, slightly deviates laterally, and projects somewhat posteriorly beyond M^3. The dorsolateral end of the process is slightly elevated and has a distinct flat area, which is bordered ventrally by a well-developed ridge fused anteriorly with a small tubercle. This area was probably the origin of the ventral portion of the dilatator nasi muscle, as in extant Tenrecidae and Solenodontidae (Gambaryan, 1989). A large area on the lateral side of the base of the zygomatic process above M^1–M^3 has a slightly concave, rough surface, which is interpreted as the origin of the maxillonasalis muscle.

Anterior to P^4, three alveoli are preserved. The anterior alveolus is identified by a small fragment of its posteromedial wall. The second alveolus looks like a small circular foramen extended slightly posteromedially. The third alveolus is the largest, widened transversely; in the middle part, it is compressed slightly longitudinally. Its anterior wall has a distinct projection, which indicates that the alveolus contained two partially fused roots. The first, second, and third alveoli preserved probably contained the posterior root of P^2, the anterior labial root of P^3, and the fused posterior labial and lingual roots of P^3, respectively. Judging from the sizes of the second and third alveoli, P^3 was relatively small and had a weakly developed lingual projection.

P^4–M^3 are three-rooted. P^4 has a long labial lobe and a relatively small lingual projection. The parastylar lobe is large, substantially projects anteriorly. The parastyle cusp is low. The paracone is high, massive, conical. A strong postcrista extends from the apex of the paracone to the metastyle. The metastylar lobe is long, the metastyle is low. The protocone is small and low,

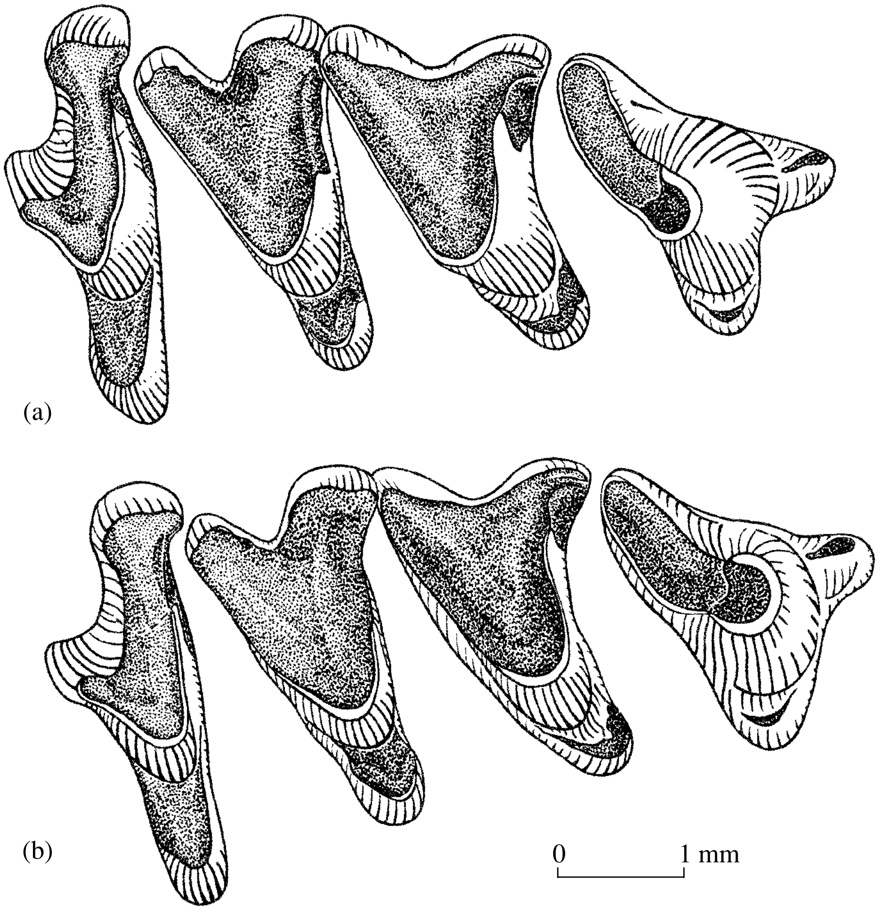


Fig. 27. *Asiapternodus mackennai* Lopatin, 2003, holotype PIN, no. 3107/400, right P^4–M^3, occlusal view: (a) strictly vertically, (b) with a slight anterior inclination; Khaychin-Ula 2 locality, Mongolia; Khaychin Formation, Middle Eocene.

with a poorly pronounced apex and small crests of the preprotocrista and postprotocrista.

The molars are narrowly triangular, short, and wide; from M^1 to M^3, they decrease in length and increase in width. M^1 has a relatively shallow ectoflexus and an anteriorly inclined lingual lobe. The metastylar lobe is larger than the parastylar lobe. The anterior margin of the parastylar lobe has a small parastyle cusp, which is isolated from the labial end of the preparacrista by an extensive depression. A weak ectocingulum, which has a small eminence in the posterolabial part of the parastylar lobe (a reduced stylocone), extends from the parastyle to the metastyle. A small precingulum, which is connected to the parastyle, borders the anterolingual side of the parastylar lobe. The metastylar lobe is extended posterolabially. The paracone is massive, triangular. The preparacrista terminates in the lingual part of the occlusal surface of the parastylar lobe, the postparacrista connects the apex of the paracone with the metastyle. The protocone is relatively large, its conical apex is displaced considerably anteriorly in relation to the apex of the paracone and is opposed to the parastyle. A small crest of the postprotocrista is present. The precingulum is very narrow and weak, particularly, in the middle part. The postcingulum is vague, interrupted; only its lingual portion, which borders the posterolingual wall of the base of the paracone, is relatively distinct; traces of other projections of the postcingulum are two elongated wear facets on the posterior side of the paracone base.

M^2 extend transversely, has a very deep ectoflexus. The parastylar lobe is substantially larger than the metastylar lobe. The labial margin of the parastylar lobe is straight. In a worn tooth, the parastyle is united with the labial part of the precingulum. The stylocone is relatively large. The ectocingulum is weak. The metastyle cusp is small. The paracone is smaller than in M^1. In a worn tooth, the labial part of the preparacrista is united with the wear facet of the parastyle and precingulum. The postparacrista connects the apex of the paracone with the metastyle. The apex of the protocone is located within the same transverse line as the apex of the paracone. The precingulum is more distinct than in M^1, extends throughout the anterior side of the para-

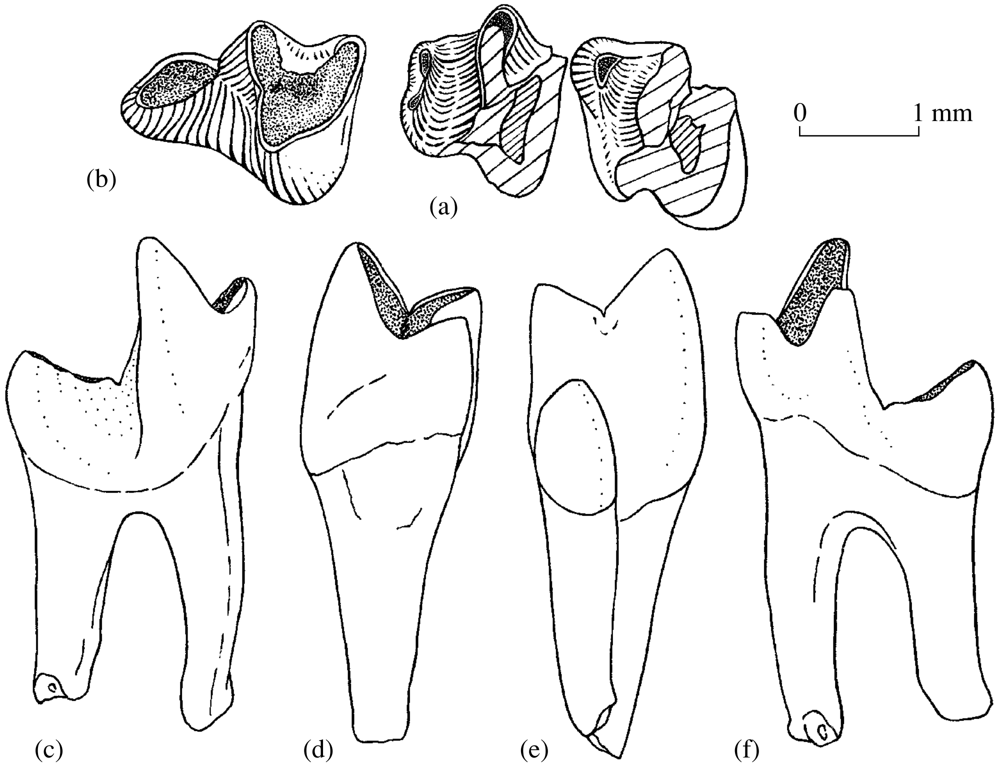


Fig. 28. *Asiapternodus mackennai* Lopatin, 2003: (a) specimen PIN, no. 3107/399, right M_1 and M_2, occlusal view; (b–f) specimen PIN, no. 3107/398, right M_3: (b) occlusal, (c) labial (d) anterior, (e) posterior, and (f) lingual views; Khaychin-Ula 2 locality, Mongolia; Khaychin Formation, Middle Eocene.

cone. The postcingulum is interrupted, looks like slightly convex sites of enamel at the base of the posterior (which are arranged similar to respective wear facets on M^1) and posterolingual sides of the paracone.

M^3 has a very large parastylar lobe located at the same transverse line as the apices of the paracone and protocone. The metastylar lobe is reduced and shifted slightly posteriorly, the metastyle is distinct. The common wear facet of the parastyle and precingulum is separated from the preparacrista. The preparacrista is strong and long, reaches the stylocone; the postprotocrista is short, connected to the metastyle. The lingual lobe is very broad, much wider than in M^1 and M^2. The protocone is low. The precingulum is developed to the same extent as in M^2. The postcingulum is absent.

It should be noted that particular elements of the occlusal surface (styles, stylocone, ectocingulum, and crests of the protocone) of M^1–M^3 of the holotype are smoothed by wear; however, their shape, arrangement, and dimensions are recognizable due to the uneven dentin, which are retained on the fused wear facets.

In the interdental spaces, the maxilla has deep oval vascularized pits (which are opposed to high trigonids of P_4–M_3); the pits increase in depth posteriorly (from P^3/P^4 to M^2/M^3). The anterior side of M^1–M^3 has distinct wear facets (Fig. 27a), which are evidence of close contact with the posterior margin of the trigonids of M_1–M_3 as the teeth occluded.

The lower jaw, as in other apternodontids (Matthew, 1903, text-fig. 2; Schlaikjer, 1934; Scott and Jepsen, 1936; Hough, 1956), is characterized by a distinctive shape of the coronoid region: the ascending ramus is considerably displaced laterally relative to the horizontal ramus and deviates substantially medially from the longitudinal axis of the tooth row; the condyle is widened and inclined anteromedially and ventromedially.

The horizontal ramus of the lower jaw is relatively massive. The lingual wall of the alveolar margin is much higher than the labial wall. The angle between the ascending and horizontal rami is about 110°. The coronoid process is high and slender. The masseteric fossa is shallow, but clearly outlined anteriorly. The strong condylar crest extends to the lateral side of the condyle and borders the masseteric fossa ventrally. The incisure between the coronoid and articular processes is broad, but shallow. The condyle is large, massive, relatively short, and wide, located at the level of the base of the molar crowns. The transverse axis of the condyle is slightly inclined anteromedially and posterolaterally. The articular surface covers a sector about 180°. Most of the articular surface faces posteroventrally. The condylar neck is short, straight, with a small depression on the medial side (the upper pterygoid fossa for a portion of the pterygoideus externus muscle) and a sharp dorsal ridge.

The mandibular foramen is large, oval, located at the level of the middle of the coronoid process; a large and deep depression is located posterior to the foramen. The incisure between the articular and angular processes is small.

M_1 and M_2 are approximately equal in length. Their structure is typical of apternodontids: the roots are massive; the crowns are compressed longitudinally; the trigonids are high, with a vertical posterior wall; the talonids are short and low, reduced. The talonid of M_1 has an oblique labial edge and the only massive cusp in the posterolingual corner. The talonid of M_2 projects substantially posterolabially at the base. The talonid cusp is relatively small, positioned posterolingually. A distinct subtransverse crest descends from its apex onto the labial projection and terminates in a weak cuspule at the base of the labial side of the talonid. This tiny cuspule is located substantially below the lingual border of the talonid and the apex of the main talonid cusp. It is undoubtedly nonhomologous to any of three talonid cusps of placentals and can be named additional ventrolabial cusp.

The trigonid of M_3 (Figs. 28b–28e) has a large paraconid, a high protoconid, and a relatively low metaconid. The talonid is long, narrow, with a longitudinally directed wear facet and a small cusp on the posterior margin.

Measurements, mm. Holotype: length of P^4–M^3 along the crowns, 6.6; tooth dimensions (length × width): P^4, 2.25 × 1.8; M^1, 1.75 × 3.1; M^2, 1.6 × 3.2; M^3, 1.15 × 3.6.

Specimen PIN, no. 3107/399: length of M_1–M_3 along alveoli, ca. 4.6; total length of M_1, ca. 1.5; talonid length, 0.5; talonid width, 0.5; total length of M_2, 1.5; talonid length, 0.55; talonid width, 0.8; metaconid height, 1.5; alveolar length of M_3, 1.6; lingual depth of the horizontal ramus of the lower jaw under M_1/M_2, 3.2; thickness under M_3, 1.35; distance from the posterior edge of the condyle to the posterior alveolus of M_3, 7.0; to the anterior base of the coronoid process, 6.0; thickness of the condyle, 1.5; width of the condylar head, 2.4; dorsal length of the condylar neck with the head, 2.0 (1.0 + 1.0).

Specimen PIN, no. 3107/398, M_3: total length, 2.1; talonid length, 1.05; trigonid width, 1.65; talonid width, 0.75; protoconid height, 2.0; metaconid height, 1.5.

Occurrence. Middle Eocene (Irdinmanhan) of Mongolia.

Material. In addition to the holotype, the type locality yielded a right dentary fragment with heavily damaged M_1 and M_2, alveoli of M_3, and partially preserved ascending ramus with the articular process (specimen PIN, no. 3107/399) and isolated right M_3 (PIN, no. 3107/398).

SUBORDER ERINACEOMORPHA GREGORY, 1910

Erinaceomorpha: Gregory, 1910, p. 464.

Diagnosis. Terrestrial (i.e., surface dwelling, nonaquatic, nonsubterranean) insectivores. Skull with middle constriction. Orbits and optic foramen relatively large; infraorbital canal relatively long; jugal, zygomatic arches, and ectopterygoid processes of alisphenoid always present. Alisphenoid canal short, with medial bony wall. Mandibular condyle narrow.

Dentition showing the following unique set of structural characters: P^3 small, triangular, occasionally, secondarily increased; P^4 always with hypocone, metacone weak or absent, crest of metacrista or postcrista strong; M^1 and M^2 subrectangular, with narrow stylar shelf and distinct hypocone and postcingulum; P_1 small, single-rooted; P_2 and P_3 simple in structure, essentially unicuspid; P_4 with short talonid, cusps of talonid strongly or completely reduced; lower molars with ridgelike paraconid, cusps of trigonid inclined anteriorly, entoconid high, hypoconid low, frequently flattened even at early stages of wear; in M_1 and M_2, talonid and trigonid equal in width or talonid slightly wider.

Composition. Five families: Erinaceidae Fischer von Waldheim, 1817, Upper Paleocene–Middle Eocene, Lower Oligocene–Upper Miocene of North America, Lower Eocene–Recent of Asia, Upper Eocene–Recent of Europe, Lower Miocene–Recent of Africa; Adapisoricidae Schlosser, 1887, Upper Paleocene–Lower Eocene of Europe; Amphilemuridae Heller, 1935 (= Dormaaliidae Quinet, 1964), Eocene of Europe and North America; Sespedectidae Novacek, 1985, Lower Eocene–Lower Oligocene of North America; and Creotarsidae Hay, 1930, Lower Eocene of North America.

Comparison. The Erinaceomorpha differ from the Soricomorpha and Chrysochloridea in the adaptive complex (erinaceomorphs do not include subterranean or semiaquatic taxa), the structure of the infraorbital and alisphenoid canals, the presence of midcranial constriction, the larger orbits and larger optic foramen, and in the special dental structure (including the absence of zalambdomorphy). In addition, the Erinaceomorpha differ from the Soricomorpha in the better developed zygomatic arches and the shape of the mandibular condyle, and from the Chrysochloridea, in the absence of a rudiment of the entotympanic bone and a more anterior position of the temporomandibular joint.

FAMILY ERINACEIDAE FISCHER VON WALDHEIM, 1817

Erinacini: Fischer von Waldheim, 1817, p. 372.

Erinacidae: Gray, 1821, p. 300.

Erinaceidae: Bonaparte, 1838, p. 111.

Type genus. *Erinaceus* Linnaeus, 1758, Pliocene–Recent of Eurasia and Africa.

Diagnosis (only dental characters). Erinaceomorph insectivores with dental formula $I^{3}/_{3-2}C^{1}/_{1}P^{4-2}/_{4-1}M^{3-2}/_{3-2}$. Deciduous generation of antemolars reduced. M^1 and M^2 subrectangular or subsquare in outline, with well-developed hypocone, which usually connected by small crest to postprotocrista. Paraconule of M^1 and M^2 reduced, metacrista long in M^1, short in M^2. M^3, if present, considerably reduced and triangular or oval in outline. In P_4 and M_1, metaconid displaced slightly anteriorly in relation to protoconid. Lower molars substantially decreasing from M_1 to M_3, exoedaenodont (labial edge of tooth strongly projecting beyond jaw edge, cusps inclined lingually), subrectangular in outline. Trigonid relatively low, inclined slightly anteriorly. Paraconid of M_1 strongly protruding, high; paracristid shearing. Paraconid of M_2 and M_3 low, directed subtransversely. Hypoconulid of M_1 and M_2 considerably reduced and located exactly or approximately in middle of posterior edge of occlusal surface.

Composition. Five subfamilies: Changlelestinae Tong et Wang, 1997, Lower Eocene of Asia; Tupaiodontinae Butler, 1988, Lower Eocene–Upper Oligocene of Asia; Galericinae Pomel, 1848, Middle Eocene–Recent of Asia (at present, only in southeastern Asia), Upper Eocene–Lower Pliocene of Europe, Lower Oligocene–Upper Miocene of North America, Miocene–Lower Pliocene of Africa; Brachyericinae Butler, 1948, Lower Oligocene–Middle Miocene of Asia, Lower Miocene of Europe (see Lopatin and Zazhigin, 2003), Miocene of North America; Erinaceinae Fischer von Waldheim, 1817, Upper Eocene–Recent of Asia, Lower Oligocene–Recent of Europe, Miocene of North America, Miocene–Recent of Africa.

Comparison. The Erinaceidae differ from the Amphilemuridae, Sespedectidae, Adapisoricidae, and Creotarsidae in the reduced deciduous generation of antemolars and, frequently, reduced dental formula; in the absence of well-pronounced bunodont molars and mesostyles on the upper molars, in the large hypocone of M^1 and M^2, the considerably reduced M^3, the shape of the paraconid of M_1, and in the reduced hypoconulid of M_1 and M_2.

SUBFAMILY GALERICINAE POMEL, 1848

Galerices: Pomel, 1848, p. 249.
Gymnurinae: Gill, 1872, p. 19.
Hylomidae: Anderson, 1879, p. 138.
Parasoricidae: Schlosser, 1887, p. 91.
Echinosoricinae: Cabrera, 1925, p. 57.
Galericini: Butler, 1948, p. 488.
Galericinae: Van Valen, 1967, p. 262.
Hylomyinae: Frost et al., 1991, p. 23.

Type genus. *Galerix* Pomel, 1848, Oligocene–Lower Pliocene of Europe, Miocene of Asia and Africa.

Diagnosis (only dental characters). Unspecialized erinaceids with dental formula $I^3/_{3-2}C^1/_1P^{4-2}/_{4-2}M^3/_3$. Rostrum and antemolar row relatively long. P^4–M^2 subsquare in outline, with large hypocone. M^3 subtriangular in outline, with well-developed metacone, three-rooted. I_1 present, I_2 approximately equal in size to I_1. P_3 present. Lower molars gradually decreasing in size from M_1 to M_3; hypoconulid absent or extremely reduced, or, occasionally, well-developed on M_3. M_3 double-rooted, with well-developed talonid; similar in structure to M_2.

Composition. Three tribes: Galericini Pomel, 1848, Middle Eocene–Recent of Asia, Upper Eocene–Lower Pliocene of Europe, Lower Oligocene–Upper Miocene of North America, Miocene–Lower Pliocene of Africa; Neurogymnurini Butler, 1948, Upper Eocene–Upper Oligocene of Eurasia (see Lopatin, 1999); and Protericini Butler, 1948, Lower Oligocene of North America.

Remarks. The tribes Neurogymnurini and Protericini are monotypic, include *Neurogymnurus* Filhol, 1877 and *Proterix* Matthew, 1903, respectively. The tribe Galericini sensu lato (after McKenna and Bell, 1997, p. 277) includes all other members of the subfamily Galericinae. Hoek Ostende (2001a) narrowed the diagnosis of this tribe and restricted it to the Oligocene–Neogene genera *Galerix, Parasorex, Schizogalerix*, and *Deinogalerix*; a classification for the genera that were not included in Galericini sensu stricto was not proposed. Below, this tribe is considered in the composition Galericini sensu lato.

Comparison. The Galericinae differ from the Changlelestinae in the large hypocone of P^4–M^2, less developed paraconule of M^1 and M^2, longer trigonid of M_1, and in the absence of distinct hypoconulid and a portion of the cristid oblique that ascends onto the trigonid in M_1 and M_2. They differ from the Tupaiodontinae in the relatively longer and narrower upper and lower molars, in the subsquare shape of P^4, the larger hypocone of M^1 and M^2, the long antemolar row, smaller I_1, the more strongly elongated trigonid of M_1, and in the admissible presence of double-rooted P_2. They differ from the Brachyericinae and Erinaceinae in the long rostrum, nonreduced or slightly reduced dental formula, in particular, the presence of I_1, P_1, P_3, and relatively well-developed $M^3/_3$.

Tribe Galericini Pomel, 1848

Galerices: Pomel, 1848, p. 249.
Galericini: Butler, 1948, p. 488.

Type genus. *Galerix* Pomel, 1848, Oligocene–Lower Pliocene of Europe, Miocene of Asia and Africa.

Diagnosis (only dental characters). Unspecialized Galericinae with dental formula $I^3/_3C^1/_1P^{4-3}/_{4-3}M^3/_3$. Rostrum and antemolar row moderately elongated. $I^1/_1$ small. P_4 nonreduced, frequently with metaconid.

Generic composition. *Protogalericius* gen. nov., uppermost Lower Eocene of Kyrgyzstan; *Eochenus* Wang et Li, 1990, Middle Eocene of China; *Eogalericius* Lopatin, 2004, *Microgalericulus* gen. nov., Middle Eocene of Mongolia; *Oligochenus* Lopatin, 2005, uppermost Eocene of Mongolia; *Galerix* Pomel, 1848 (= *Tetracus* Aymard, 1850, = *Pseudogalerix* Gaillard, 1929), Oligocene–Lower Pliocene of Europe, Miocene of Asia and Africa; *Parasorex* Meyer, 1865, Middle Miocene–Lower Pliocene of Europe; *Schizogalerix* Engesser, 1980, Middle Miocene–Lower Pliocene of Asia, Upper Miocene of Europe and Africa; *Deinogalerix* Freudenthal, 1972, Upper Miocene of southern Western Europe; *Ocajila* Macdonald, 1963, Oligocene–Lower Miocene of North America; *Lantanotherium* Filhol, 1888, Middle–Upper Miocene of Eurasia, Africa, and North America; *Thaiagymnura* Meng et Ginsburg, 1997, Lower Miocene of southeastern Asia; *Echinosorex* Blainville, 1838, Middle Miocene–Recent of southeastern Asia; *Hylomys* Müller, 1839 (= *Neotetracus* Trouessart, 1909, = *Neohylomys* Shaw et Wong, 1959), Lower Miocene–Recent of southeastern Asia; *Podogymnura* Mearns, 1905, Recent, Philippines.

Comparison. In the structure of the dentition, the tribe Galericini differs from Protericini in the longer anterior part of the tooth row, small anterior incisors, large number and greater size of premolars; and from Neurogymnurini, usually in the shorter antemolar row. In addition, Galericini differ from Neurogymnurini and Protericini in the shape and structure of P_4, including the usual development of the metaconid.

Genus *Eogalericius* Lopatin, 2004

Eogalericius: Lopatin, 2004c, p. 84.

Type species. *Eogalericius butleri* Lopatin, 2004, Middle Eocene of Mongolia.

Diagnosis. Dental formula $I^3/_3C^1/_1P^4/_4M^3/_3$. P^4–M^2 short and wide, with small hypocones. Parastyle of P^4 large. Stylar lobes of M^1 and M^2 large, strongly projecting. Hypocone of M^1 and M^2 detached from protocone. Postmetaconule crest long, connected to postcingulum. M^3 short. C_1 small. P_2 and P_3 weakly reduced. P_4 relatively small (not higher than M_1 and no more than 75–80% of its length), with well-developed paraconid and metaconid. M_2 slightly shorter than M_1 (approximately 85–95% as long), M_3 much shorter than M_2 (75–85%). Trigonid of M_1 short, paracristid subtransverse. M_3 with hypoconulid which closely positioned or fused with entoconid. Paracristid of M_3 long. Two mental foramina, under P_2 and P_3, present.

Species composition. Type species.

Comparison. *Eogalericius* differs from all known genera of Galericini, except for *Eochenus,* in the relatively small hypocones of P^4–M^2, large parastyle of P^4, strongly projecting stylar lobes of M^1 and M^2, relatively small P_4, short trigonid and subtransverse paracristid of M_1, and presence of the hypoconulid on M_3, and obligatory presence of two mental foramina. It differs from *Eochenus* in the long postmetaconule crest and detached hypocone of M^2, small C_1, larger P_2 and P_3, less massive and lower P_4 (in *Eochenus,* P_4 is 86–94% of the M_1 length, see Wang and Li, 1990, table 1), better developed metaconid of P_4, ratio of the lengths of the lower molars (in *Eochenus* M_2 is relatively smaller, 80–85% as long as M_1, whereas M_3 is almost equal to M_2, 90–100%), and in the longer paracristid of M_3.

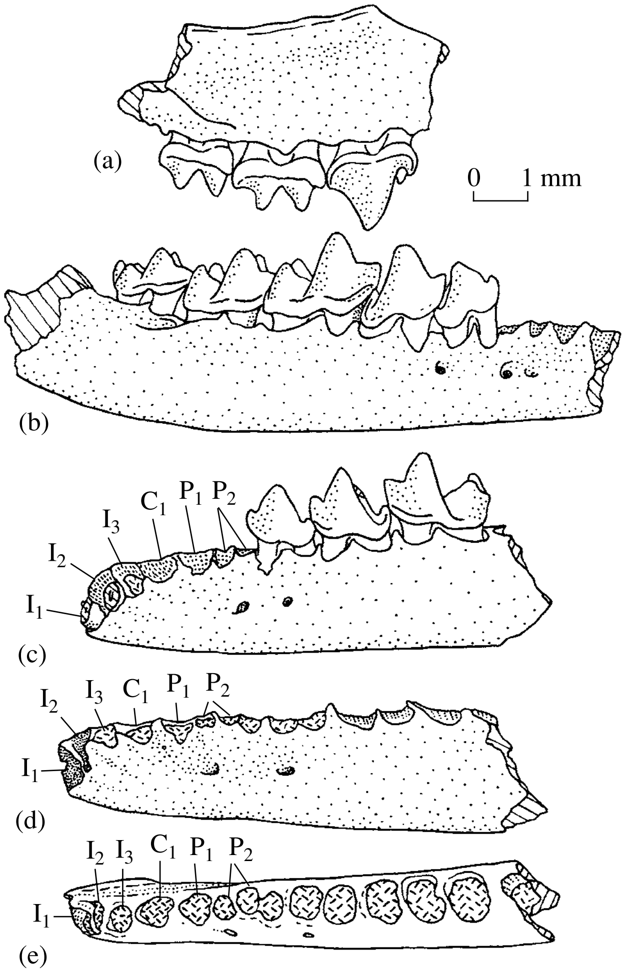


Fig. 29. *Eogalericius butleri* Lopatin, 2004: (a) holotype PIN, no. 3107/420, right maxillary fragment with P^4–M^2, labial view; (b) specimen PIN, no. 3107/422, right dentary fragment with P_3–M_3 and alveoli of C_1–P_2, labial view; (c) specimen PIN, no. 3107/425, left dentary fragment with P_3–M_1, fragmentary I_1 and I_2, and alveoli of I_3–P_2, labial view; (d, e) specimen PIN, no. 3107/440, left dentary fragment with alveoli of I_1–M_1: (d) labial and (e) occlusal views; Khaychin-Ula 2 locality, Mongolia; Khaychin Formation, Middle Eocene.

Eogalericius butleri Lopatin, 2004

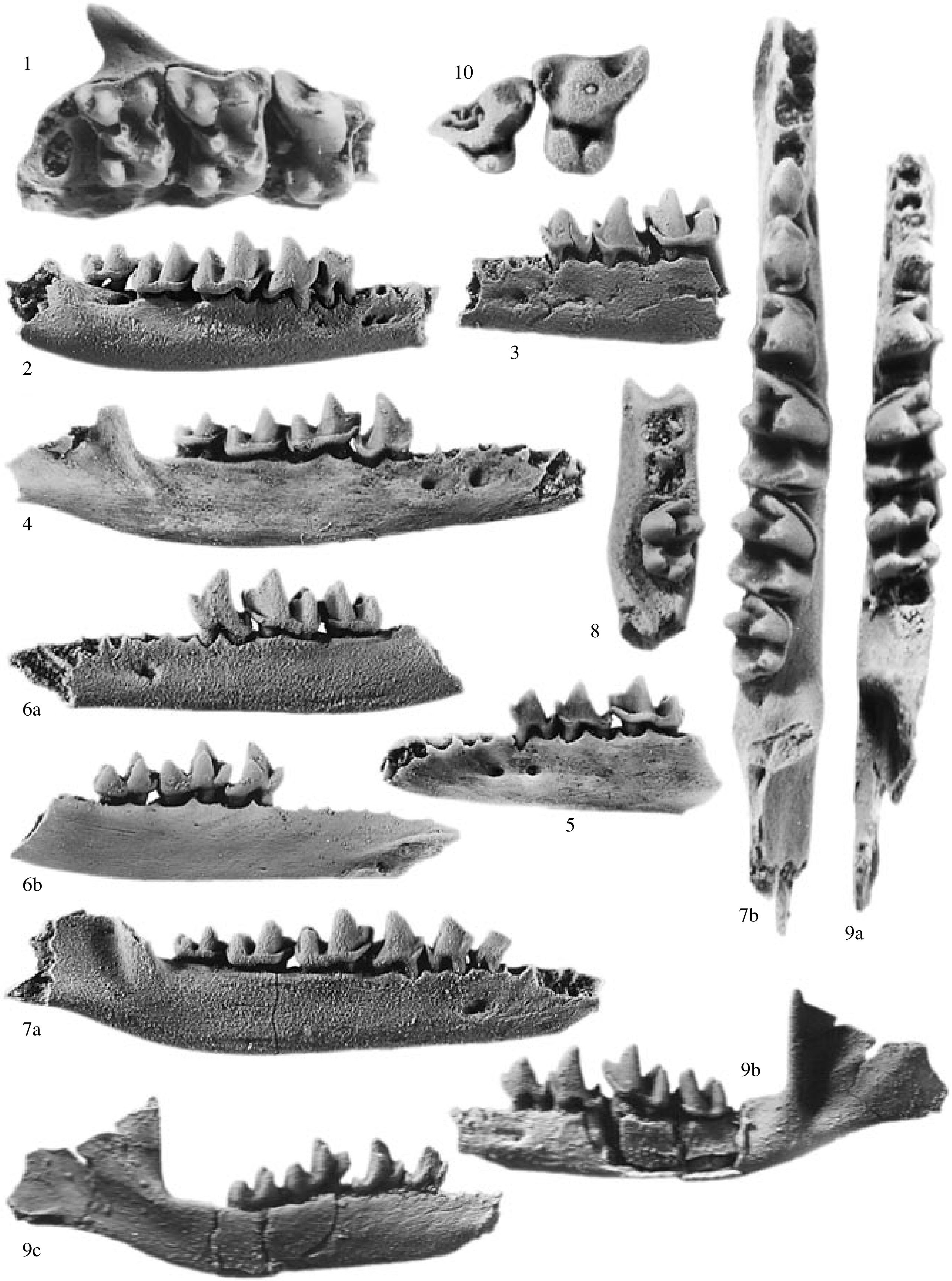
Plate 7, figs. 1–8

Eogalericius butleri: Lopatin, 2004c, p. 85, pl. XI, figs. 1–10, text-figs. 1 and 2.

Holotype. PIN, no. 3107/420, right maxillary fragment with P^4–M^2; Mongolia, Khaychin-Ula 2 locality; Middle Eocene, Khaychin Formation.

Description (Figs. 29, 30). The base of the zygomatic process of the maxilla is located in line with

Plate 7



the posterior labial root of M^1. The upper margin of the zygomatic process is thin, ridgelike. The base of the zygomatic arch and adjacent area on the lateral side of the maxilla above M^1 and M^2 form an extensive depression for the maxillonasalis muscle. The infraorbital foramen is small and located in line with P^3. The posterior foramen of the infraorbital canal is above the space between P^4 and M^1. The infraorbital canal is narrow.

P^4–M^3 are three-rooted, including one lingual root. P^4 has a high paracone, a strong postcrista, and a well-developed lingual lobe. The parastyle is relatively large, projects anteriorly. The ectocingulum is narrow. The protocone is compressed slightly longitudinally, and the preprotocrista is long and connected to the crest, which extends along the anterior margin of the occlusal surface to the parastyle. The hypocone is small, conical, approximately half as high as the protocone, and markedly projects lingually. The postcingulum is strong.

The occlusal surface of M^1 and M^2 is trapezoid, the lingual lobe is slightly shorter than the labial lobe (Pl. 7, fig. 1; Fig. 30a). The stylar lobes are large; in the middle region (in line with the conules), the anterior and posterior sides of the crown are noticeably concave. The ectoflexus is weak. The stylar shelf is narrow; the ectocingulum is narrow but distinct, continuous. The precingulum is well-pronounced, but short, extends at the base of the anterior side of the crown in line with the paraconule and preprotocrista. The parastylar and metastylar lobes strongly project anterolabially and posterolabially, respectively. The parastylar crest is weak, the metacrista is well developed, and it is particularly long and strong in M^1. The paracone and metacone are widely spaced, with pointed apices, approximately equal in height and stoutness. In M^2, the labial cusps are more widely spaced and the centrocrista is weaker than in M^1. The protocone is large and massive. The preprotocrista and postprotocrista are short, connected to conules. The transversely extended paraconule is substantially smaller than the metaconule. The preparaconule crest is strong, extends to the parastylar lobe. The postparaconule crest is short and thin, terminates at the base of the lingual wall of the paracone. The metaconule is relatively massive. The premetaconule crest is short and weak, connected to the base of the lingual wall of the metacone. The postmetaconule crest is long and strong, extends posterolabially and fuses with the labial portion of the postcingulum. The lingual portion of the postcingulum is clearly pronounced at the level of the metaconule and postprotocrista posterolabial to the hypocone apex. The hypocone is relatively small, conical, its apex is completely isolated from the trigon (there is no crest connected to the postprotocrista). M^2 is slightly shorter and substantially narrower than M^1.

Judging from the alveoli, M^3 was substantially smaller than M^2 in both length and width and was in the shaped of a narrow triangle. This last character means that M^3 lacks a hypoconal shelf and is distinguished by the noticeably reduced area of the metacone and metastyle.

The horizontal ramus of the lower jaw is relatively narrow and low. The symphysial region extends posteriorly to the midlength, or the posterior root, of P_2. Its posteroventral part contains a small symphysial foramen. Two mental foramina usually present under P_2 and P_3 (Pl. 7, figs. 3–5; Figs. 29c–29e); rarely, there are three foramina: under the anterior and posterior roots of P_2 and under P_3 (Pl. 7, fig. 2; Fig. 29b); and, occasionally, two small foramina are fused in one large and deep fossa located under the posterior root of P_2 and the anterior root of P_3 (Pl. 7, figs. 6a, 7a).

The anterior edge of the base of the coronoid process is straight. The ascending and horizontal rami are positioned at an angle of approximately 105°. The masseteric crest is massive, the masseteric fossa is superficial. The mandibular foramen is located at the level of the molar crowns above the alveolar margin of the horizontal ramus. There is a relatively weak medial crest at the base of the coronoid process. The lower margin of the coronoid region forms a typical dorsal curvature.

The incisors, canine, and P_1 are single-rooted, while the other teeth are double-rooted. Judging from the preserved tooth fragments and alveoli, the size ratios of the single-rooted antemolars are $C_1 > P_1 > I_2 = I_1 > I_3$ (Figs. 29c–29e). P_2 is small, compressed later-

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Explanation of Plate 7

Figs. 1–8. *Eogalericius butleri* Lopatin, 2004: (1) holotype PIN, no. 3107/420, right maxillary fragment with P^4–M^2 and alveoli of M^3, occlusal view, ×11; (2) specimen PIN, no. 3107/422, right dentary fragment with P_3–M_3 and alveoli of C_1–P_2, labial view, ×7; (3) specimen PIN, no. 3107/426, left dentary fragment with P_3–M_1 and alveoli of P_1–P_2, labial view, ×7; (4) specimen PIN, no. 3107/421, right dentary fragment with P_4–M_3, fragmentary I_1 and I_2, and alveoli of I_3–P_3, labial view, ×7; (5) specimen PIN, no. 3107/425, left dentary fragment with P_3–M_1, fragmentary I_1 and I_2, and alveoli of I_3–P_2, labial view, ×7; (6) specimen PIN, no. 3107/427, left dentary fragment with P_4–M_2 and alveoli of I_2–P_3 and M_3, ×7: (6a) labial and (6b) lingual views; (7) specimen PIN, no. 3107/430, right dentary fragment with P_2–M_3 and alveoli of I_2–P_1: (7a) labial view, ×7, and (7b) occlusal view, ×11; (8) specimen PIN, no. 3107/429, left dentary fragment with M_3 and alveoli of M_2, occlusal view, ×11; Mongolia, Khaychin-Ula 2 locality; Middle Eocene, Khaychin Formation.

Fig. 9. *Microgalericulus esuriens* sp. nov., holotype PIN, no. 3403/300, left dentary fragment with P_3–M_2: (9a) occlusal view, ×11, (9b) labial and (9c) lingual views, ×7; Mongolia, Khaychin-Ula 3 locality; Middle Eocene, Khaychin Formation.

Fig. 10. *Protogalericius averianovi* sp. nov., holotype ZIN, no. 89009, left maxillary fragment with P^3 and P^4, ×11; Andarak 2 locality, Kyrgyzstan; uppermost Lower Eocene, lower part of the Alai Beds.

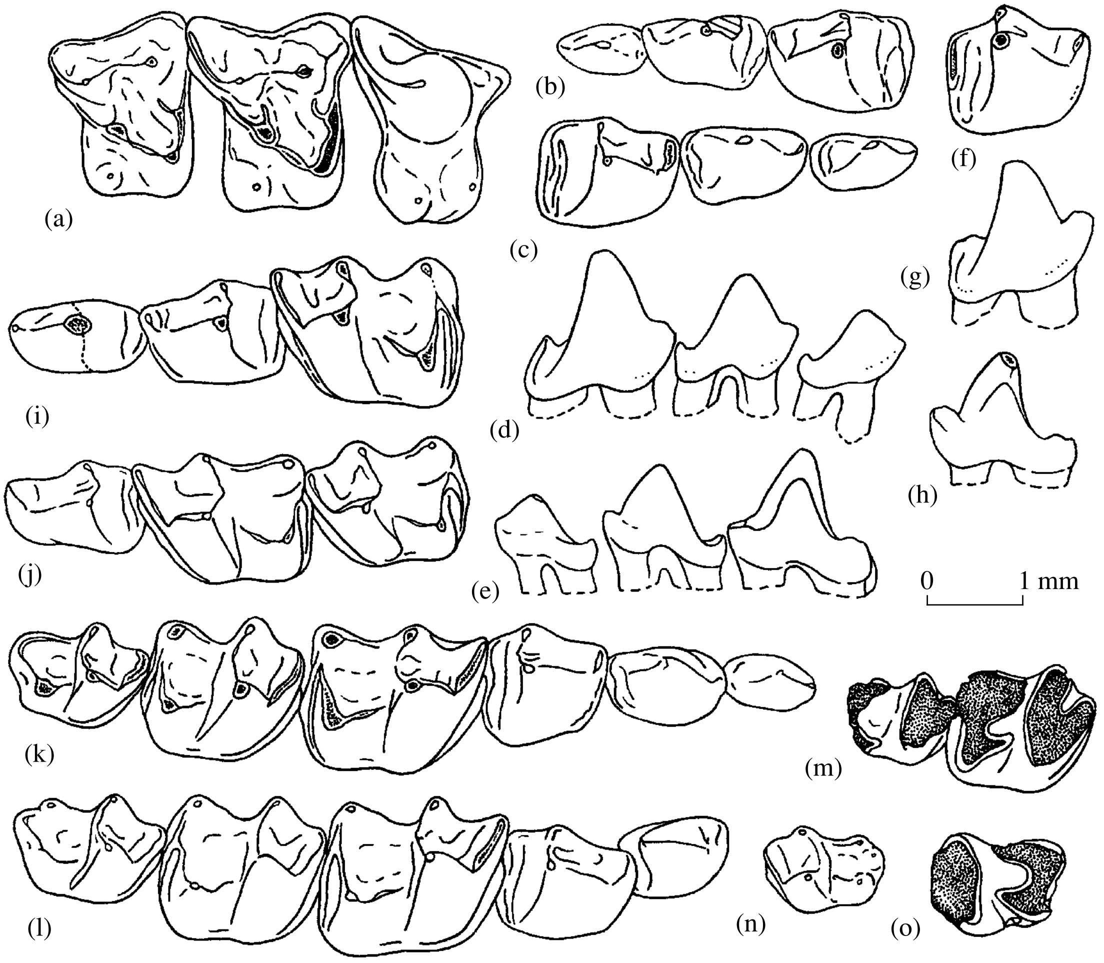


Fig. 30. *Eogalericius butleri* Lopatin, 2004: (a) holotype PIN, no. 3107/420, right P^4–M^2, occlusal view; (b) specimen PIN, no. 3107/424, left P_2–P_4, occlusal view; (c–e) specimen PIN, no. 3107/431, right P_2–P_4: (c) occlusal, (d) labial, and (e) lingual views; (f–h) specimen PIN, no. 3107/433, right P_4: (f) occlusal, (g) labial, and (h) lingual views; (i) specimen PIN, no. 3107/426, left P_3–M_1, occlusal view; (j) specimen PIN, no. 3107/427, left P_4–M_2, occlusal view; (k) specimen PIN, no. 3107/430, right P_2–M_3, occlusal view; (l) specimen PIN, no. 3107/422, right P_3–M_3, occlusal view; (m) specimen PIN, no. 3107/436, heavily worn right M_2 and M_3, occlusal view; (n) specimen PIN, no. 3107/429, left M_3, occlusal view; and (o) specimen PIN, no. 3107/437, heavily worn left M_3, occlusal view; Khaychin-Ula 2 locality, Mongolia; Khaychin Formation, Middle Eocene.

ally, with a tiny paraconid and a low and short talonid. The paraconid is elevated, connected by a short and bladelike crest to the apex of the protoconid. P_3 is substantially longer, wider, and higher than P_2; however, it is similar to this tooth in its general proportions and structure and differs in the more massive protoconid, better detached paraconid, and distinct talonid. The postcingulid is well developed. The precingulids of P_2 and P_3 are absent.

P_4 is partially molarized, with a clearly differentiated trigonid and a very short talonid. The paraconid is relatively high, conical or more or less ridgelike, separated from the protoconid by a clear notch. The protoconid is massive and high, the metaconid is substantially smaller and approximately half as high as the protoconid. The crest on the anterior side of the protoconid is weakly or moderately developed. The apices of the protoconid and metaconid are positioned within the same transverse line. The protocristid has a deep notch. The precingulid is usually weak, narrow, and confined to a small area under the paracristid; sometimes, it is completely lost. The talonid has a single low cusp, which is located in the central or lingual region of the transverse postcingulid crest; however, it never occupies the extreme posterolingual corner of the talonid. The talonid basin is small, closed lingually by a narrow metastylid crest, which descends along the posterolingual edge of the metaconid and adjoins the postcingulid crest. The postcingulid crest descends ventrolabially and usually terminates in the posterolabial corner of the crown; sometimes (where it is transformed into the proper postcingulid), it extends on the labial side to the level of the anterior part of the posterior root.

The lower molars are low, transversely expanded, $M_1 > M_2 \geqslant M_3$. In M_1, the talonid is slightly wider than the trigonid. The trigonid basin is open. The paraconid is elevated, ridgelike, directed anterolingually. The shearing paracristid has a well-developed carnassial notch. The protoconid and metaconid are widely spaced. The protocristid has a deep notch. The apex of the metaconid is located somewhat anterior to the apex of the protoconid. The precingulid and ectocingulid are fused into an integral labial cingulid, which terminates anterior to the base of the hypoconid. The hypoflexid is superficial. The talonid basin is closed. The hypoconid and entoconid are positioned opposite to each other, with the latter being much higher. The entocristid is high and long, reaches the base of the metaconid. The cristid oblique low, connected to the middle of the base of the posterior wall of the protoconid. The lingual region of the postcristid (which ascends onto the entoconid) is narrow, poorly pronounced, sometimes, completely absent (Fig. 30j). The postcingulid is strong, connected to the postcristid at the posterolabial corner of the base of the entoconid; from this point, the postcingulid descends ventrolabially to the base of the hypoconid.

M_2 is similar in structure to M_1; however, its trigonid is relatively shorter, while the paracristid is lower, shorter, and transversely positioned. The talonid is equal in width to the trigonid, or slightly narrower.

M_3 is similar in trigonid structure to M_2, but its talonid is narrower. The entocristid is complete, the postcingulid is absent. In contrast to M_1 and M_2, M_3 has a well-developed hypoconulid positioned close to the entoconid and fused with it at the base. The apical notch between the hypoconulid and the entoconid ranges from deep to superficial (Pl. 7, fig. 8; Figs. 30l, 30n); sometimes, the two cusps are completely fused (Pl. 7, fig. 7b; Fig. 30k).

Measurements, mm. Length of P^4–M^2 along the tooth crowns, 4.7; length of P^4–M^3 along alveoli, 5.25 (holotype). Length of I_1–M_3 along alveoli, 10.3 (specimen PIN, no. 3107/421).

For measurements of the upper teeth, see Table 24, the lengths of the tooth row are in Table 25, dimensions of the lower teeth are in Tables 26 and 27.

Depth of the horizontal ramus of the lower jaw: under P_2, 1.75–2.0; under P_3, 1.65–2.2; under P_4, 2.0–2.4; under M_1, 2.05–2.5; under M_2, 2.05–2.5; under M_3, 2.0–2.5. In a young animal (specimen PIN, no. 3107/429), the depth of the horizontal ramus under M_2, 1.8; under M_3, 1.5.

Occurrence. Middle Eocene (Irdinmanhan) of Mongolia.

Material. In addition to the holotype, the collection of PIN contains 19 dentary fragments (PIN, nos. 3107/421–438, 440) from the type locality: one with P_2–M_3, one with P_3–M_3, two with P_2–P_4, two with

Table 24. Measurements of the upper cheek teeth of *Eogalericius butleri* Lopatin, 2004, holotype PIN, no. 3107/420

Tooth	Length		Width	
	labial	lingual	parastyle–protocone	metastyle–hypocone
P^4	1.7	1.05	1.7	2.0
M^1	1.7	1.3	2.0	2.15
M^2	1.4	1.25	1.9	1.65

Table 25. Length of the lower cheek teeth rows of *Eogalericius butleri* Lopatin, 2004

Tooth row	Length	Specimen PIN, no.
P_2–M_3	8.2	3107/430
P_3–M_3	7.1	3107/422
	7.25	3107/430
P_3–M_3	6.0	3107/421
	6.05	3107/430
P_2–P_4	3.45	3107/430
	3.6	3107/424
	3.8	3107/431
P_2–P_3	2.1	3107/430
	2.15	3107/424
P_3–P_4	2.3–2.8	3107/422, 424–426, 430
P_3–M_1	4.2–4.55	3107/422, 425, 426, 430
P_4–M_2	4.55–4.95	3107/421–423, 427, 430, 435
P_4–M_1	3.0–3.3	3107/421–423, 425–428, 430, 435
M_1–M_3	4.7–4.95	3107/421, 422, 430
M_1–M_2	3.25–3.5	3107/421–423, 430, 434
M_2–M_3	2.55	3107/436
	2.9	3107/421
	3.0	3107/430
	3.15	3107/422

Table 26. Measurements of the lower antemolars of *Eogalericius butleri* Lopatin, 2004 (collection of PIN; in I_1 and I_2, diameters of roots; in I_3–P_1, diameters of alveoli)

Tooth	Length			Width		
	N	limits	Δ	*N*	limits	Δ
I_1	1	0.4	–	1	0.6	–
I_2	2	0.4	–	2	0.5–0.6	0.55
I_3	4	0.25–0.35	0.3	3	0.5–0.6	0.57
C_1	5	0.7–0.9	0.74	5	0.6–0.7	0.63
P_1	10	0.55–0.7	0.61	10	0.45–0.6	0.56
P_2	3	0.95–1.05	1.0	3	0.5–0.55	0.53
P_3	7	1.1–1.4	1.22	6	0.7–0.77	0.73
P_4	12	1.35–1.5	1.44	12	0.95–1.1	1.03

Table 27. Measurements of the lower molars of *Eogalericius butleri* Lopatin, 2004 (collection of PIN)

Tooth	Length					Width				
	N	total		trigonid		*N*	trigonid		talonid	
		limits	Δ	limits	Δ		limits	Δ	limits	Δ
M_1	10	1.8–1.9	1.85	0.9–1.0	1.0	10	1.3–1.4	1.34	1.3–1.45	1.36
M_2	8	1.45–1.7	1.61	0.75–0.9	0.79	8	1.3–1.35	1.32	1.2–1.35	1.28
M_3	6	1.1–1.5	1.32	0.6–0.75	0.67	6	0.9–1.0	0.98	0.7–0.9	0.82

P_3–M_1, one with P_3–P_4, one with P_4–M_3, three with P_4–M_2, one with P_4–M_1, one with P_4, one with M_1 and M_2, two with M_2 and M_3, one with M_3, and two without teeth (one with alveoli of I_1–M_1, another with alveoli of M_2 and M_3).

Genus *Microgalericulus* Lopatin, gen. nov.

Etymology. From the Greek *micros* (small), *gale* (small predator), and the Latin *ericulus* (little hedgehog).

Type species. *Microgalericulus esuriens* sp. nov.

Diagnosis. Known dental formula P_4M_3. P_3 is slightly reduced, compressed laterally. P_4 small (83% as long as M_1), narrow, with relatively long talonid. Paraconid well-developed; metaconid small, weakly separated from protoconid and displaced anteriorly; talonid with lingual cusp. Molars relatively narrow, with high trigonids, without ectocingulids. Paracristid of M_1 inclined anteriorly, elongated. M_2 substantially smaller than M_1 (less than 85% as long as M_1), with small paraconid. Mental foramen located under anterior part of P_3.

Species composition. Type species, Middle Eocene (Irdinmanhan) of Mongolia.

Comparison. The new genus differs from all known genera of Galericini, except for *Eogalericius*, in the weakly reduced P_3 and relatively small P_4 with a well-developed paraconid. It differs from *Eogalericius* in the laterally compressed P_3, narrow P_4 with longer talonid and less developed metaconid, in the lingual position of the talonid cusp of P_4, different length ratio of M_1 and M_2 (in *Eogalericius*, M_2 is 85–95% as long as M_1), relatively narrower and higher M_1 and M_2 without ectocingulids, the elongated and more longitudinally directed paracristid of M_1, small paraconid of M_2, and in the presence of only one mental foramen (*Eogalericius* has two or three; see above).

Microgalericulus esuriens Lopatin, sp. nov.

Plate 7, fig. 9

Etymology. From the Latin *esuriens* (hungry).

Holotype. PIN, no. 3403/300, left dentary fragment with P_3–M_2; Mongolia, Khaychin-Ula 3 locality; Middle Eocene, Khaychin Formation.

Description (Fig. 31). A small-sized hedgehog. The horizontal ramus of the lower jaw is narrow and low. The mental foramen is located in line with the apex of the protoconid of P_3. The anterior edge of the base of the coronoid process is straight, the angle between the ascending and horizontal rami is approximately 100°. The masseteric crest is strong, the masseteric fossa is relatively deep. The mandibular foramen is located at the same level as the molar crowns. The medial crest at the base of the coronoid process is weak. The lower margin of the jaw in the coronoid region forms a typical dorsal curvature.

P_1 is single-rooted (the alveolus is preserved), other cheek teeth are double-rooted. P_2 is much smaller than P_3. P_3 is small, compressed laterally, with a narrow protoconid, small paraconid, and low and short talonid. The postcingulid is well-developed, a small cuspule is present in its middle part.

P_4 is much longer and higher than P_3, with a differentiated trigonid and a relatively long talonid. The paraconid is low, ridgelike, separated from the protoconid by a distinct notch. The protoconid is massive and high, a weak crest is located on its anterior side. The metaconid is reduced, substantially lower and less massive than the protoconid, and weakly separated from it. The apex of the metaconid is located anterior to the apex of the protoconid; therefore, the protocristid is inclined substantially anteriorly. The protocristid notch is superficial and narrow. The precingulid is thin, but distinct. The talonid is relatively large, with a single low cusp, which is located in the lingual part of the transverse postcingulid crest and occupies the posterolingual corner of the talonid. The shallow talonid basin is open lingually because the metastylid crest is undeveloped. The sharp postcingulid crest descends ventrolabially and terminates in the posterolabial corner of the talonid.

The lower molars are relatively narrow and high, $M_1 > M_2 \geqslant M_3$. In M_1, the talonid is equal in width to the trigonid. The trigonid and talonid considerably differ in height, this difference is seen not only between the protoconid and hypoconid, but also between the metaconid and entoconid. The trigonid basin is widely open. The paraconid is raised, ridgelike. The paracristid is relatively long, shearing, with a well-developed carnassial notch. This crest is directed anterolingually but, terminally, deviates slightly anteriorly and, hence, it

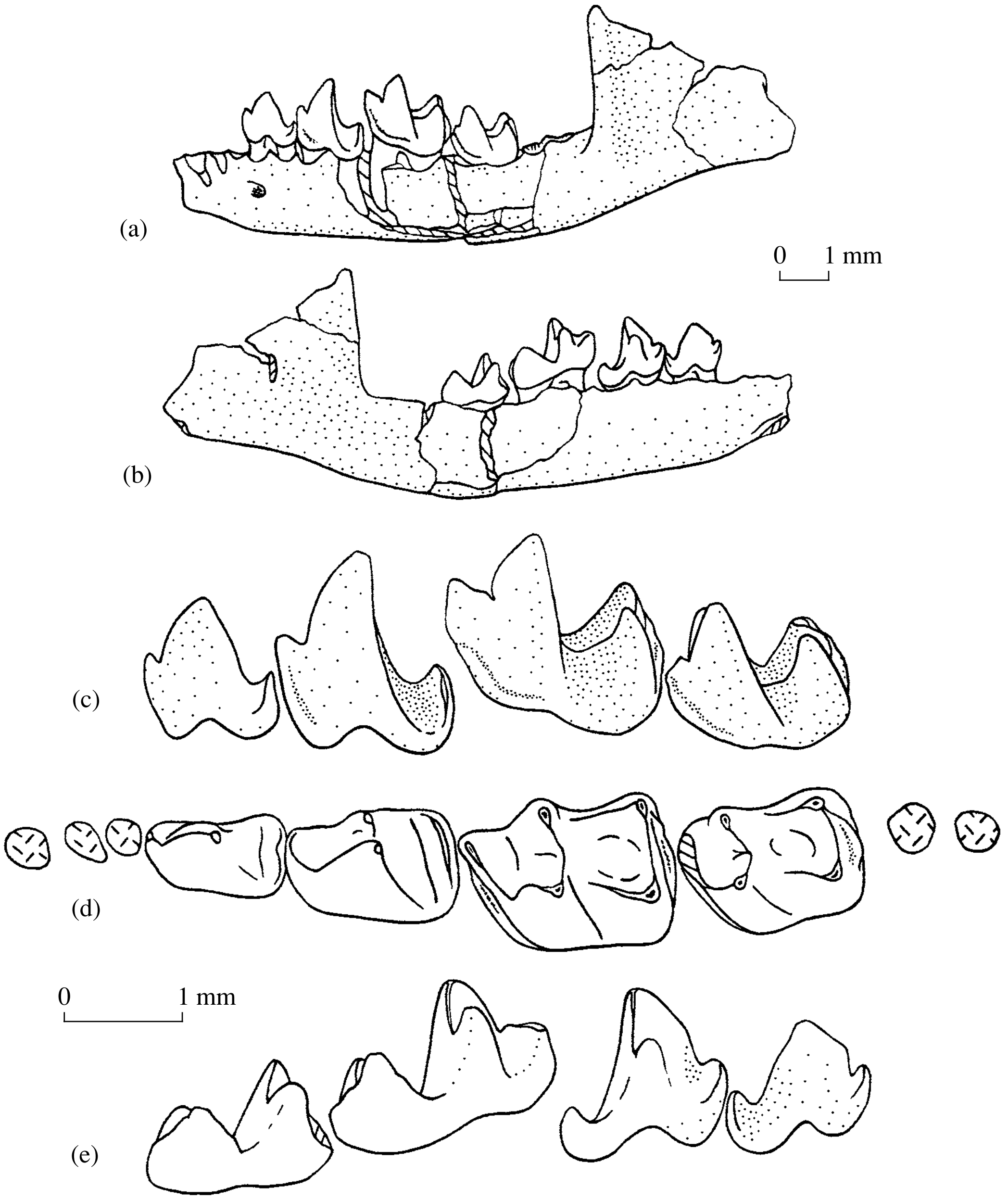


Fig. 31. *Microgalericulus esuriens* sp. nov., holotype PIN, no. 3403/300, left dentary fragment with P_3–M_2 and alveoli and P_1, P_2, and M_3: (a) labial and (b) lingual views, (c) P_3–M_2, labial view, (d) P_3–M_2 and alveoli of P_1, P_2, and M_3, occlusal view, and (e) P_3–M_2, lingual view.

seems not to be subtransverse. The protoconid and metaconid are widely spaced, the protocristid notch is deep. The apex of the metaconid is displaced substantially anteriorly in relation to the apex of the protoconid. The precingulid is narrow, terminates posteriorly in line with the apex of the protoconid. The ectocingulid is absent. The hypoflexid is superficial. The talonid basin is closed lingually by a high and long entocristid, which reaches the base of the metaconid. The hypoconid and entoconid are positioned opposite to each other, the entoconid is much higher. The cristid oblique is low and narrow, connected to the middle of the base of the posterior wall of the protoconid. The postcristid is well developed, complete. The postcingulid is moderately developed, extends from the posterior base of the hypoconid to the posterolabial part of the base of the entoconid and is not connected to the postcristid (Figs. 31c, 31d).

M_2 is much shorter and somewhat narrower than M_1, with a shorter trigonid and a low, short, and trans-

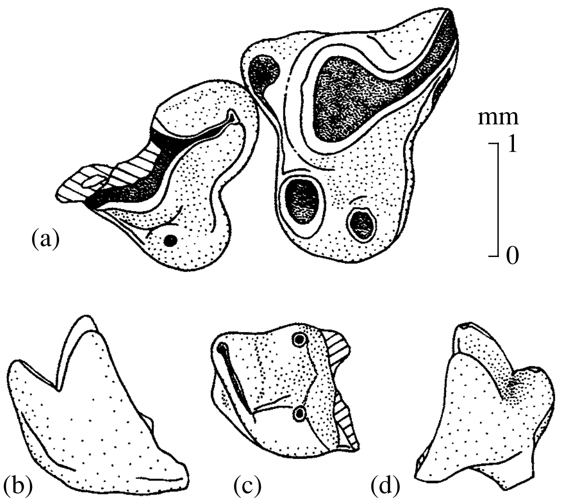


Fig. 32. *Protogalericius averianovi* sp. nov.: (a) holotype ZIN, no. 89009, left P^3–P^4, occlusal view; (b–d) specimen ZIN, no. 89010, fragmentary left M_1: (b) labial, (c) occlusal, and (d) lingual views; Andarak 2 locality, Kyrgyzstan; lower part of the Alai Beds, uppermost Lower Eocene.

verse paracristid. The talonid is slightly narrower than the trigonid. The postcingulid is weak, connected to the point of fusion between the postcristid and entoconid.

Judging from the alveoli, M_3 was substantially smaller than M_2.

Measurements, mm. Holotype: length of P_2–M_3 along alveoli, 7.8; length of P_3–M_2, 5.2; alveolar length of P_1, 0.4; P_2, 0.7; dimensions of premolars (length × width): P_3, 1.2 × 0.7; P_4, 1.45 × 0.95; dimensions of molars: total length of M_1, 1.75; trigonid length, 0.85; trigonid width, 1.3; talonid width, 1.3; total length of M_2, 1.45; trigonid length, 0.75; trigonid width, 1.2; talonid width, 1.15; alveolar length of M_3, 1.0; depth of the horizontal ramus of the lower jaw: under P_3, 1.7; under P_4, 1.85; under M_1, 1.7; under M_2, 1.6; under M_3, 1.7.

Material. Holotype.

Genus *Protogalericius* Lopatin, gen. nov.

Etymology. From the Greek *protos* (the very first), *gale* (small predator), and the Latin *ericius* (hedgehog).

Type species. *Protogalericius averianovi* sp. nov.

Diagnosis. P^4 massive, relatively long and narrow, with large parastyle and weak cingula. Trigonid of M_1 narrow; paracristid short, subtransverse.

Species composition. Type species, uppermost Lower Eocene of Kyrgyzstan.

Comparison. *Protogalericius* differs from *Eogalericius* in the more massive P^4 with a large parastyle and less developed cingula, and in the narrow trigonid and the short and more transversely positioned paracristid of M_1. The structural characters of the trigonid of M_1 distinguish *Protogalericius from Microgalericulus, Eochenus*, and all later Galericini.

Protogalericius averianovi Lopatin, sp. nov.

Plate 7, fig. 10

Etymology. The species is named in honor of the Russian paleontologist A.O. Averianov.

Holotype. ZIN, no. 89009, left maxillary fragment with P^3 and P^4; Kyrgyzstan, Andarak 2 locality; uppermost Lower Eocene, lower part of the Alai Beds.

Description (Fig. 32). P^3 is triangular in outline, with a massive paracone and a large metastylar lobe strongly projecting posterolabially. The metastyle cusp is small, the postcrista is narrow and low. The ectocingulum is weak. The lingual projection is small, the protocone cusp is small. The precingulum and postcingulum are well developed.

P^4 has a massive paracone, strong postcrista, and well-developed lingual lobe. The parastyle is very large, projects anteriorly. The ectocingulum is narrow, hardly discernible. The protocone is compressed slightly longitudinally, the preprotocrista is connected to a crest extending on the anterior margin of the occlusal surface to the parastyle. The hypocone is small, conical, approximately half as high as the protocone. The postcingulum is moderately developed.

The trigonid of M_1 is relatively narrow. The paraconid is elevated, ridgelike, directed almost transversely. The paracristid is short, shearing; the carnassial notch is well developed. The trigonid basin has a narrow lingual opening. The protoconid and metaconid are positioned opposite to each other, the protocristid notch is deep. The precingulid and ectocingulid are well developed, separated by a gap at the level of the protoconid apex.

Measurements, mm. Holotype: length of P^3–P^4, ca. 3.4; labial length of P^3, ca. 1.7; lingual length, 0.8; width, 1.4; labial length of P^4, 1.85; lingual length, 1.15; width at the parastyle–protocone line, 1.8; width at the metastyle–hypocone line, 2.15.

Specimen ZIN, no. 89010, fragment of M_1: trigonid length, 1.0; trigonid width, 1.25.

Material. In addition to the holotype, a fragment of left M_1 (ZIN, no. 89010) from the type locality (collected by A.O. Averianov in 1993).

ORDER DIDYMOCONIDA LOPATIN, 2001

Didymoconida: Lopatin, 2001, p. 106.

Diagnosis. Medium-sized and large insectivores. Bony rostrum formed of nasals and premaxillae present. The jugal considerably reduced, lacking contact with lacrimal, but zygomatic arch massive. Maxilla in orbit bordered by frontal, separating palatine from lacrimal. Tympanic bulla completely ossified, formed of fused ectotympanic and entotympanic bones. Walls of external auditory meatus formed of squamosal and mastoid. Dental formula reduced to varying degree, $I^{3-?}/_{2-0}C^{1}/_{1}P^{3-?}/_{3-2}M^{2}/_{2}$. Incisors small, chisel-shaped. Canines large, of carnivorous type. Premolars simple in structure, $P^{4}/_{4}$ molarized to greater or lesser extent. Upper molars with high twinned cusps of paracone and metacone, lower molars with low reduced paraconid and high twinned protoconid and metaconid.

Composition. One family, Didymoconidae Kretzoi, 1943, Paleogene of Asia.

Comparison. The Didymoconida differ from the Lipotyphla in the structure of its tympanic bulla and external auditory meatus, massive zygomatic arch, the presence of bony rostrum, dental formula, better developed canines, and the structure of the trigonid of lower molars. The Didymoconida differ from the Leptictida in the more reduced jugal bone, the presence of contact between the maxilla and frontal, and the absence of contact between the palatine and lacrimal inside the orbit, in the structure of the tympanic bulla (in the Leptictida, it is formed by the expanded entotympanic bone), the exclusion of the parietals from the formation of the occipital region, the absence of a large suprameatal foramen in the squamosal, more reduced dental formula, and distinctive structure of the trigonid of lower molars.

FAMILY DIDYMOCONIDAE KRETZOI, 1943

Didymoconidae: Kretzoi, 1943, p. 194.

Tshelkariidae: Gromova, 1960, p. 42.

Type genus. *Didymoconus* Matthew et Granger, 1924, Oligocene of Mongolia, China, and Kazakhstan.

Diagnosis. The same as the diagnosis of the order.

Composition. Three subfamilies: Ardynictinae Lopatin, 1997, Upper Paleocene–Upper Eocene of Central Asia; Didymoconinae Kretzoi, 1943, Middle Eocene–Upper Oligocene of Central Asia and Kazakhstan; and Kennatheriinae subfam. nov., Lower Paleocene–Middle Eocene of Central Asia.

SUBFAMILY ARDYNICTINAE LOPATIN, 1997

Ardynictinae: Lopatin, 1997, p. 119; 2003c, p. 82; Tong, 1997, p. 153; Morlo and Nagel, 2002, p. 125.

Type genus. *Ardynictis* Matthew et Granger, 1925, Middle–Upper Eocene of Mongolia, China, and Kazakhstan.

Diagnosis. Dental formula: $I^{3}/_{2}C^{1}/_{1}P^{3}/_{3}M^{2}/_{2}$. P^3 lacking metacone. P^4 partially molarized, much longer and narrower than molars; metacone fused with paracone; hypocone absent. Stylar shelf of P^4–M^2 wide. Hypocone of M^1 and M^2 undeveloped or very small, in shape of rudimentary cusp on postcingulum (hypoconal shelf). P^2 single- or double-rooted, P_2 single-rooted. P_4 slightly molarized, without metaconid and distinct cusps of talonid. Talonid of M_1 and M_2 uni- or bicuspid (entoconid and/or hypoconulid reduced); open lingually; with high, shearing cristid oblique. Coronoid process of lower jaw high, narrow, and straight; angular process deflecting strongly medially.

Generic composition. *Archaeoryctes* Zheng, 1979, Upper Paleocene–Middle Eocene of Central Asia; *Wanolestes* Huang et Zheng, 2002, Upper Paleocene of China; *Hunanictis* Li, Chiu, Yan et Hsien, 1979, Lower Eocene of China; *Ardynictis* Matthew et Granger, 1925, Middle–Upper Eocene of Mongolia, Middle Eocene of China, Upper Eocene of eastern Kazakhstan; *Jiajianictis* Tong, 1997, Middle Eocene of China; and *?Mongoloryctes* Van Valen, 1966, Middle Eocene of China.

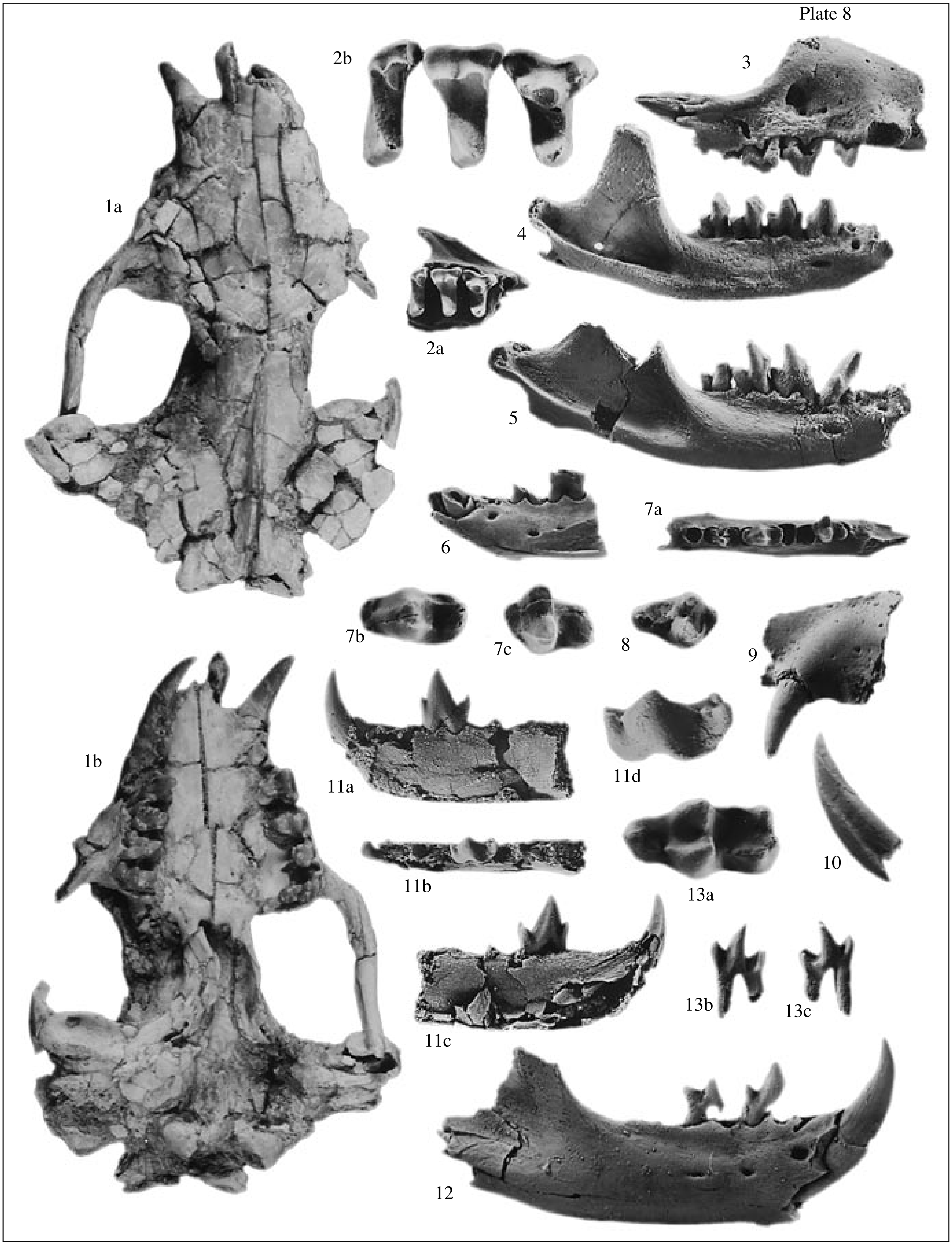
Comparison. The Ardynictinae differ from the Didymoconinae in the absence of metacone on P^3, less molarized P^4 and P_4, the absence or rudimentary character of the hypocone of P^4–M^2, wide stylar shelf of P^4–M^2, single-rooted P_2, and structure of the talonid of P_4–M_2, and in the shape of the coronoid and angular processes of the lower jaw.

Remarks. Tong (1997) independently divided the family Didymoconidae into the subfamilies Didymoconinae and Ardynictinae. My paper appeared in print in January, 1997, dated January–February; the publication by Tong was not dated more precisely than 1997; consequently, according to the International Code of Zoological Nomenclature (ICZN), the name Ardynictinae Lopatin, 1997 takes priority. Tong's classification is also based on the structure of $P^{4}/_{4}$, hypocones of M^1 and M^2, and talonids of M_1 and M_2. He assigned the genera *Ardynictis, Zeuctherium*, and *Hunanictis* to the Ardynictinae, while the Didymoconinae was considered to comprise *Didymoconus, Archaeoryctes, Jiajianictis*, and, presumably, *Kennatherium*. The assignment of *Archaeoryctes* to the Didymoconinae was probably caused by the presence of the hypoconal shelf on its upper molars. *Jiajianictis* was referred to the Didymoconinae based on the presence of semimolarized P_4 with the metaconid. However, the only specimen of the only species of this genus, *J. muricatus,* belongs to a young individual, M_2 of which has not erupted and, consequently, its DP_4 has not been replaced (about the order of tooth replacement in the Didymoconidae, see Morlo and Nagel, 2002; Lopatin, 2003a). Semimolarized DP_4 is characteristic of the other Ardynictinae (Matthew and Granger, 1925b; Lopatin, 2003a); therefore, it is highly probable that *Jiajianictis* belongs to this subfamily.

Wanolestes lii Huang et Zheng, 2002 from the Gashatan of China was referred in the original description to Soricomorpha (Huang and Zheng, 2002). It is characterized by a reduced paraconid and a high trigonid with twinned protoconid and metaconid of M_1 and M_2, by the absence of metaconid on P_4 and entoconid on M_1 and M_2. These characters suggest that *Wanolestes* belongs to the Ardynictinae (see Lopatin, 2004a).

The genus *Mongoloryctes* is tentatively placed in Ardynictinae, based only on the similarity of the gen-

Plate 8



eral structural pattern of M^1 of *M. auctus* (Matthew and Granger, 1925b; Van Valen, 1966) and unquestionable ardynictines.

Zeuctherium Tang et Yan, 1976 from the Lower Paleocene of China (Tang and Yan, 1976) and *Kennatherium* Mellett et Szalay, 1968 from the Middle Eocene of northern China and Mongolia are placed below in a distinct subfamily, the Kennatheriinae subfam. nov.

In the Didymoconidae, the angular process of the lower jaw is deflected medially to a greater or lesser extent, while in the Ardynictinae, a small medial flank is formed. Such structure is usually associated in placentals with enlarged tympanic bullae and provides the maintenance of a fixed distance between the braincase and lower jaw (see Sánchez-Villagra and Smith, 1997).

Genus *Archaeoryctes* Zheng, 1979

Archaeoryctes: Zheng, 1979, p. 360.

Type species. *Archaeoryctes notialis* Zheng, 1979, Upper Paleocene of China.

Diagnosis. From small-sized to large Didymoconidae. P^2 single-rooted. P^3 with parastyle and well-developed protocone. Stylar shelf of P^4–M^1 well-developed. M^1 and M^2 with rudimentary hypocone; metastylar wing of M^1 and parastylar wing of M^2 large; metacone of M^2 slightly reduced. Protoconid of P_4 transversely compressed, bladelike. Paraconid of M_1 and M_2 large, talonid with hypoconid and hypoconulid, entoconid absent.

Species composition. *A. notialis* Zheng, 1979, Upper Paleocene (Nongshanian) of China; *A. euryalis* Lopatin, 2001, Upper Paleocene (Gashatan) of Mongolia; and *A. borealis* Meng, 1990, upper Lower Eocene (Arshantan) of China.

Comparison. *Archaeoryctes* differs from *Ardynictis* in the presence of a rudimentary hypocone on M^1 and M^2 and a parastyle on P^3; the better developed metacone of M^2, better developed stylar wings of M^1–M^2; the bladelike protoconid of P_4; the presence of the hypoconulid on P_4–M_2, the absence of entoconid on M_1; nonreduced talonid of M_2, and in the single-rooted P^2. It differs from *Hunanictis* in the better developed protocone of P^3 and the stylar shelf of P^4; from *Mongoloryctes*, in the better developed styles of M^1; from *Wanolestes*, in the relatively large and less elevated paraconid of M_1 and M_2; and from *Jiajianictis*, in the presence of the hypoconulid on M_1 and M_2.

Archaeoryctes euryalis Lopatin, 2001

Plate 8, fig. 1

Archaeoryctes euryalis: Lopatin, 2001a, p. 97, text-figs. 1–5.

Holotype. PIN, no. 3104/292, almost complete skull with canines and both cheek tooth rows; Mongolia, Tsagan-Khushu locality; Upper Paleocene, Naran-Bulak Formation, Zhigden Member.

Description (Figs. 33–35). A relatively large member of the family, the skull is approximately 100 mm long. In general, the skull is wedge-shaped; the skull base is broad, the zygomatic arches are widely spaced, the facial and, particularly, the rostral region are narrowed.

The skull is strongly distorted, crushed and crooked somewhat to the right side. Most of the bones are fragmentary, some are displaced. The right premaxilla, most of the right zygomatic arch, and some bone fragments from the skull base are lost. As a result of distortion, the lateral part of the left squamosal is strongly raised; therefore, being pasted together, the posterior end of the zygomatic arch appeared under this bone.

The premaxillae, judging from the position of the fragment preserved, formed the lateral and ventral walls of the narrow, anteriorly extended rostrum, which is closed dorsally by the nasals. The lateral portion of the suture between the premaxilla and maxilla is located at the base of the rostrum, in line with the alveolus of the canine. At the boundary of the lateral and dorsal surfaces of the rostrum, a suture between the pre-

Explanation of Plate 8

Fig. 1. *Archaeoryctes euryalis* Lopatin, 2001, holotype PIN, no. 3104/292, skull, ×1: (1a) dorsal and (1b) ventral views; Tsagan-Khushu locality, Mongolia; Upper Paleocene, Naran-Bulak Formation, Zhigden Member.

Figs. 2–8. *Ardynictis captor* Lopatin, 2003: (2) holotype PIN, no. 3107/333, right maxillary fragment with P^4–M^2, occlusal view: (2a) general appearance, ×3, and (2b) P^4–M^2, ×8; (3) specimen PIN, no. 3107/330, right maxillary fragment with P^2–P^4, the base of M^1, and alveoli of C^1 and M^2, labial view, ×3; (4) specimen PIN, no. 3107/362, right dentary fragment with P_3–M_2, labial view, ×3; (5) specimen PIN, no. 3107/372, right dentary fragment with P_3–M_2, labial view, ×3; (6) specimen PIN, no. 3107/340, left dentary fragment with broken off C_1 and P_3–P_4, labial view, ×3; (7) specimen PIN, no. 3107/346, left dentary fragment with P_4 and M_2, occlusal view: (7a) general appearance, ×3, (7b) P_4, ×8, and (7c) M_2, ×8; (8) specimen PIN, no. 3107/345, right M_2, occlusal view, ×8; Khaychin-Ula 2 locality, Mongolia; Middle Eocene, Khaychin Formation.

Figs. 9–13. *Khaichinula lupula* sp. nov.: (9) specimen PIN, no. 3107/324, left maxillary fragment with C^1, labial view, ×3; (10) specimen PIN, no. 3107/392, right C_1, lingual view, ×3; (11) specimen PIN, no. 3403/305, left dentary fragment with DC_1 and DP_3: (11a) labial view, ×3, (11b) occlusal view, ×3, (11c) lingual view, ×3, and (11d) DP_3, occlusal view, ×8; (12) specimen PIN, no. 3107/323, right dentary fragment with DC_1 and C_1 in early stage of eruption, partially damaged DP_3 and DP_4 and alveoli of P_2, M_1, and M_2, labial view, ×3; (13) holotype PIN, no. 3403/326, left P_4: (13a) occlusal view, ×8, (13b) labial view, ×3, and (13c) lingual view, ×3; (9, 10, 12, 13) Khaychin-Ula 2 and (11) Khaychin-Ula 3 localities, Mongolia, Middle Eocene, Khaychin Formation.

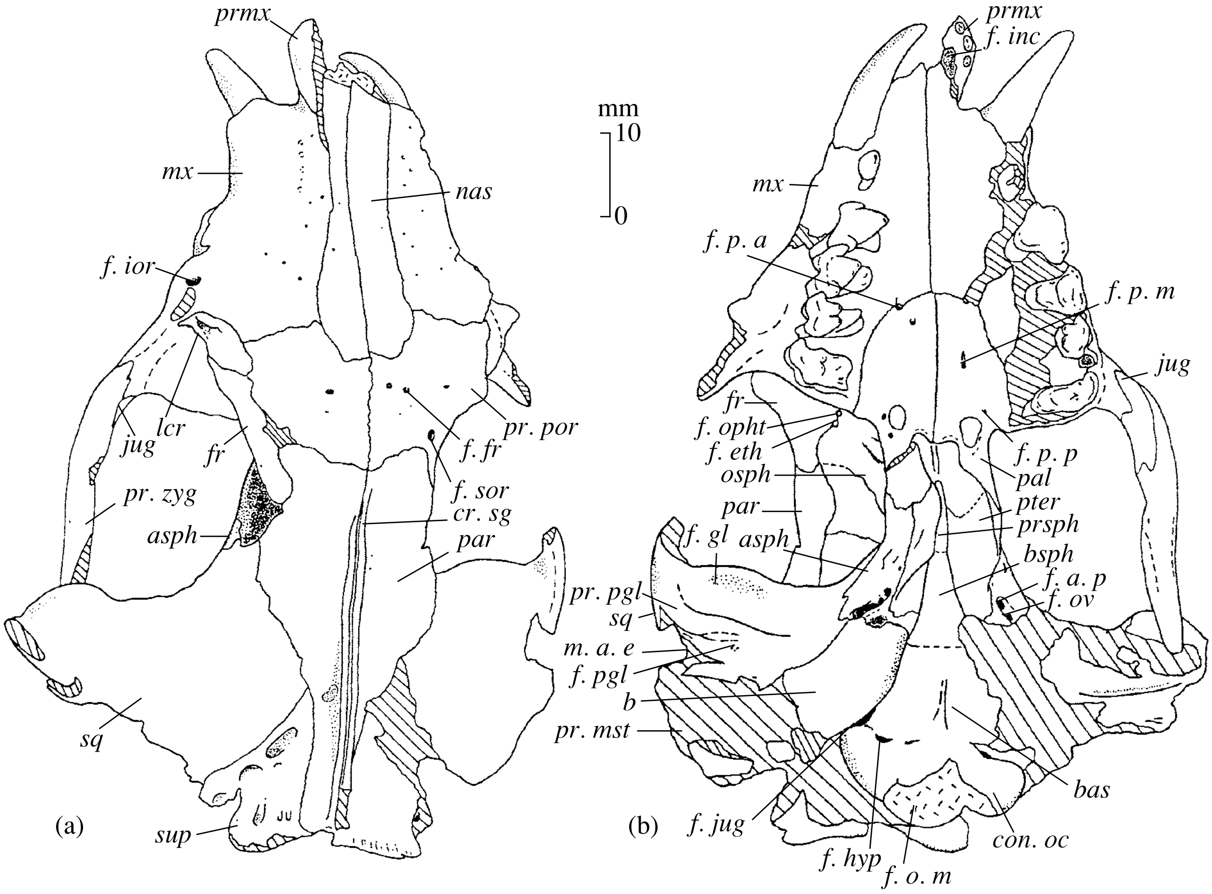


Fig. 33. *Archaeoryctes euryalis* Lopatin, 2001, holotype PIN, no. 3104/292, skull: (a) dorsal and (b) ventral views. Designations: (*asph*) os alishenoideum, (*b*) bulla ossea, (*bas*) basioccipitale, (*bsph*) os basisphenoidale, (*con. oc*) condylus occipitalis, (*cr. sg*) crista sagittalis, (*f. a. p*) foramen alare posterius, (*f. eth*) foramen ethmoideum, (*f. fr*) foramen frontalis, (*f. ior*) foramen infraorbitale, (*f. gl*) fossa glenoidalis, (*f. hyp*) foramen hypoglossum, (*f. inc*) foramen incisivum, (*f. jug*) foramen jugulare, (*f. o. m*) foramen occipitale magnum, (*f. opht*) foramen ophtalmaticus, (*f. ov*) foramen ovale, (*f. p. a*) foramen palatinum anterius, (*f. pgl*) fossa postglenoidalis, (*f. p. m*) foramen palatinum medius, (*f. p. p*) foramen palatinum posterius, (*fr*) os frontale, (*f. sor*) foramen supraorbitale, (*jug*) os jugale, (*lcr*) os lacrimale, (*m. a. e*) meatus acusticus externus, (*osph*) os orbitosphenoideum, (*mx*) os maxillare, (*nas*) os nasale, (*pal*) os palatinum, (*par*) os parietale, (*pr. mst*) processus mastoideus, (*prmx*) os praemaxillare, (*pr. pgl*) processus postglenoidalis, (*pr. por*) processus postorbitalis, (*prsph*) os praesphenoideum, (*pr. zyg*) processus zygomaticus ossis squamosi, (*pter*) os pterygoideum, (*sq*) os squamosum, and (*sup*) os supraoccipitale.

maxilla and nasal is clearly seen. Thus, the dorsal component of the premaxilla is absent. In the anterolateral part, directly above the alveolus of I^1, there is a small circular foramen. The lateral surface is convex in the region of incisors, particularly, near I^2. The ventral portion of the suture between the premaxilla and maxilla is short. The incisive foramen, which is located between these bones, is large, extended oval. Anteriorly, the premaxilla is broken off; therefore, it is impossible to judge the extent to which it projected anteriorly beyond the incisors.

The nasals are narrow and long, convex in the anterior part, extend posteriorly slightly farther than the beginning of the zygomatic arches. Since the most anterior regions of both nasals are broken off, it is difficult to infer the position of their anterior edge. In the middle part, close to the lateral edge, there are two dorsally open foramina; the anterior foramen is small, while the posterior foramen is somewhat larger. The sutures between the nasals and maxillae are distinct and widened because the bones are displaced by distortion. The suture between the nasals and frontals is W-shaped in horizontal plane.

The maxillae form most of the facial region and the anterior part of the zygomatic arches. Dorsally, they come in contact with the premaxillae, nasals, frontals, and lacrimals. The dorsal and lateral surfaces of the rostral portion are rough, fine-pitted, with many small pits and foramina. Near the boundary between the nasals, there are relatively large rounded depressions, each contains several tiny pits. In the better preserved left bone, three depressions of this type form a regular longitudinal row (Pl. 8, fig. 1a; Fig. 33a). In the first two, all pits are superficial; in the third, one pit is relatively deep but blind. The rostral portion also has nutrient foramina: two very small foramina and a larger foramen ahead of the longitudinal row of depressions (all face anterodorsally); one small dorsal foramen is between the middle and posterior depressions, two are medial to the posterior depression, and one is posterolateral to it. Three small foramina are on the dorsolateral surface of the facial portion. The medial of these foramina faces dorsally, and other two face posterolaterally. The pits and depressions could have been the origins of tendons of the nasolabialis profundus superficialis muscle, which moved the elongated snout.

The lateral wall of the maxilla is pierced by a short rounded infraorbital canal, which opens anteriorly as a large infraorbital foramen located in line with P^4. Lateral to the infraorbital canal, the base of the zygomatic process has a rough, slightly concave region, which was probably the origin of the maxillonasalis muscle. The zygomatic process of the maxilla is broad and massive. Within the zygomatic arch, it contacts with the zygomatic process of the squamosal (dorsally and laterally) and the jugal. The maxilla forms the anteroventral part of the orbit and its floor. The anterior region of the orbital floor is perforated by small rounded foramina and pierced by the lingual root of M^2. In the orbital wall, the maxilla comes in contact with the frontal and, thus, separates the lacrimal from the palatine. The boundary between the maxilla and lacrimal passes above the posterior foramen of the infraorbital canal and reaches the anterior boundary between the lacrimal and frontal. The position of the palatine–maxillary suture and the sphenopalatine foramen remains uncertain because of distortion of the specimen.

On the ventral side of the skull, the surface of the palatine processes of the maxillae is rough, fine-pitted. The anterior palatine foramen is located medial to P^4, within the palatine–maxillary suture and is connected anteriorly to a wide and shallow groove. The palatine–maxillary suture extends from the posteromedial edge of the posterior molar and passes almost parallel to the longitudinal axis of the skull along the lingual side of the tooth row to the middle of P^4, where it turns medially and comes in contact with the suture between the opposite pair of bones.

The jugal forms a relatively small segment of the zygomatic arch. This is a small, longitudinally extended element in the anterior quarter of the ventromedial side of the zygomatic arch, which is clearly visible only from the ventral side of the skull. It is bordered laterally, posteriorly, and dorsomedially by the zygomatic process of the squamosal, while anteriorly and anteromedially, by the zygomatic process of the maxilla. Thus, it disjoins the zygomatic processes of the maxilla and squamosal ventrally and medially; however, it allows contact between these processes on the dorsal and lateral sides of the zygomatic arch. The ventral portion of the squamosal–jugal suture begins from the most lateral point of the zygomatic arch anterior to its caudal curvature, extends along the middle of the arch for one-fourth of its length and abruptly turns dorsomedially; on the dorsomedial surface, it meets the squamosal–maxillary suture and passes into the jugal–maxillary suture, which extends anteroventrally on the same side and is closed at the bend of the zygomatic arch.

On the ventral side, the edge of the palatines is in line with P^4. A relatively small oval middle palatine foramen is observed in the left bone at the level of M^1; anteriorly, it is connected to a short, shallow groove. This foramen contains two separate foramina: the larger lateral foramen opens in anteromedially, while the smaller medial foramen faces anterolaterally. In the right bone, the foramen located opposite M^1 is slitlike and opens anteriorly. A small posterior palatine foramen is located posteromedial to M^2. It is oval in shape, opens ventrally. At the posterior margin, the palatine processes form a massive postpalatine torus. On each bone, this torus has a raised circular area (probably, for attachment of epithelial fascicles) just ahead of the choanae. The torus is pierced on the lateral side by relatively large circular foramina (open laterally). Each foramen is probably connected by a canal to respective posterior palatine foramen. At the level of the choanal orifices, the postpalatine torus is divided into three processes. The lateral processes are narrow, long, extend to the anterior base of the alisphenoid and pterygoid. The central postpalatine process separating the choanal orifices extends posteriorly to the presphenoid.

The palatine is represented in the orbit by a small element bordered by a process of the frontal and by the alisphenoid. It is impossible to recognize contacts between the palatine and other bones forming the orbital wall because of distortion.

The lacrimals are small, with a large orbital portion and a small facial process (which are visible from the dorsal side because of distortion of the specimen, Fig. 33a). The facial process is a very narrow band, the medial part of which forms a small lacrimal tubercle overhanging a large fossa, which contains the lacrimal foramen and is bordered anteriorly and posteriorly by ridgelike thickenings of the bone. The opening of the lacrimal duct is small, faces posterolaterally. Within the orbit, the lacrimal is bordered anteriorly and ventrally by the lacrimal–maxillary suture and, posteriorly, by the lacrimal–frontal suture. Most of its orbital surface is flat, located medially and posteriorly to the fossa of the lacrimal foramen. The short lateral process overlies the maxilla above the posterior half of the infraorbital canal. The ventral portion of the lacrimal–maxillary suture passes slightly above this canal, so that the lacrimal does not participate in the formation of the dorsal wall of the posterior opening of the infraorbital canal.

The frontals are short, approximately one-third as long as the parietals and half as long as the nasals. The anterior edges of the bones are approximately in line with the infraorbital canals, while the posterior edges are slightly posterior to the postorbital processes. The surface of these bones is flat. The left bone contains two foramina for the rami of V_1, i.e., a large frontal foramen in the anterior part (open dorsally) and a much smaller foramen posterior of it (slitlike, open anterodorsally). In the right bone, the number of these structures is doubled; in addition, a relatively large foramen is present near the postorbital process (open anterodorsally). The surface of the postorbital process is covered with many small grooves and pits, which are tentatively interpreted as traces of attachment of a tendon that closed the orbit posteriorly. The frontal–parietal sutures extend transversely relative to the skull axis, located at the narrowest region of the skull roof.

On the lateral side, the frontal descends into the orbit and forms a significant part of the orbital wall. Here, it is bordered anteriorly by the lacrimal, ventrally, by the maxilla and palatine, and, posteriorly, by the orbitosphenoid and alisphenoid. A stout supraorbital crest extends posteriorly from the lacrimal tubercle and terminates in the postorbital process, which is followed by a circular supraorbital foramen. Within the frontal–orbitosphenoid suture, there are two relatively large foramina (ethmoidal and ophthalmic).

The parietals form the major part of the skull roof. They gradually expand posteriorly up to the area overlapped by the squamosals. The medial area of the convex dorsal surface of the parietals rise abruptly upwards and form a stout sagittal crest. It extends gradually increasing in height from the boundary of the frontals to the posterior edge of the dorsal surface of the skull proceeds, where it lowers rather abruptly. The wedge-shaped posterior parts of the parietals overlap the dorsal exposure of the supraoccipital and divide it into two triangular portions. The lateral extent of the parietals is small.

The squamosals are considerably fragmented. These are the largest bones of the skull, which form most of the temporal region and basicranium. Anteriorly and posteriorly, they are bordered by the squamosal–parietal and squamosal–supraoccipital sutures, respectively. The dorsal surface is smooth and slightly concave.

The zygomatic process of the squamosal is directed at the base anteriorly and dorsally. It forms most of the zygomatic arch, approximately three-fourths of its total extent. Judging from the preserved fragment of the left arch, the zygomatic process is relatively high and wide, gently curved. Dorsally and laterally, it is bordered by the zygomatic process of the maxilla; ventrally and medially, it embraces the jugal. In the middle third, it is pierced by a narrow canal providing passage for a nerve or vessel; the anterior foramen of this canal is on the medial side, while the posterior foramen is on the lateral side of the bone. The lateral surface is convex, smooth, with a distinct low ridge in the lower part of the middle third of the arch; the ridge separates a rough ventrolateral area for attachment of muscular fibers. A considerably larger, clearly outlined, rough region for muscles is in the posterior part of the medial surface just posterior to the foramen.

The glenoid fossae and postglenoid processes are well developed, large. The anterior border of the glenoid fossa is distinct, slightly curved anteriorly. The articular surface is smooth, deeply concave in the center, inclined anteroventrally, crescentic in shape (in lateral view). The postglenoid process is broad, rounded triangular (in posterior view); posteriorly, it is connected to the mastoid process of the petrosal; medially, it is bordered by the ectotympanic. A true postglenoid foramen is absent. However, a relatively large fossa is located in the center of the posterior surface of the postglenoid process; the fossa contains three small foramina (one in each lateral wall and one in the posterior wall), which were probably connected with the venous emissaries. The lateral foramen is the largest. The suture between the right squamosal and alisphenoid is seen in ventral view on the lateral side of the ectopterygoid process. Posteriorly, this suture terminates at the anterolateral corner of the tympanic bulla. The suture between the squamosal and ectotympanic extends posteriorly. Despite the fracture, it is visible in lateral view that the squamosal forms the dorsal, anterior, and ventral walls of the external auditory canal (posteriorly, it is closed by the mastoid). The external auditory meatus was apparently oval.

The presphenoid is narrow triangular, connected laterally to the pterygoid and, posteriorly, to the basisphenoid. The basisphenoid is trapezoid, bordered laterally by the alisphenoid and tympanic bulla and, posteriorly, by the basioccipital.

The pterygoids are distinctly separated from the alisphenoids, palatines, and presphenoid. They participate in the formation of the internal walls of the posterior nasal passage and are connected to the presphenoid on the roof of the internal naris. The entopterygoid crests are compressed transversely and slightly inclined (the right crest is considerably distorted).

The alisphenoids form a large part of the lateral walls of the braincase. Their dorsal processes closely approach the skull roof and come in contact with the parietals. Anteriorly, the alisphenoid is bordered by the frontal and orbitosphenoid and, within the sphenorbital fissure, is connected to the palatine. The palatine–alisphenoid suture curves anterior to the sphenorbital fissure and extends posteriorly on the lateral side of the ectopterygoid process onto the ventral side of the skull. Posteriorly, there is distinct contact with the squamosal. In the temporal region, the alisphenoid–squamosal suture extends vertically, passes along the crest lateral to the ectopterygoid process, which marks the boundary between the lateral wall and the floor of the braincase. The ventral portion of the suture curves posteriorly and extends on the lateral side of the ectopterygoid crest to the tympanic bulla. The anterior edge of the alisphenoid reaches the middle part of the lateral side of the posterior process of the palatine. The palatine–alisphenoid suture meets there with the pterygoid–alisphenoid suture. The last suture extends posteriorly

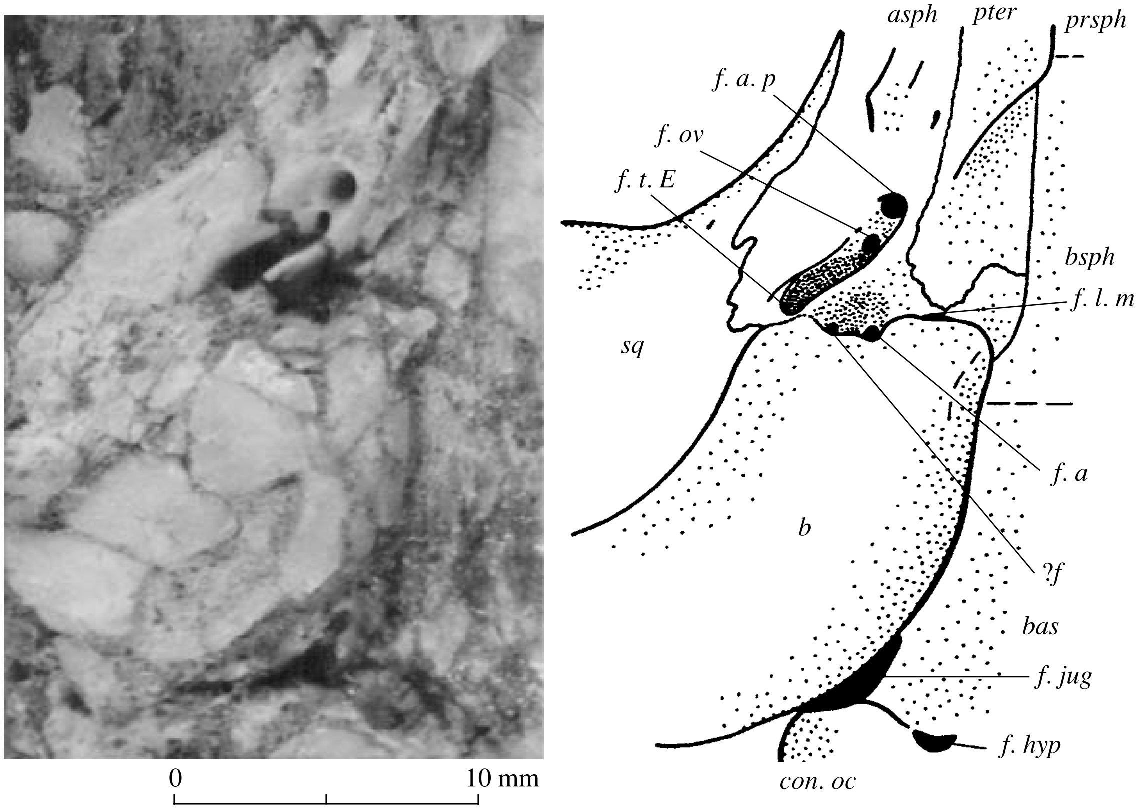


Fig. 34. *Archaeoryctes euryalis* Lopatin, 2001, holotype PIN, no. 3104/292, skull, structure of the ear region, right side. Designations: (*?f*) presumable foramen of the internal carotid nerve, (*f. a*) foramen of the internal carotid artery, (*f. l. m*) foramen lacerum medium, and (*f. t. E*) foramen tubae Eustachii s. auditivae. For other designations, see Fig. 33.

on the lateral base of the entopterygoid process and has in this region a characteristic serrated shape. The narrow posterior portion of the suture ascends along the medial wall of the choanae and is connected with the pterygoid–presphenoid suture.

Anterior to the tympanic bulla, the alisphenoid has the elements described below (Fig. 34). The ectopterygoid process of the alisphenoid is located lateral to the process of the pterygoid. It is compressed transversely, with a broad base and a narrow tip turned ventrolaterally. Medial to it, near to the pterygoid–alisphenoid suture, there is a small circular foramen continued posteriorly by a short, deep groove. A large, longitudinally extended depression containing three large foramina is located at the posterior base of the ectopterygoid process. Two foramina are in its anterior wall, open posteriorly. The larger of the two foramina is the posterior opening of the alisphenoid canal. It is circular in shape and located in the anteroventral part of the depression. A narrow bony bridge separates it from the second foramen, i.e., the foramen ovale, which is half as large as the first, located dorsally and slightly posteriorly. Another very small foramen is located a little ventrally, in the lateral wall of the depression (only on the right side of the skull). Posteriorly, the depression narrows and forms a deep trough, with a small narrow foramen in the posterior wall. It faces anteriorly and is located somewhat dorsal to the foramen ovale. Since it is located in a long groove, this is probably the anterior foramen of the bony part of the Eustachian tube. Medially, the depression and the groove are bordered over the entire extent by a high ridge. Another deep depression is located medial to the posterior half of this ridge, directly ahead of the tympanic bulla. Its posterior wall (that is, the anterior wall of the tympanic bulla) is pierced by two foramina separated from each other by a vertical lamina; the medial foramen is relatively large, while the lateral foramen is smaller. The first is regarded as an exit of the internal carotid artery. The second probably provided passage for the internal carotid nerve. The middle lacerate foramen is separate, located in the medial part of the base of the anterior wall of the tympanic bulla. It is large, broad, oval in shape.

The orbitosphenoid is surrounded anteriorly, posteriorly, and ventrally by the frontal, alisphenoid, and palatine, respectively. Its central part retains a wide groove, which descends posteroventrally and is bordered posteriorly by a high ridge. It probably terminated in the optic foramen. A large sphenorbital fissure is located posteroventrally.

The occipital bones are considerably fragmented and displaced. The foramen magnum is large, oval. The

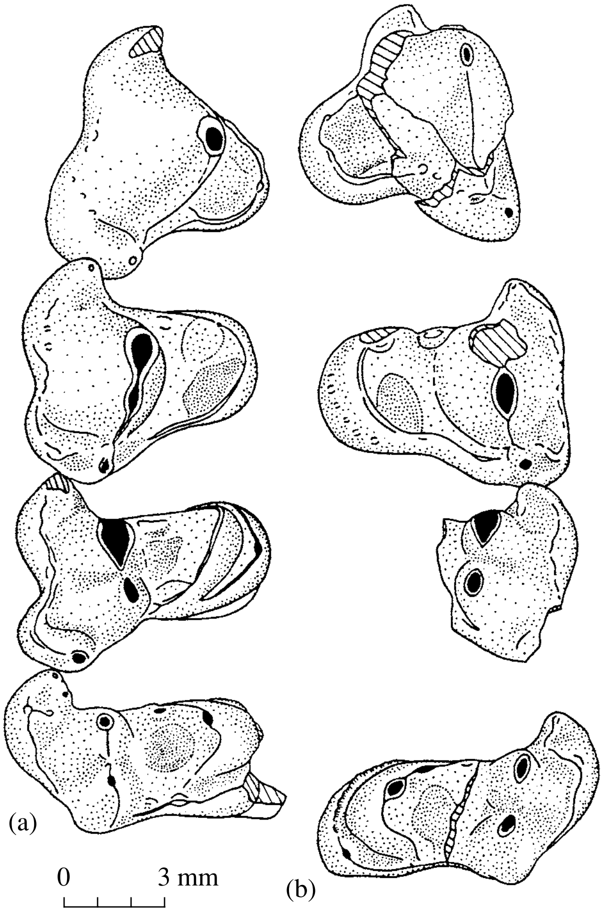


Fig. 35. *Archaeoryctes euryalis* Lopatin, 2001, holotype PIN, no. 3104/292, P^3–M^2, occlusal view: (a) right and (b) left.

supraoccipital is pentagonal in outline. It is very thick, with a slightly concave central part. The well-developed dorsal process is exposed on the skull roof; it is divided by the parietals into two approximately equal triangular portions. Two large oval depressions are located near the squamosal–supraoccipital suture. The posterior margin has a grooved surface. The occipital–mastoid suture passes ventrally from the lambdoid crest to the lateral side of the occipital condyle. The basioccipital, which is bordered anteriorly by the basisphenoid and, laterally, by the tympanic bulla and mastoid, is visible in ventral view. The bone gradually expands posteriorly and has a weak longitudinal keel. The occipital condyles are relatively small, convex; their anterior edge curves slightly posteriorly. A large hypoglossal foramen is located directly anterior to each condyle. Slightly anteriorly and laterally, a slitlike jugular foramen is located at the boundary between the tympanic bulla, occipital, and petrosal bones.

At the skull base, the mastoid process of the petrosal forms a semicircular region bordered anteriorly and laterally by the squamosal and, anteromedially, by the tympanic bulla. A small, ventrolaterally open foramen is located on the right side posterior and slightly medial to the postglenoid fossa. The mastoid is strongly flattened on the occipital side. A detailed description is impossible because of both mastoids are considerably fragmented.

The tympanic bulla is completely ossified, bean-shaped; its long axis is inclined anteromedially. On the lateral side, it is slightly flattened, the medial part is convex. The anterior edge is located almost in line with the transverse axis of the glenoid fossa. The tympanic bulla encloses completely the tympanic cavity, is bordered by the alisphenoid anteriorly, by the squamosal laterally, by the mastoid posteriorly, and, by the basisphenoid and basioccipital medially. Hence, its walls are only formed by tympanic bones. The ventral surface of the tympanic bulla lacks a suture.

The teeth (Fig. 35) are well preserved: the left row has a canine, P^2–M^2, and alveoli of three incisors; the right row has a canine and P^2–M^2; the canines and almost all cheek teeth are complete.

Judging from the alveoli, the incisors were very small, rounded. Apparently, $I^1 < I^2 > I^3$. The canine is large, slightly curved, of the carnivorous type. P^2 is single-rooted, simple conical, compressed slightly transversely. P^3–M^2 are three-rooted, with a large lingual and two smaller labial roots. In M^2, the posterior labial root is considerably reduced. P^3 and P^4 are substantially longer than molars. The stylar shelf of P^3–M^2 is well-developed.

P^3 has a single large and high cusp, the paracone. The parastyle and metastyle are well-pronounced, the ectocingulum is absent. The lingual projection is relatively large; however, the protocone only slightly raises above its surface and bordering ridges.

P^4 differs from P^3 in the greater molarization, that is, it has a weak ectocingulum, a rudimentary metacone (completely fused with the paracone, but having a separate apical wear facet), and a well-developed protocone. A small paraconule is present. A small depression is seen in the posterolingual part of the occlusal surface, which probably marks the initial stage of development of the postcingulum. The lingual side of the crown of left P^4 is sculptured with small, widely spaced tubercles in the middle part.

M^1 is Y-shaped. The parastylar wing projects strongly anterolabially, the metastylar wing projects posterolabially. A distinct ectocingulum connects the styles. The paracone and metacone are detached for approximately one-fourth of their height. The paracone is substantially more massive than the metacone and has a larger wear facet. The protocone is triangular, connected by long, low crests to the basal parts of the lingual walls of the paracone and metacone. The conules are weak. The postcingulum in the shape of a relatively wide border is located much more dorsally than the occlusal surface of the lingual lobe. It has a small rudimentary cusp of the hypocone. A very narrow

Table 28. Measurements of the upper teeth of *Archaeoryctes euryalis* Lopatin, 2001, holotype PIN, no. 3104/292; (sin) left, (dex) right, incisors measured along alveoli

Parameter	I^1 sin	I^2 sin	I^3 sin	C^1		P^2 dex	P^3		P^4		M^1 dex	M^2	
				sin	dex		sin	dex	sin	dex		sin	dex
Length	1.9	2.3	2.0	5.5	5.5	3.3	7.5	7.3	6.0	6.2	5.5	4.8	4.8
Width	1.8	2.3	2.0	4.0	4.0	2.0	6.3	6.0	7.3	7.0	7.9	8.0	–

anterolingual cingulum with a fine-tuberculate structure is connected to the postcingulum.

The crown of M^2 is inverted L-shaped in outline, because its parastylar wing is well-developed and projects far anterolabially, while the metastyle is considerably reduced. In addition to the parastyle, the parastylar wing has two small cuspules in the anterior part. The ectocingulum extends from the parastyle to the line of the middle of the metacone. Other structural elements of the occlusal surface are similar to those of M^1, although the metacone is developed to a much lesser extent, the postcingulum is wider and looks like a hypoconal shelf, and the rudimentary cusp of the hypocone is displaced posteriorly in relation to the protocone to a greater extent.

Measurements, mm. Holotype: condylobasal skull length, ca. 95; basal length, ca. 102 (because of transverse and vertical distortion, only longitudinal measurements are listed; in addition, note that the anterior region of the rostrum is broken off).

Length of tooth rows: I^1–M^2, 49; C^1–M^2, 39; P^2–M^2, 28; P^3–M^2, 24 (right) and 26 (left); P^4–M^2, 17 (right) and 18 (left).

Tooth measurements are given in Table 28.

Comparison. *Archaeoryctes euryalis* differs from *A. notialis* in the larger size, better developed lingual projection of P^3, relatively shorter P^4, the structure of M^2 (strongly developed parastylar part and reduced metastylar part), and in the better developed postcingulum of M^1 and M^2. The distinctions from *A. borealis*, which is only represented by the lower teeth, consist in the considerably larger size of *A. euryalis.*

Remarks. *Archaeoryctes euryalis* is closely similar to *A. notialis* in the shape and structure of P^3–M^2 (Zheng, 1979, pl. I, fig. 1b; Gingerich, 1981, p. 534, text-fig. 4A). The well-developed postcingulum of M^1 and M^2 and the large size of *A. euryalis* suggest that it is more advanced evolutionary than *A. notialis,* which agrees with the geological ages of these taxa.

Occurrence. Upper Paleocene (Gashatan) of Mongolia.

Material. Holotype.

Genus *Ardynictis* Matthew et Granger, 1925

Ardynictis: Matthew and Granger, 1925b, p. 2.

Type species. *Ardynictis furunculus* Matthew et Granger, 1925, uppermost Eocene of Mongolia.

Diagnosis. Small and medium-sized Didymoconidae. P^2 double-rooted. P^3 with well-developed protocone, without parastyle. M^1 and M^2 without hypocone, metastylar wing of M^1 and parastylar wing of M^2 moderately developed, metacone of M^2 considerably reduced. Protoconid of P_4 conical. Talonid of M_1 with hypoconid and entoconid, talonid of M_2 considerably reduced, having only hypoconid.

Species composition. *A. furunculus* Matthew et Granger, 1925, uppermost Eocene (Ergilian) of Mongolia; *A. zhaii* Tong, 1997, Middle Eocene (Irdinmanhan) of China; *A. captor* Lopatin, 2003, Middle Eocene (Irdinmanhan) of Mongolia.

Comparison. *Ardynictis* differs from *Archaeoryctes* in the absence of a rudimentary hypocone on M^1 and M^2, parastyle on P^3; reduction of the metacone of M^2; the weaker stylar shelves of M^1–M^2; the conical shape of the protoconid of P_4, the absence of hypoconulid on P_4–M_2, the presence of the entoconid on M_1, reduction of the talonid of M_2; and in the double-rooted P^2. It differs from *Hunanictis* in the better developed protocone of P^3 and stylar shelf of P^4 and in the double-rooted P^2. It differs from *Mongoloryctes* in the better developed styles of M^1, from *Wanolestes* and *Jiajianictis* in the presence of the entoconid on M_1.

Ardynictis captor Lopatin, 2003

Plate 8, figs. 2–8; Plate 10, figs. 3 and 4

Ardynictis captor: Lopatin, 2003c, p. 82, text-figs. 1–3, 4a, 4b, and 5.

Holotype. PIN, no. 3107/333, right maxillary fragment with P^4–M^2; Mongolia, Khaychin-Ula 2 locality; Middle Eocene, Khaychin Formation.

Description (Figs. 36–38). A small-sized *Ardynictis*: the P_2–M_2 row is 10–11 mm long, the P_4–M_2 row is 6–7 mm long, the lower jaw is about 27 mm long, and the reconstructed skull is approximately 40 mm long. The rostral region of the skull is very narrow (in specimen PIN, no. 3107/330, the palatal process of the maxilla at P^2 is 3.2 mm wide; at P^3/P^4, 5.2 mm wide). The lateral region of the maxilla is smooth, convex, pierced by several small nutrient foramina near the nasal–maxillary suture and infraorbital foramen. Rough sites are located dorsal to alveoli of the canine and P^2, anterior to the infraorbital foramen, and on the base of the zygomatic arch.

The infraorbital canal is short, its anterior foramen is located in line with the posterior labial root of P^4, and

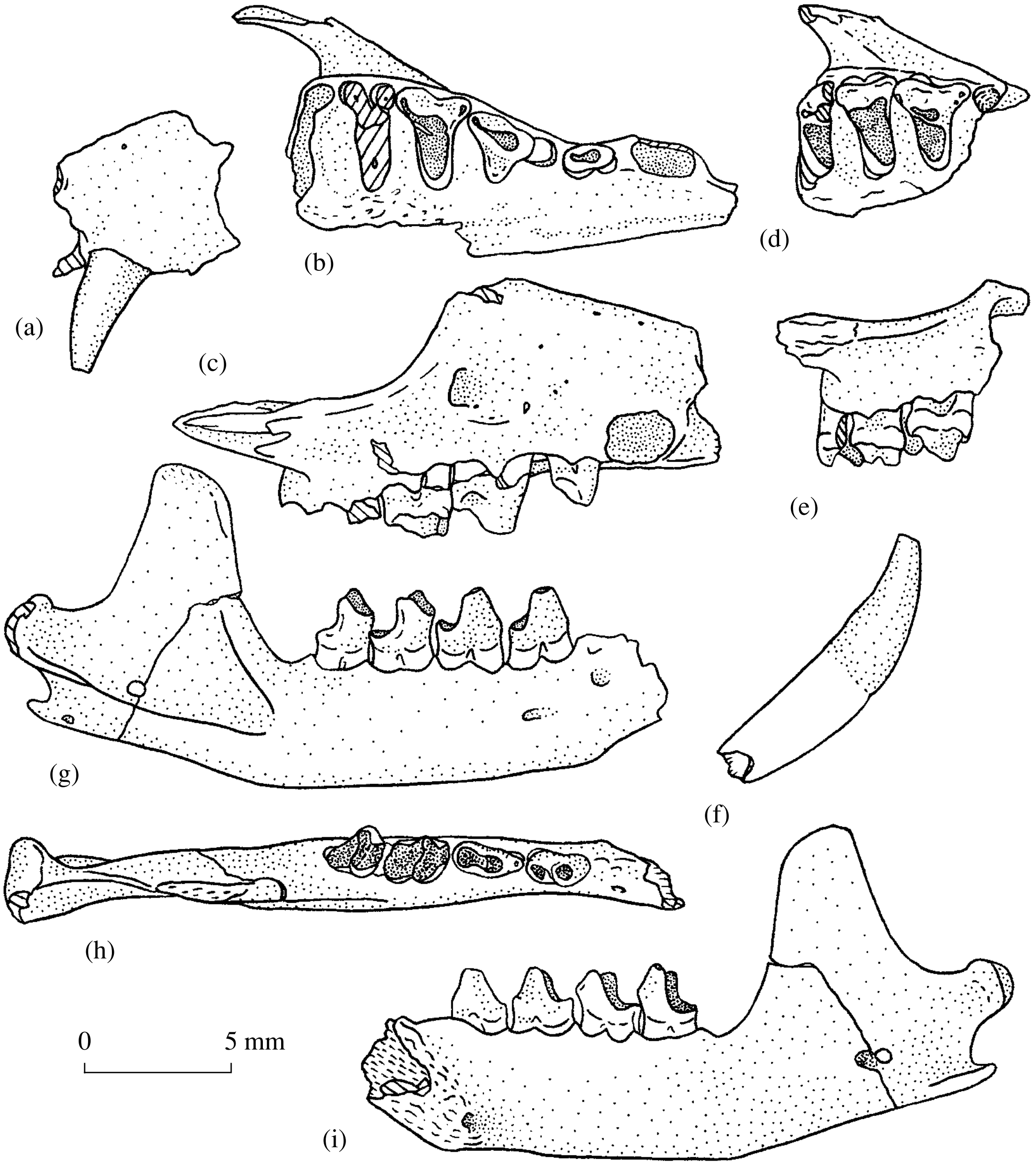


Fig. 36. *Ardynictis captor* Lopatin, 2003: (a) specimen PIN, no. 3107/329, left maxillary fragment with C^1, labial view; (b, c) specimen PIN, no. 3107/330, right maxillary fragment with P^2–P^4, the base of M^1, and alveoli of C^1 and M^2: (b) occlusal and (c) labial views; (d, e) holotype PIN, no. 3107/333, right maxillary fragment with P^4–M^2: (d) occlusal and (e) labial views; (f) specimen PIN, no. 3107/335, right C$_1$, labial view; (g–i) specimen PIN, no. 3107/362, right dentary fragment with P$_3$–M$_2$: (g) labial, (h) occlusal, and (i) lingual views; Khaychin-Ula 2 locality, Mongolia; Khaychin Formation, Middle Eocene.

the posterior foramen is in line with the middle part of M^1. The foramina are rounded angular in shape (the lateral and dorsal walls of the canal are straight). Ventromedial to the anterior foramen of the infraorbital canal, there is an opening of a small canal for a vessel and nerve, which extends to P^3. The orbital floor is pierced by massive lingual roots of P^4 and molars. The lacrimal and maxilla come in contact dorsal to the infraorbital canal.

The posterior edge of the base of the zygomatic arch is located in line with the parastylar wing of M^2. The zygomatic arch is slender. Judging from the preserved arch fragment (specimen PIN, no. 3107/330; Pl. 8, fig. 3; Fig. 36b), the zygomatic process of the squamosal and jugal overlain laterally the zygomatic process of the maxilla, the anterior border of contact between these bones is in line with M^2.

The upper incisors are not preserved. The canine is relatively short and massive, slightly curved, compressed substantially transversely (Fig. 36a). P^2 is small, its anterior root is much more narrower than the posterior root. The crown is elongated, the wear facet of the paracone extends on its posterior side to the hardly discernible metastyle. P^2 is separated from the canine and P^3 by small spaces.

P^3–M^1 are three-rooted. The lingual root is long and massive, the labial roots are small. M^2 is double-rooted, the labial roots are completely fused.

P^3 is triangular. The paracone is large, high; in a worn tooth, a strong shearing crest connects it with a well-developed metastyle. The lingual projection is weak, the protocone is small. The parastyle and ectocingulum are absent.

P^4 is partially molarized. The stylar shelf is large, the parastyle and metastyle are well-developed, large; a distinct ectocingulum is present. A small supplementary cusp (stylocone) is located lingual to the parastyle; in a heavily worn tooth, it is fused with the parastyle. The paracone is large, the metacone is relatively small, poorly detached. The shearing crest of the metacrista connects the metacone to the metastyle. The protocone projects considerably lingually, so that the crown is T-shaped in outline. M^1 is substantially shorter than P^4 and differs from it in the presence of a well differentiated metacone, and less developed styles and ectocingulum. The parastyle is substantially larger than the metastyle. In M^2, the metacone is very small, the metastylar wing is absent; M^2 is much shorter than M^1. The posterior cheek teeth slightly increase in width from P^4 to M^2.

The lower jaw has a slender and low horizontal ramus and a long coronoid region. The symphysis reaches the line of the middle of P_3. A deep postsymphysial fossa is present. The anterior mental foramen is located under P_2, the posterior foramen is in line with the posterior root of P_3 or the space between P_3 and P_4; another relatively large foramen is located on the anterior side of the dentary under incisors. Sometimes, small supplementary foramina are observed under the anterior root of P_3 or P_4 and at the level of incisors and canines.

The lower edge of the dentary is slightly curved. The angle between the ascending and horizontal rami is about 110–120°. The masseteric fossa is deep, distinctly outlined; its anterior edge reaches the level of the base of the anterior slope of the coronoid process. A sharp condylar crest extends from the lateral side of the condyle and borders the masseteric fossa ventrally. The coronoid process is high, bladelike, with a gently sloping posterior edge and a rounded thickened tip with a rough surface. The articular process is long. The neck of the condyle is elongated, deviating slightly dorsally. The condyle is broad, high, located at the level of the cheek teeth crowns. The transverse axis of the condyle is inclined slightly posterolaterally. The articular surface covers a sector about 180°, most of its area faces posterodorsally. The mandibular foramen is oval in shape, located at the level of the incisure between the coronoid and articular processes slightly anterodorsal to the angular process. In one case (senescent specimen, PIN, no. 3107/362), a circular through foramen is located just posterior to the mandibular foramen (Pl. 8, fig. 4; Figs. 36g, 36i); the regular shape and smoothed edges of this foramen suggest that it was formed during the animal's life as an obvious aberration. The incisure between the articular and angular processes is relatively deep. The angular process is small, pointed, curves considerably medially.

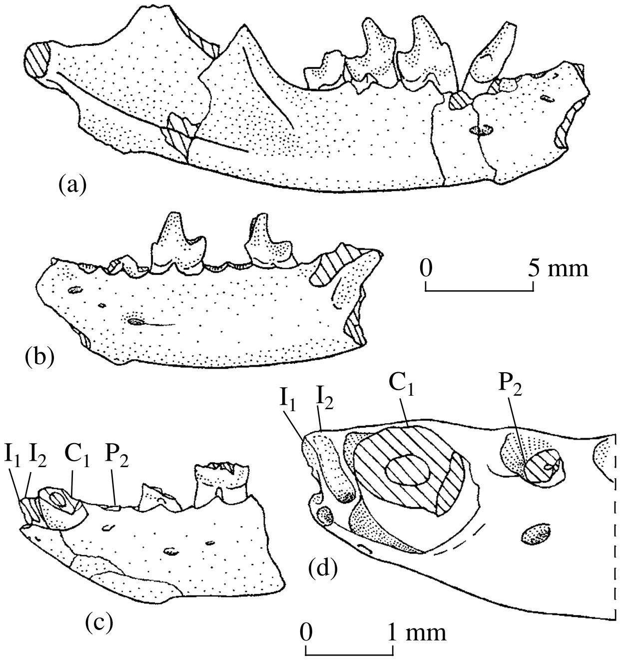


Fig. 37. *Ardynictis captor* Lopatin, 2003: (a) specimen PIN, no. 3107/372, right dentary fragment with P_3–M_2, labial view, one of the largest individuals; (b) specimen PIN, no. 3107/346, left dentary fragment with P_4 and M_2, labial view, a medium-sized individual; (c, d) specimen PIN, no. 3107/340, left dentary fragment with damaged C_1, P_3, and P_4: (c) general appearance, labial view, and (d) anterior part of the horizontal ramus, dorsolabial view; Khaychin-Ula 2 locality, Mongolia; Khaychin Formation, Middle Eocene.

The lower incisors are not available. In one specimen (PIN, no. 3107/340; Pl. 8, fig. 6; Figs. 37c, 37d), alveoli of two incisors are preserved anterior to the canine; they are located along the tooth row axis and inclined slightly anteriorly. The anterolabial edge of the jaw is completely preserved; its shape suggests that the third alveolus was not formed. A small rounded foramen located slightly ventrolateral to the alveolus of the anterior incisor (Figs. 37c, 37d) undoubtedly represents the mental foramina (it is also present in the other Didymoconidae). Thus, only two incisors were present. The statement that *Ardynictis* has three pairs of lower incisors (Matthew and Granger, 1925b; Gromova, 1960) is incorrect.

C_1 is compressed slightly transversely, has a long massive root and a relatively short, slightly curved

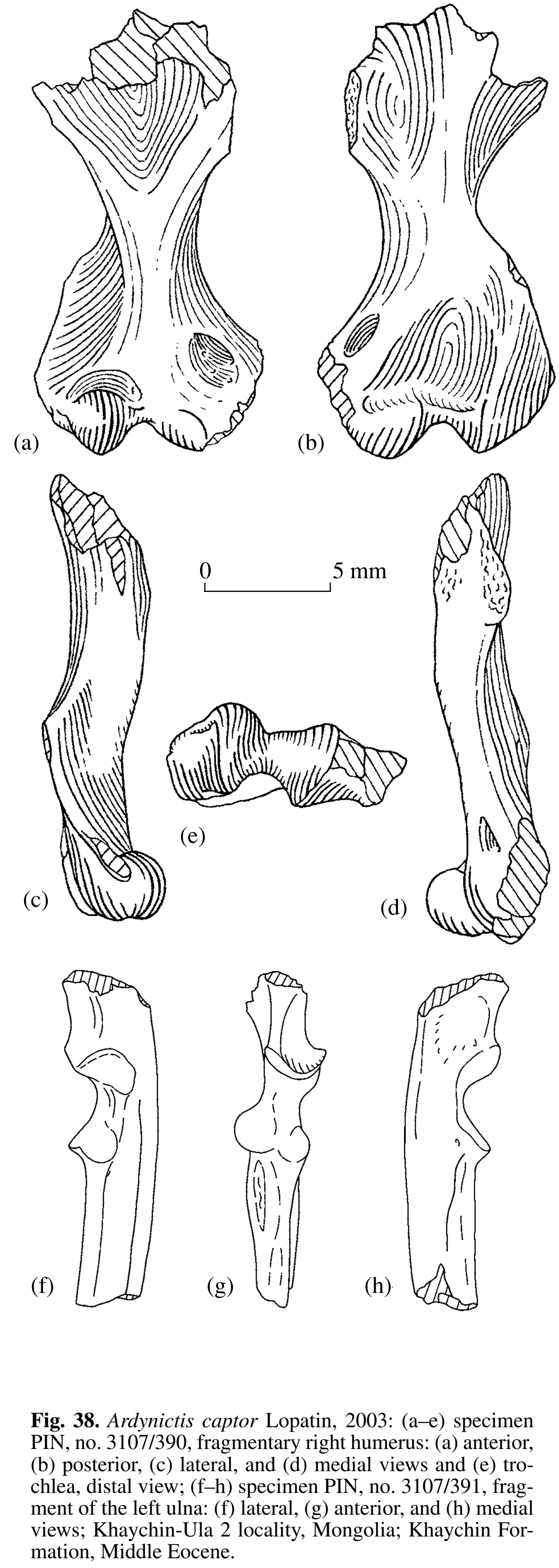


Fig. 38. *Ardynictis captor* Lopatin, 2003: (a–e) specimen PIN, no. 3107/390, fragmentary right humerus: (a) anterior, (b) posterior, (c) lateral, and (d) medial views and (e) trochlea, distal view; (f–h) specimen PIN, no. 3107/391, fragment of the left ulna: (f) lateral, (g) anterior, and (h) medial views; Khaychin-Ula 2 locality, Mongolia; Khaychin Formation, Middle Eocene.

crown, with a flattened lingual surface and a weak posterior edge (Fig. 36f).

The P_2–M_2 row is separated from C_1 by a small space. P_2 has not been found. Its alveolus is small, circular. In one senescent animal with heavily worn cheek teeth (PIN, no. 3107/362), the alveolus of P_2 is absent; its place is occupied by weak rugosity and superficial depressions (Figs. 36g, 36h). This tooth was probably lost during the animal's life, and its alveolus was filled with bony tissue (similar cases were recorded in other extinct mammals: Palmqvist et al., 1999; Lopatin, 2001b). The absence of P_2 and its alveolus may be caused not only by the loss of a broken or affected tooth, but also by the fact that the anterior premolar of Didymoconidae could have belonged to the deciduous generation. Actually, the large root of the deciduous canine and the development of the permanent canine left no room for an anlage of P_2; therefore, DP_2 could have retained and functioned during almost the whole of the life; as it was loss at the late stages of ontogeny, the alveolus became closed (see also Morlo and Nagel, 2002, p. 139).

P_3 is narrow, with a high protoconid and a poorly pronounced supplementary posterior cuspule. The protoconid of P_4 is high, massive, conical, widened slightly transversely, and has an apical wear facet, which descends along the posterior wall of the protoconid. The paraconid is well-developed, relatively low, narrow or having a broad base. The talonid is higher than the paraconid, comparable in width with the protoconid. The cristid oblique is well-developed. The wear facet of the talonid is connected to the wear facet of the posterior wall of the protoconid. Sometimes, the talonid has a small, but distinct projection at the base of the posterior part of the lingual wall (Pl. 8, fig. 7b).

M_1 has a broad trigonid and a narrow talonid. The paraconid is much higher than the talonid, widened transversely, and displaced slightly lingually. The protoconid and metaconid are fused at the base, the notch between their apices is large. The protoconid is slightly more massive and higher than the metaconid. The apices of the hypoconid and entoconid are displaced to the posterior margin of the occlusal surface. The entoconid is compressed strongly longitudinally, substantially smaller than the hypoconid.

M_2 has a small paraconid, broad trigonid, and considerably reduced, short, and narrow talonid. The paraconid is semicircular in outline. The protoconid is much higher and more massive than the metaconid. The talonid has the only cusp, the hypoconid, which projects strongly posterolabially.

The humerus is characterized by a relatively short and wide diaphysis, symmetrical distal epiphysis, general shortening and flattening and weak development of the distal part of the deltopectoral crest (Pl. 10, fig. 3; Figs. 38a–38e). Most of the humerus, with the distal epiphysis, is preserved. The proximal region is very broad. The head is broken off. The crest of the greater tubercle (crista tuberculi majoris) projects strongly laterally. The crest of the lesser tubercle (crista tuberculi minoris) is relatively strong, with a rough surface. Posterior to this crest, there is a large elongated teres tubercle (for the musculus teres major), with a rough flattened surface, which forms a thick ridgelike projection. The crests of the lesser and greater tubercles, which are strong in the proximal part, descend along the anterior surface of the bone to the middle of the diaphysis, becoming indistinct. A large, slightly concave triangular area is located between them. The posterior surface of the bone is flat; near the projection of the teres tubercle, it is considerably deepened.

The diaphysis is widely oval in section, poorly pronounced; in fact, it is marked by an insignificant constriction between the proximal and distal epiphyses. The distal region is broad. The crest of the lateral epicondyle (crista epicondyli lateralis) is large, projects strongly; proximally, it closely approaches the middle of the diaphyses. The medial epicondyle (extensor insertion) is also well-developed, large (its end is broken off). A large, elongated oval entepicondylar foramen is located above the medial epicondyle. The trochlea is divided anteriorly by a deep groove into two condyles, the hemispheric lateral (for the radius) and flattened medial (for the ulna) condyles. The medial region projects distally to a slightly greater extent than the lateral region. The olecranon fossa is relatively large (for Didymoconidae), but shallow; this suggests that the forelimbs of the animal were mostly semiflexed (O'Leary and Rose, 1995; O'Leary, 1998).

The ulna (Pl. 10, fig. 4; Figs. 38f–38h) is trough-shaped laterally, flat medially, convex posteriorly, and carinate anteriorly. The olecranon (partially broken off, but the tubercle of the olecranon is preserved) is relatively large, approximately as long as the semilunar incisure, narrow, curving anteromedially, with a keel-shaped anterior side. Its lateral surface is strongly concave, the medial surface has a small depression. The coronoid and anconeal processes project substantially anteriorly. The semilunar incisure expands considerably distally. The radial incisure is well-pronounced, the supinator crest is extended and strong.

Measurements, mm. Measurements of cheek teeth are given in Tables 29 and 30; horizontal ramus of the lower jaw, in Table 31; ascending ramus, in Table 32.

Length of P^4–M^2, 5.35 (holotype); alveolar length of C^1–M^2, 13.0; P^2–M^2, 8.5; alveolus of C^1 (length × width), 2.2 × 1.8 (specimen PIN, no. 3107/330).

External length of the crown of C^1 (PIN, no. 3107/329) along straight line, 3.6; diameters at the base, 1.75 × 1.35. Diameters at the base of C_1: 1.7 × 1.2 (PIN, no. 3107/335), 2.0 × 1.3 (PIN, no. 3107/336), and 2.2 × 1.3 (PIN, no. 3107/340).

Alveolus of P_2 (length × width), 0.9 × 0.9 (PIN, no. 3107/361), 1.0 × 0.9 (PIN, no. 3107/337), 1.05 × 0.95 (PIN, no. 3107/346), 1.1 × 1.0 (PIN, no. 3107/340), 1.15 × 0.8 (PIN, no. 3107/363), 1.2 × 0.9 (PIN, no. 3107/359, 385), 1.3 × 0.95 (PIN, no. 3107/372), and 1.4 × 0.9 (specimen PIN, no. 3107/364).

Table 29. Measurements of the upper cheek teeth of *Ardynictis captor* Lopatin, 2003

Specimen PIN, no.	Tooth	Length	Width
3107/330	P^2	1.6	0.85
	P^3	2.65	1.9
	P^4	2.35	3.2
3107/332	P^3	2.4	2.1
3107/334	P^4	2.05	3.0
	M^1	1.7	3.2
3107/333 (holotype)	P^4	2.2	2.8
	M^1	1.95	3.0
	M^2	~1.2	3.1

Table 30. Measurements of the lower cheek teeth of *Ardynictis captor* Lopatin, 2003

Specimen PIN, no.	Tooth	Length	Width	
			trigonid	talonid
3107/341	P_3	1.95	1.2	
3107/362	P_3	1.95	1.0	
	P_4	2.25	1.15	
	M_1	2.15	1.5	1.25
	M_2	1.9	1.7	1.1
3107/361	P_3	2.1	1.05	
	M_2	–	–	0.9
3107/340	P_4	2.4	1.2	
3107/343	P_4	2.45	1.35	
3107/372	P_4	2.4	1.1	
	M_1	2.35	–	1.3
	M_2	2.0	–	0.9
3107/344	M_1	2.45	1.75	1.3
3107/346	P_4	2.5	1.3	
	M_2	2.05	1.5	1.05
3107/345	M_2	2.0	1.45	0.9
3107/359	M_2	–	–	0.9

Alveolar length of P_2–M_2, 9.3 (PIN, no. 3107/385), 10.0 (PIN, no. 3107/359), 10.2 (PIN, no. 3107/346), 10.8 (PIN, nos. 3107/337, 361), and 11.0 (PIN, no. 3107/372).

Length of P_4–M_2, 6.0 (PIN, no. 3107/359), 6.35 (PIN, no. 3107/362), 6.5 (PIN, no. 3107/346), 6.7 (PIN, no. 3107/361), 6.75 (PIN, no. 3107/372), and 7.0 (PIN, no. 3107/337).

Table 31. Measurements of the horizontal ramus of the lower jaw of *Ardynictis captor* Lopatin, 2003

Parameter		Specimen PIN, no. 3107/										
		337	338	340	346	359	361	362	363	364	372	385
Height	under P_3	3.7	–	3.8	4.0	3.8	3.9	3.7	3.8	3.8	4.4	3.2
	under P_4	4.25	–	4.2	4.45	4.3	4.9	4.0	–	4.0	4.5	2.9
	under M_1	4.25	–	–	4.6	4.5	5.0	3.9	–	–	4.6	3.3
	under M_2	4.1	4.3	–	4.4	4.25	4.9	3.8	–	–	4.5	3.6
Thickness at M_2		2.3	2.15	–	2.35	2.2	2.35	2.0	–	–	2.6	2.4

Table 32. Measurements of the ascending ramus of the lower jaw of *Ardynictis captor* Lopatin, 2003

Parameter	Specimen PIN, no.	
	3107/362	3107/372
Height of coronoid region	9.5	–
Distance from posterior edge of condyle to posterior edge of M_2	10.2	12.5
Distance from posterior edge of condyle to anterior base of coronoid process	9.0	12.0
Distance from posterior edge of condyle to anterior edge of masseteric fossa	9.0	12.0
Thickness of condyle	1.9	2.3
Width of articular head	2.8	3.4
Dorsal length of neck with head	3.0 (2.0 + 1.0)	3.5 (2.2 + 1.3)
Length of angular process	3.0	–
Height of angular process	1.6	–

Humerus (PIN, no. 3107/390): width of the diaphysis at the narrowest point (above the crista epicondyli lateralis), 3.8; thickness of the diaphysis, 2.8.

Ulna (PIN, no. 3107/391): length of the olecranon anteriorly, ca. 4.2; length of the semilunar incisure, 4.3; width at the distal part of the semilunar incisure, 2.9; width at the anconeal process, 2.6; thickness at the anconeal process, 3.5.

Variability. The lower jaw fragments examined enable the estimation of ontogenetic and, probably, sexual variation in size in *Ardynictis captor.*

Specimen PIN, no. 3107/385 represents a juvenile stage, before the eruption of M_2. The alveolar margin of the jaw is not formed, it is low on the labial side. Alveoli of DP_3 and DP_4 are smaller than alveoli of P_3 and P_4 in adults and have thicker interalveolar septa. The septum between alveoli of M_1 is undeveloped. Only the anterior alveolus of M_2 is open, in which the protoconid and metaconid are seen. The alveolus of P_2 is similar in shape and structure to that of adults. The horizontal ramus of the lower jaw of this specimen is on average 75–80% as deep as that of adults. The senescent stage (specimen PIN, no. 3107/362) is characterized by heavily worn teeth and, probably, by the loss of P_2 (DP_2).

Adult and senescent individuals irrespective of the degree of tooth wear (and, hence, individual age) can be divided into two size groups. In the first, the P_2–M_2 row is about 10 mm long and the horizontal ramus of the lower jaw under these teeth is at most 4.5 mm deep. Two larger specimens (PIN, nos. 3107/361 and 372) are distinguished by the stout jaw, the depth of the horizontal ramus (4.6–5.0 mm), and the length of cheek tooth row (about 11 mm). It is possible to assume that these distinctions are connected with sexual dimorphism.

Comparison. *Ardynictis captor* differs from *A. furunculus* in the half as large dimensions, the shape and structure of P^4 (the protocone is compressed strongly longitudinally, the styles are well developed, and a small, slightly detached metacone), less developed metastyle of M^1, and in the structural details of M_1 and M_2, in particular, in the high position of the paraconid and relatively lower trigonid (in *A. captor*, the trigonid is approximately twice as high as the talonid; in *A. furunculus*, this ratio is 3.5). *A. captor* differs from *A. zhaii* in the much smaller size (M_2 of *A. zhaii* is 4.1 mm long, see Tong, 1997, p. 154).

Remarks. The humerus (specimen PIN, no. 3107/390) is typical in structure for Didymoconidae (see Gromova, 1960, text-fig. 6), but differs from the previously known specimens in the shorter diaphysis and general flatness. It is referred to *Ardynictis captor* based on the accordance in size with the jaws of this species (didymoconid species from the Khaychin Fauna are clearly differentiated in size and most of them are represented by limb bones, see below). The short, wide, and flat humerus suggests a better pronounced fossorial specialization of *Ardynictis* in comparison with *Didymoconus* (see Gromova, 1960). The ulna (specimen PIN, no. 3107/389) corresponds in size to the humerus discussed.

Occurrence. Middle Eocene (Irdinmanhan) of Mongolia.

Material. In addition to the holotype, the collection of PIN contains the following specimens from the type locality: three fragments of maxillae: with C^1 (PIN, no. 3107/329), with P^2–M^1 and the base of the zygomatic arch (PIN, no. 3107/330), and with P^4–M^1 (PIN, no. 3107/334); isolated P^3 (PIN, no. 3107/332); 13 dentary fragments: with alveoli of I_1 and I_2, the base of C_1, and damaged P_3–P_4 (PIN, no. 3107/340); with P_3, P_4, and M_2 (PIN, no. 3107/361), with P_3–M_2 and ascending ramus (PIN, nos. 3107/362, 372), with P_3–P_4 (PIN, no. 3107/363), with P_4 (PIN, no. 3107/343), with P_4 and M_1 (PIN, no. 3107/344), with P_4 and M_2 (PIN, nos. 3107/346, 359), with nonerupted M_2 (PIN, no. 3107/385), and without teeth (PIN, nos. 3107/337, 338, 364); four isolated lower teeth: two C_1 (PIN, nos. 3107/335, 336), P_3 (PIN, no. 3107/341), and M_2 (PIN, no. 3107/345); incomplete right humerus (PIN, no. 3107/390); and proximal half of the left ulna (PIN, no. 3107/391).

SUBFAMILY DIDYMOCONINAE KRETZOI, 1943

Type genus. *Didymoconus* Matthew et Granger, 1924, Oligocene of Mongolia, China and Kazakhstan.

Diagnosis. Dental formula $I^3/_2C^1/_1P^3/_3M^2/_2$. P^3 with metacone. P^4 clearly molarized, approximately equal in length and width to M^1, metacone and paracone separate. Stylar shelf of P^4–M^2 narrow. Hypocone of P^4–M^2 well-developed. P^2 double-rooted, P_2 single or double-rooted. P_4 molariform. Talonid of P_4–M_2 tri- or bicuspid, having hypoconid, entoconid, and hypoconulid (positioned close to hypoconid) or only hypoconid and entoconid; cusps located at posterior margin of occlusal surface. Coronoid process of lower jaw low, angular process deflected slightly medially.

Generic composition. *Khaichinula* gen. nov., Middle Eocene of Mongolia; *Ergilictis* Lopatin, 1997, Upper Eocene of Mongolia; *Didymoconus* Matthew et Granger, 1924 (= *Tshelkaria* Gromova, 1960), Lower–Upper Oligocene of Mongolia, northern China, and Kazakhstan; *Archaeomangus* Lopatin, 1997, Lower Oligocene of Mongolia; and *Tshotgoria* Lopatin, 1997, Upper Oligocene of Mongolia.

Comparison. The Didymoconinae differ from the Ardynictinae in the presence of the metacone on P^3, completely molarized P^4 and P_4, the narrow stylar shelf and well-developed hypocone of P^4–M^2, the structure of the talonid of P_4–M_2, and in the ascending ramus of the lower jaw.

Remarks. The upper teeth of the genera *Khaichinula, Ergilictis*, and *Tshotgoria* have not been recorded; however, the structure of lower teeth enables the assignment of these taxa to the subfamily Didymoconinae.

Genus *Khaichinula* Lopatin, gen. nov.

Etymology. From the Khaychin-Ula locality.

Type species. *Khaichinula lupula* sp. nov.

Diagnosis. Small-sized didymoconine. P_2 single-rooted. P_4 with high, anteriorly projecting paraconid and distinct paracristid. The talonid of P_4 short and narrow, tricuspid, hypoconulid positioned close to hypoconid, rudimentary entocristid present.

Species composition. Type species, Middle Eocene (Irdinmanhan) of Mongolia.

Comparison. *Khaichinula* differs from all other genera of Didymoconinae in the presence of the entocristid and distinct paracristid on P_4, and the single-rooted P_2. In addition, it differs from all members of the subfamily, except for *Ergilictis*, in the presence of well-developed hypoconulid and large, detached paraconid on P_4. The differences from *Ergilictis* include the lesser degree of molarization of P_4, which has a larger and higher paraconid and a relatively short and narrow talonid.

Khaichinula lupula Lopatin, sp. nov.

Plate 8, figs. 9–13; Plate 10, fig. 5

Etymology. From the Latin *lupula* (small female wolf).

Holotype. PIN, no. 3107/326, isolated left P_4; Mongolia, Khaychin-Ula 2 locality; Middle Eocene, Khaychin Formation.

Description (Figs. 39–41). Dimensions are relatively small, a little smaller than in *Didymoconus rostratus* (Gromova, 1960): length of C_1–M_2 along alveoli, 18–20 mm, P_2–M_2, 15.5–16.5 mm. The rostral region is narrow (at P^2, the palatal process of the maxilla is approximately 4 mm wide). The dorsal surface of maxilla has small nutrient foramina near the nasal–maxillary suture. A relatively large foramen is located on the lateral side of the maxilla. A small area anterior to the alveolus of the canine is covered with small pits. An area above P^2 for an attachment of a muscle also has a fine-pitted surface.

C^1 is oval in section, the edge on its posterior side is poorly pronounced. Judging from the alveoli, P^2 is double-rooted, the posterior root is larger than the anterior root.

The lower jaw is relatively short, massive, with a deep symphysis (reaches the line of the middle of the crown of P_3) and relatively abrupt beginning of the rise of the coronoid region. The mental foramina are located under P_2 and the posterior root of P_3. Posterior to the

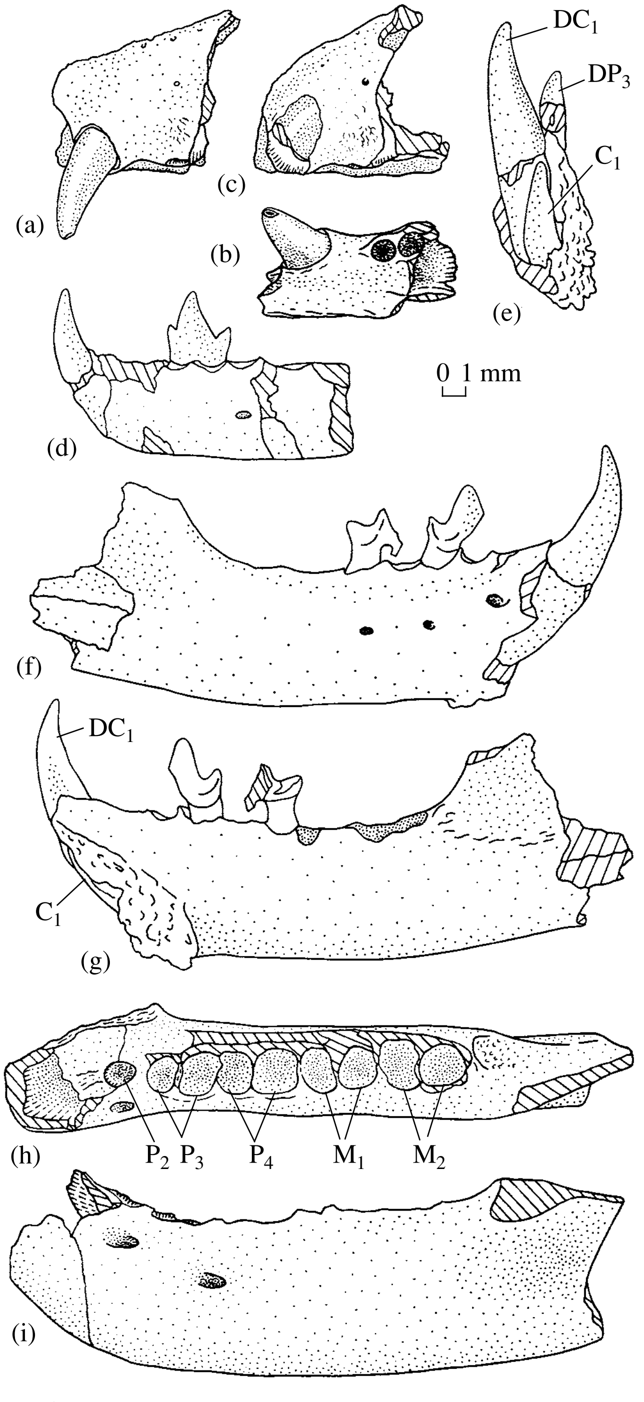


Fig. 39. *Khaichinula lupula* sp. nov.: (a, b) specimen PIN, no. 3107/324, left maxillary fragment with C^1: (a) labial and (b) occlusal views; (c) specimen PIN, no. 3107/360, left maxillary fragment with a damaged C^1, labial view; (d) specimen PIN, no. 3403/305, left dentary fragment with DC_1 and DP_3, labial view; (e–g) specimen PIN, no. 3107/323, right dentary fragment with DC_1 and C_1 at the initial stage of eruption, partially disrupted DP_3 and DP_4, and alveoli of P_2, M_1, and M_2: (e) anterior, (f) labial, and (g) lingual views; (h, i) specimen PIN, no. 3107/355, left dentary fragment with alveoli of C_1–M_2: (h) occlusal and (i) labial views; (a–c, e–i) from the Khaychin-Ula 2 locality and (d) from the Khaychin-Ula 3 locality, Mongolia; Khaychin Formation, Middle Eocene.

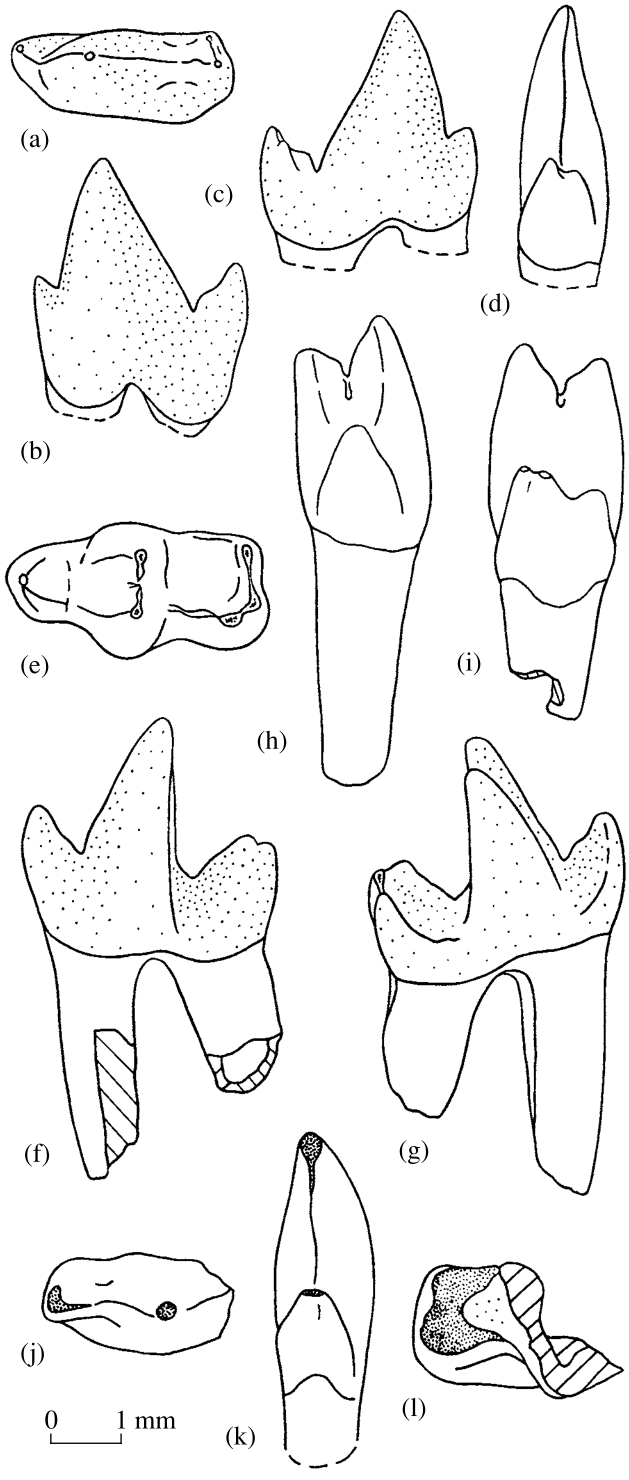


Fig. 40. *Khaichinula lupula* sp. nov.: (a–d) specimen PIN, no. 3403/305, unworn left DP_3: (a) occlusal, (b) labial, (c) lingual, and (d) posterior views; (e–i) holotype PIN, no. 3107/326, left P_4: (e) occlusal, (f) labial, (g) lingual, (h) anterior, and (i) posterior views; (j–l) specimen PIN, no. 3107/323: (j, k) fragmentary right DP_3: (j) occlusal and (k) posterior views; (l) fragmentary worn right DP_4, occlusal view; (e–l) from the Khaychin-Ula 2 locality and (a–d) from the Khaychin-Ula 3 locality, Mongolia; Khaychin Formation, Middle Eocene.

alveolus of M_2, the lingual projection of the bone has a distinct trace of insertion of a large portion of the masseter; this area has a fine-pitted surface and a sharp anterior border (specimen PIN, no. 3107/355).

DC_1 is large, long, pointed, and slightly lyre-shaped at the apex. The permanent canine at the state of eruption is located lingual to the deciduous canine. A completely erupted C_1 has a weak posterior edge, a relatively sharp edge on the anterolingual side of the crown, and a flattened lingual surface, which is slightly concave at the base. The alveolus of C_1 terminates posteriorly at the anterior root of P_3.

P_2 (DP_2) has one alveolus, which is relatively large, elongated; separated from the canine by a small diastema. The alveoli of P_3–M_2 are located closely to one another, without intervals. The septum between the alveoli of the posterior root of P_3 and the anterior root of P_4 is partially resorbed.

Unworn DP_3 (specimen PIN, no. 3403/305) is compressed transversely, its high protoconid is inclined anteriorly, has well-pronounced anterior and posterior crests. The paraconid is in the shape of a small cuspule close to the midheight of the anterior side of the protoconid. The talonid is relatively long, with a longitudinal crest, a high terminal cuspule, and another small, low, transversely extended cuspule located anterolingual to the first. In a worn DP_3 (specimen PIN, no. 3107/323), the crown has a high, conical protoconid and a well-developed cuspule at the posterior margin. A bulge in the lingual part of the talonid corresponds to the lingual cusp of an unworn tooth. The fragment preserved of DP_4 demonstrates a lingually open talonid, which has at the posterior margin of the occlusal surface a large hypoconid (probably, fused with the hypoconulid) connected to a longitudinally compressed entoconid.

P_4 is narrow and long, with a large and clearly detached paraconid. The labial part of the posterior base of the paraconid is connected by a narrow crest to the anterior base of the protoconid (the angle of the notch is about 90°). The protoconid and metaconid are equally massive, closely fused at the base, and separated apically by a superficial notch (the angle is 95°). The protoconid is slightly higher than the metaconid. The talonid is substantially shorter, narrower, and lower than the trigonid, open lingually. The hypoconid is connected to the protoconid by a narrow cristid oblique, which extends on the labial border of the occlusal surface. A relatively large hypoconulid with its own wear facet is fused with the posterolingual side of the hypoconid. A small, longitudinally compressed entoconid is separated from the hypoconulid by a distinct notch (the angle is about 110°). The hypoconulid projects posteriorly to a greater extent than the entoconid. A very narrow and low entocristid, which does not reach the trigonid, is present.

The structure of molars is not known.

The shape of the ulna (Pl. 10, fig. 5; Fig. 41) is typical for didymoconines (see Gromova, 1960, text-fig. 7); however, it lacks a distinct depression on the medial side of the base of the olecranon, and its olecranon is apparently relatively small. The bone body is more massive and almost straight distal to the semilunar incisure. The lateral side of the bone body is trough-shaped, the medial side is flat, the posterior side is convex, and the anterior side is carinate. The olecranon is narrow, curves somewhat anteromedially. The coronoid and anconeal processes substantially project anteriorly relative to the bone body. The semilunar incisure expands substantially distally, the radial incisure is poorly pronounced, the supinator crest is moderately developed.

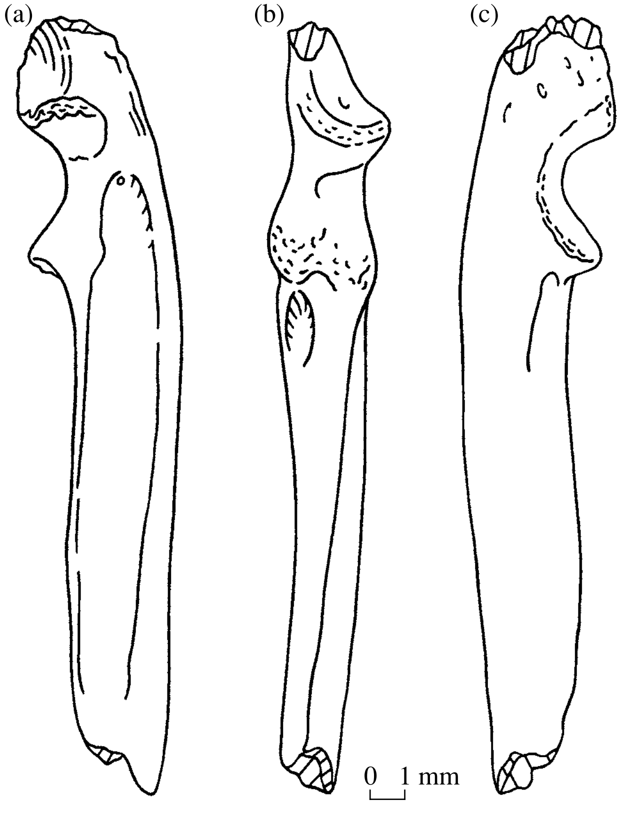


Fig. 41. *Khaichinula lupula* sp. nov., specimen PIN, no. 3107/393, fragment of the left ulna: (a) lateral, (b) anterior, and (c) medial views; Khaychin-Ula 2 locality, Mongolia; Khaychin Formation, Middle Eocene.

Measurements, mm. Holotype, P_4: total length, 3.6; trigonid, 2.0 (in particular, paraconid, 1.0); talonid, 1.6; trigonid width, 1.9; talonid width, 1.5; crown height at the paraconid, 2.0, protoconid, 3.15, metaconid, 2.6, hypoconid, 1.5, hypoconulid, 1.3, and entoconid, 1.2.

External length of the crown of C^1 along a straight line, 5.0; diameters of the base, 2.2 × 1.8 (specimen PIN, no. 3107/324), 2.5 × 1.85 (PIN, no. 3107/360); distance between C^1 and P^2, 1.9; length of P^2 along alveoli, 2.3 (PIN, no. 3107/360). Diameters of the base of C_1, 2.8 × 1.85 (PIN, no. 3107/392).

Alveoli of the lower teeth (length × width): P_2, 1.6 × 1.35 (PIN, no. 3107/355); 2.0 × 1.25 (PIN, no. 3107/323); P_3, 3.3 × 1.9; P_4, 3.6 × 2.0 (PIN, no. 3107/355); M_1, 3.3 × 2.0 (PIN, no. 3107/323); 3.4 × 2.0 (PIN, no. 3107/355); M_2, 3.2 × 2.25 (PIN, no. 3107/323); and 4.0 × 2.2 (PIN, no. 3107/355).

Deciduous teeth (PIN, no. 3107/360): crown length of DC_1, 5.0; length of DP_3, ca. 3.0; width, 1.25; length of DP_4, ca. 3.7; talonid width, 1.5. Specimen PIN, no. 3403/305, DP_3: total length, 2.95; trigonid, 1.7 (in particular, paraconid, 0.4); talonid, 1.25; trigonid width, 1.2, talonid width, 1.05; crown height at the paraconid, 2.0, protoconid, 3.1, and talonid, 2.1.

Horizontal ramus of the lower jaw, specimen PIN, no. 3107/323: depth under DP_4, 6.2; under M_2, 6.2; thickness under M_2, 3.9; specimen PIN, no. 3107/355: depth under P_4, 7.0; under M_2, 7.2; thickness under M_2, 4.0; specimen PIN, no. 3403/305: depth under DP_4, 5.0.

Ulna (PIN, no. 3107/393): length of the semilunar incisure, 5.2; width in the distal part of the semilunar incisure, 3.4; width at the anconeal process, 3.2, thickness at the anconeal process, 4.2.

Remarks. The dentary of a young individual (specimen PIN, no. 3107/323) has DC_1 and heavily worn DP_3 and DP_4 combined with the completely formed alveoli of M_2 and the presence of the crown of a permanent canine in the alveolus. Using *Didymoconus colgatei* Matthew et Granger, 1924 from the Oligocene of Mongolia as an example, Morlo and Nagel (2002) described in part the sequence of eruption of the lower teeth in the Didymoconidae: M_2 and C_1 begin to emerge simultaneously; M_2 is completely erupted; P_3 begins eruption, then does P_4; P_3 is completely erupted, then does P_4; finally, eruption of C_1 is accomplished; P_2 (or DP_2) is not replaced. Based on a preliminary study of extensive material of Oligocene Didymoconidae from Mongolia, which is stored in PIN (collected by the Joint Soviet–Mongolian Paleontological Expedition; subsequently, Joint Russian–Mongolian Paleontological Expedition), it is possible to recognize that deciduous incisors are replaced before the beginning of eruption of M_2 and the sequence of tooth replacement is as follows (0–6 are code stages of tooth replacement):

(0) $DI_1DI_2DC_1DP_2DP_3DP_4M_1$,
(1) $I_1DI_2DC_1DP_2DP_3DP_4M_1$,
(2) $I_1I_2DC_1DP_2DP_3DP_4M_1$,
(3) $I_1I_2DC_1DP_2DP_3DP_4M_1M_2$,
(4) $I_1I_2C_1DP_2DP_3DP_4M_1M_2$,
(5) $I_1I_2C_1DP_2P_3DP_4M_1M_2$,
(6) $I_1I_2C_1DP_2P_3P_4M_1M_2$.

Thus, specimen PIN, no. 3107/323 represents ontogenetic stage 3 (young).

An even smaller individual, with a canine and unworn premolar in the position of P_3 (specimen PIN, no. 3403/305) is interpreted by me as a juvenile (stage 0–1). The preserved premolar is determined as a deciduous tooth based on the partially molarized talonid, which is atypical for permanent P_3 of Didymoconidae. Since DP_3 is unworn, the canine of this specimen is considered to belong to the deciduous generation. The small depth and thickness of the horizontal ramus of the lower jaw and the incomplete preservation of the tooth row cast doubt on the species identification of this specimen; however, the similarity in size and structure of DP_3 with specimen PIN, no. 3107/323, in my opinion, allows the assignment of this specimen to *Khaichinula lupula.*

Material. In addition to the holotype, the collection of PIN contains the following specimens from the type locality: fragments of maxillae with canine and alveoli of P^2 (PIN, nos. 3107/324, 360) and dentary fragments: with complete DC_1 and C_1 at the initial stage of eruption, partially disrupted DP_3 and DP_4, and alveoli of P_2, M_1, and M_2 (PIN, no. 3107/323); with C_1 (PIN, no. 3107/325); with alveoli of C_1–M_2 (PIN, no. 3107/355); an isolated fragment of C_1 (PIN, no. 3107/392); and incomplete left ulna (PIN, no. 3107/393). In addition, a dentary fragment with DC_1 and DP_3 (specimen PIN, no. 3403/305) from the Khaychin-Ula 3 locality is stored in PIN.

SUBFAMILY KENNATHERIINAE LOPATIN, SUBFAM. NOV.

Type genus. *Kennatherium* Mellett et Szalay, 1968, Middle Eocene of Central Asia.

Diagnosis. Dental formula $I^{?}/_{?-0}C^{1}/_{1}P^{3-?}/_{3-2}M^{2}/_{2}$. Metacone of P^3 weakly developed. P^4 completely molarized, corresponding in length and width to M^1. Stylar shelf of P^4–M^2 very narrow, styles reduced, metacone and paracone separate, low; hypocone absent. P_2 rudimentary or absent. P_4 molariform. Protoconid and metaconid of P_4–M_2 relatively low. Talonid of P_4–M_2 elongated, tricuspid, with hypoconid, entoconid, and median, considerably reduced hypoconulid fused with entoconid. Cristid obliqua distinct. Coronoid process of lower jaw high, hooked posteriorly; angular process large, deflected moderately medially.

Generic composition. *Zeuctherium* Tang et Yan, 1976, Lower Paleocene of China; *Kennatherium* Mellett et Szalay, 1968, Middle Eocene of northern China and Mongolia; *Erlikotherium* gen. nov., Middle Eocene of Mongolia.

Comparison. The Kennatheriinae differ from the Didymoconinae in the weakly developed metacone of P^3, the absence of hypocone of P^4–M^2, and in the structure of the trigonid and talonid of P_4–M_2 (in particular, a trend towards fusion of the hypoconulid with the entoconid rather than with the hypoconid). The new subfamily differs from the Ardynictinae in the presence of the metacone of P^3, the narrow stylar shelf and reduced styles of P^4–M^2, completely molarized $P^4/_4$, and in the structure of M_1 and M_2. In addition, it differs from the Didymoconinae and Ardynictinae in the shape of the coronoid and angular processes of the lower jaw.

Remarks. The lower teeth and jaws are characterized based on *Kennatherium* and *Erlikotherium*, the upper teeth are characterized based on *Kennatherium* and *Zeuctherium* (*Z. niteles*, see Tang and Yan, 1976, p. 95, text-fig. 2, pl. 2, fig. 2).

Genus *Kennatherium* Mellett et Szalay, 1968

Kennatherium: Mellett and Szalay, 1968, p. 3.

Type species. *Kennatherium shirense* Mellett et Szalay, 1968, Middle Eocene of northern China and Mongolia.

Diagnosis. Known dental formula $C^1/_1P^3/_3M^2/_2$. P_2 present. P^3 short, with small protocone. P^4 relatively large, with elongated labial lobe. M^1 and M^2 lingually hypsodont. Paraconid of P_3 absent. Trigonid of M_1 and M_2 compressed strongly longitudinally; paraconid substantially reduced, displaced lingually; rudimentary precingulid present. In M_2, hypoconulid absent, roots completely fused.

Species composition. Type species.

Comparison. *Kennatherium* differs from *Zeuctherium* in the shorter P^3 with a weakly developed protocone, relatively larger P^4, and well-pronounced lingual hypsodonty of M^1 and M^2; it differs from *Erlikotherium* gen. nov. in the presence of P_2, the absence of paraconid on P_3, the structure of the paraconid region in P_4–M_2, and in the absence of hypoconulid and the fused roots of M_2.

Remarks. According to the grammar of Greek and Latin languages and ICZN, the correct spelling of the name of the type species should be *Kennatherium shirense* rather than *K. shirensis*, as was in the original description and later works (see Mellett and Szalay, 1968; Gingerich, 1981; Sánchez-Villagra and Smith, 1997).

Kennatherium shirense Mellett et Szalay, 1968

Plate 9, figs. 1–9; Plate 10, figs. 6 and 7

Kennatherium shirensis: Mellett and Szalay, 1968, p. 3, text-figs. 1 and 2.

Holotype. AMNH, no. 26295, fragment of the posterior part of the left dentary with M_1 and alveoli of M_2; China, Inner Mongolia, North Mesa, Shara Murun Area, Chimney Butte Quarry locality; Middle Eocene, Ulan Shireh Formation.

Description (Figs. 42, 43). Small-sized didymoconid: the C_1–M_2 row is about 8 mm long, the P_2–M_2 row is about 6.5 mm long, and P_4–M_2 row is about 4 mm long. The maxilla strongly narrows at P^3. The infraorbital foramen (in specimen PIN, no. 3107/349, its dimensions are 0.8 × 0.65 mm) is located above the posterior part of P^3. The infraorbital canal is short (the posterior foramen is in line with the anterior root of P^4); the lacrimal does not participate in its formation, dorsal to the canal, a clear trace of a suture with this bone is seen. Ventromedial to the posterior foramen of the infraorbital canal, there is a small deep pit (0.4 × 0.25 mm) with tiny foramina in the floor, which are connected to the floor of the alveolus of the lingual root of P^3. The posterior margin of the base of the zygomatic arch is in line with the middle of M^1. The base of the zygomatic arch is narrow, with a ventrally curved dorsal edge; it is formed by a process of maxilla, while the jugal does not contribute to its formation. A large area for the origin of the maxillonasalis muscle is located above P^4. The orbital floor is perforated by numerous small foramina and pierced by large lingual roots of M^1 and M^2.

P^2 is not preserved; judging from the alveoli, it is double-rooted.

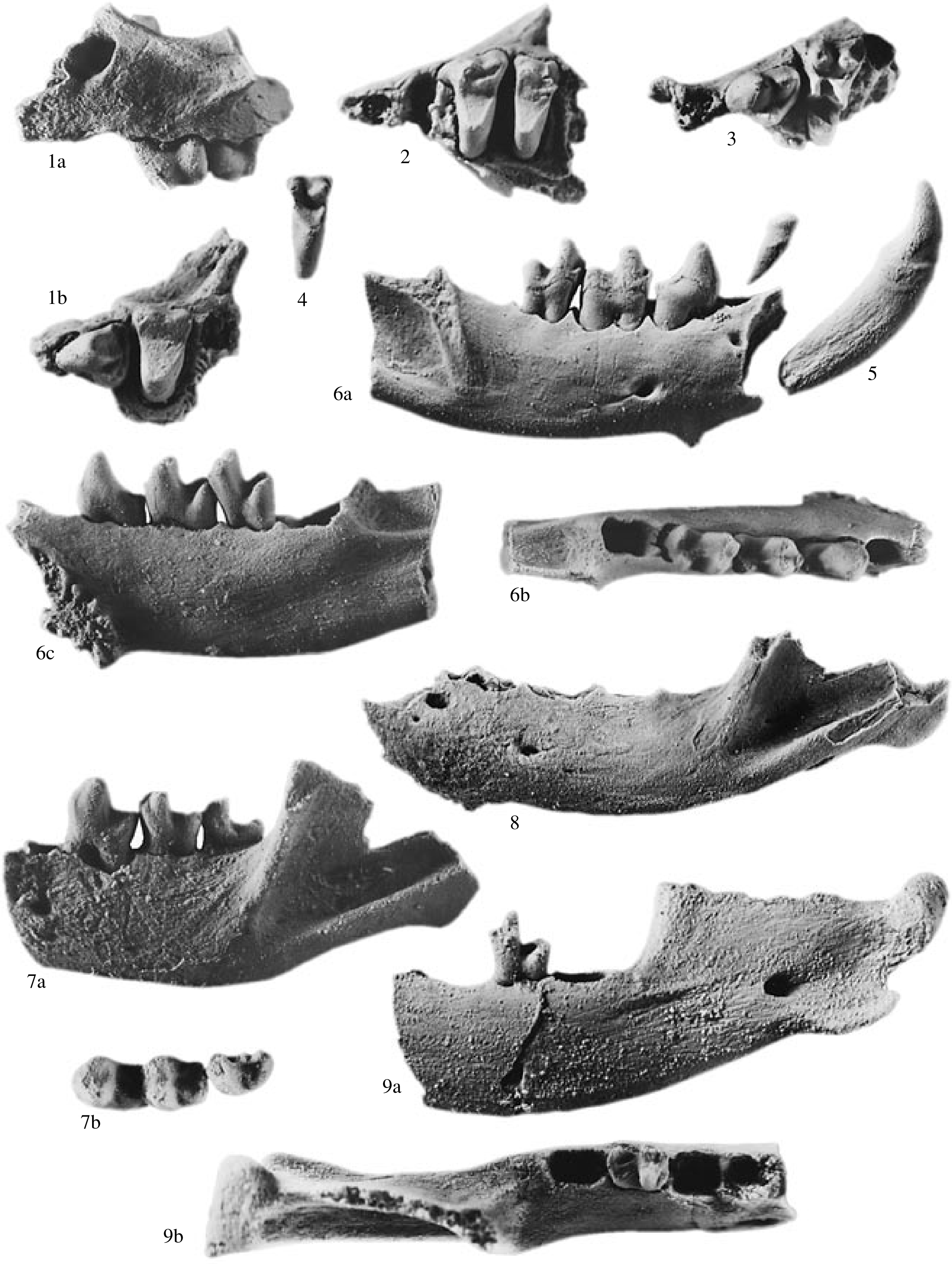
P^3 is elongated slightly longitudinally, the occlusal surface is rounded triangular in outline. The lingual projection is weak, the protocone is small and low. The ectocingulum is absent, the parastyle is absent or hardly discernible, and the metastyle is weak. The largest cusp, paracone, is conical. The metacone is smaller and lower (almost half as high as the paracone), but relatively massive, located at the posterior base of the paracone. The apex of the protocone is slightly elevated above the surface of the lingual projection, on a level with the base of the paracone. In a heavily worn condition, the metacone completely disappears; the major wear facet combines the distal surface of the paracone and the smoothed region of the metacone and metastyle. The wear facet of the protocone is connected to the major facet in the posterior part. The tooth is three-rooted; the lingual and posterior labial roots are partially fused. With reference to the tooth row, P^3 is positioned more lingually than the labial margin of P^4–M^2.

P^4–M^1 are narrow triangles in outline (in occlusal view), considerably widened transversely due to the expansion of the protocone (the width to length ratios of P^4, M^1, and M^2 are 1.5–1.6, 1.8, and 2.1, respectively). The lingual root is long and massive, the labial roots are weak; the lingual side of the crown is much higher than the labial side.

In P^4, the metastylar lobe projects substantially posterolabially. The styles are small, the ectocingulum is absent. The paracone and metacone are low, fused at the base; the angle of the notch between them is approximately 105°; the paracone is slightly more massive than the metacone. As the tooth is worn, their wear facets are united with a large wear facet in place of the trigon basin. A considerably concave worn occlusal surface looks like a triangle with the apices in places of the paracone, metacone, and protocone. The apex of the protocone is inclined somewhat anteriorly.

M^1 is similar in structure to P^4, but has less projecting stylar lobes and much smaller labial length. In M^2, the metastylar projection is reduced, the metacone is much smaller than the paracone. The paracone and metacone are widely spaced, their apices are on a level with the anterior and posterior margins of the occlusal surface, respectively. A strong crest of the preprotocrista extends from the apex of the protocone to the base of the anterolingual side of the paracone. The postprotocrista terminates at the base of the posterolingual

Plate 9



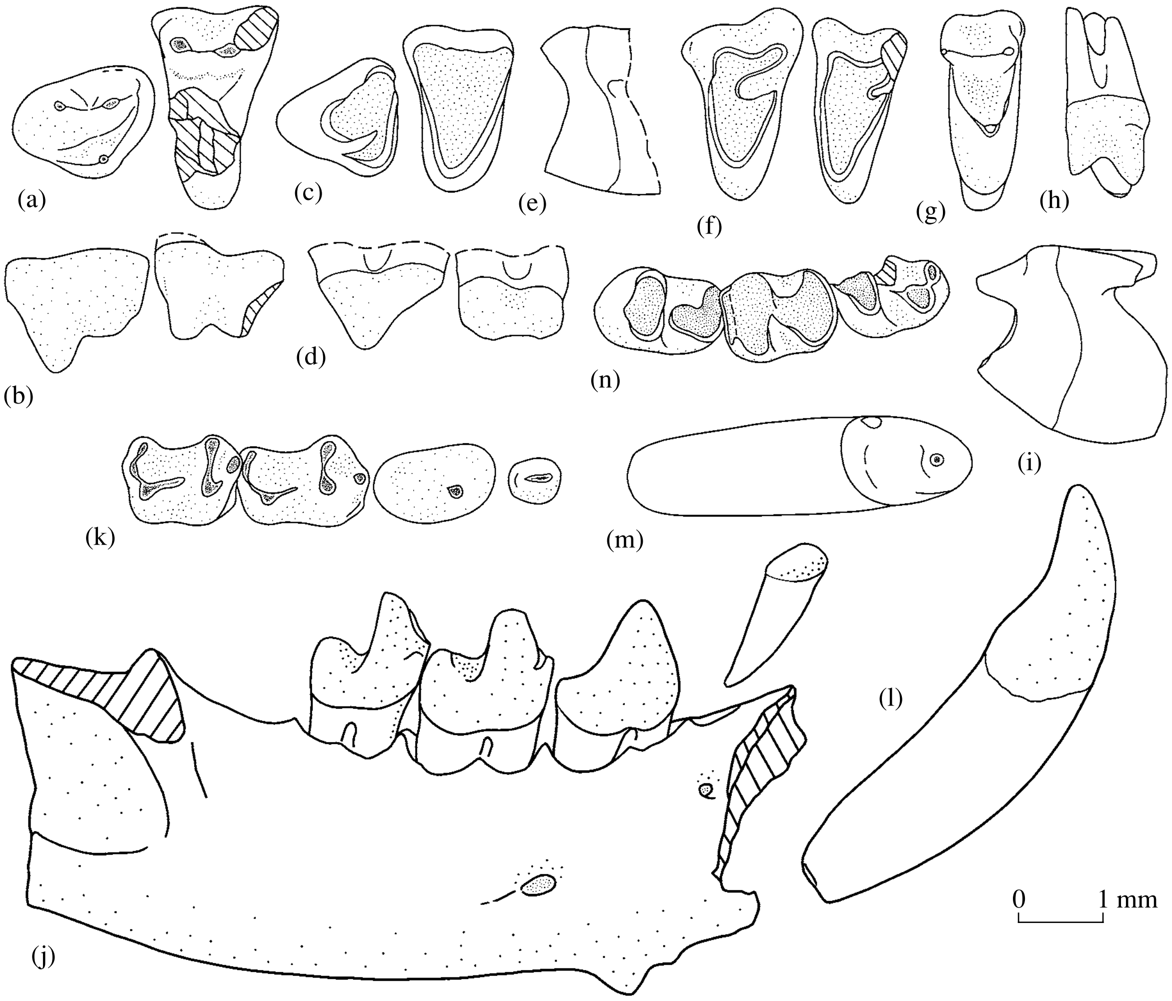


Fig. 42. *Kennatherium shirense* Mellett et Szalay, 1968: (a, b) specimen PIN, no. 3107/348, left P^3 and P^4: (a) occlusal and (b) labial views; (c–e) specimen PIN, no. 3107/347, left P^3 and P^4: (c) occlusal and (d) labial views, (e) P^4, posterior view; (f) specimen PIN, no. 3107/349, left P^4–M^1, occlusal view; (g–i) specimen PIN, no. 3107/365, right M^2: (g) occlusal, (h) labial, and (i) anterior views; (j, k) specimen PIN, no. 3107/353, right dentary fragment with P_2–M_1 (P_2 is drawn out of its alveolus): (j) general appearance, labial view, and (k) P_2–M_1, occlusal view; (l, m) specimen PIN, no. 3107/351, right C_1: (l) labial and (m) occlusal views; (n) specimen PIN, no. 3107/366, left P_4–M_2, occlusal view; Khaychin-Ula 2 locality, Mongolia; Khaychin Formation, Middle Eocene.

side of the metacone. The trigon basin is small, the conules are undeveloped; however, each crest of the protocrista has a distinct expansion in the middle part. At the base of the posterior side of the protocone, there is a hardly discernible enamel expansion.

The horizontal ramus of the lower jaw is relatively slender and low. The symphysial part reaches the line of the middle of P_3. The postsymphysial fossa is deep. The anterior mental foramen is under P_2 or the space between P_2 and P_3, the posterior mental foramen is in

Explanation of Plate 9

Figs. 1–9. *Kennatherium shirense* Mellett et Szalay, 1968, ×8: (1) specimen PIN, no. 3107/347, left maxillary fragment with P^3 and P^4: (1a) labial and (1b) occlusal views; (2) specimen PIN, no. 3107/349, left maxillary fragment with P^4–M^1, occlusal view; (3) specimen PIN, no. 3107/348, left maxillary fragment with unworn P^3 and P^4, occlusal view; (4) specimen PIN, no. 3107/365, right M^2, occlusal view; (5) specimen PIN, no. 3107/351, right C_1, labial view; (6) specimen PIN, no. 3107/353, right dentary fragment with P_2–M_1: (6a) labial view (P_2 is take out of its alveolus), (6b) occlusal view (without P_2), and (6c) lingual view (without P_2); (7) specimen PIN, no. 3107/366, left dentary fragment with P_4–M_2: (7a) labial view and (7b) P_4–M_2, occlusal view; (8) specimen PIN, no. 3107/350, left dentary fragment without teeth, with the angular process preserved, labial view; (9) specimen PIN, no. 3107/354, right dentary fragment with M_1 and partially preserved ascending ramus: (9a) lingual and (9b) occlusal views; Khaychin-Ula 2 locality, Mongolia; Middle Eocene, Khaychin Formation.

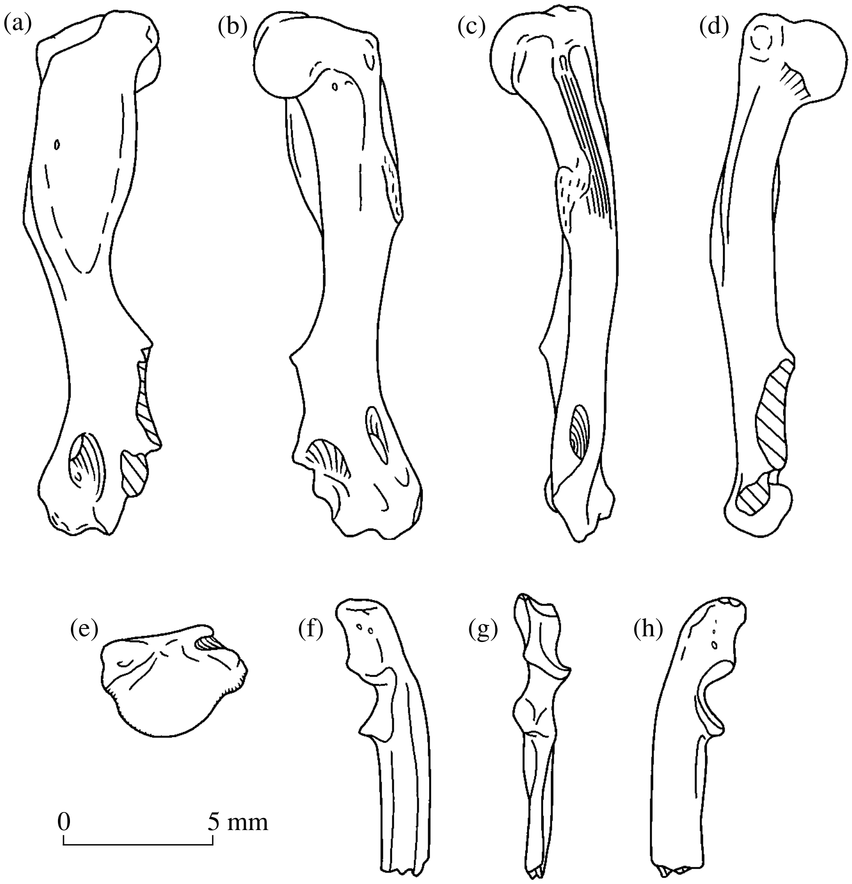


Fig. 43. *Kennatherium shirense* Mellett et Szalay, 1968: (a–e) specimen PIN, no. 3107/388, left humerus: (a) anterior, (b) posterior, (c) medial, (d) lateral, and (e) proximal views; (f–h) specimen PIN, no. 3107/389, fragment of the left ulna: (f) lateral, (g) anterior, and (h) medial views; Khaychin-Ula 2 locality, Mongolia; Khaychin Formation, Middle Eocene.

line with the anterior root of P_4 or the space between P_3 and P_4 (sometimes, three foramina are present: under P_2, under the posterior part of P_3, and under the middle of P_4). The body of the dentary gently curves from the symphysis to the angular process. The base of the coronoid process is gently sloping (the angle between the ascending and horizontal rami is about 140°). The masseteric fossa is very deep and clearly outlined, its anterior part reaches the line of the alveolus of the posterior root of M_2. The strong condylar crest, which borders ventrally the masseteric fossa, extends to the lateral side of the condyle. The condyle is massive, the articular surface covers a sector about 180°. The neck of the condyle is inclined slightly dorsally, so that most of its articular surface faces posterodorsally and is located at the level of the cheek teeth crowns. The transverse axis of the condyle is inclined slightly posterolaterally.

Posterior to the alveoli of M_2, the medial surface of the lower jaw has a massive triangular postalveolar projection with a fine-pitted or smooth surface, which was apparently the origin of a large portion of the masseter. The postalveolar projection is continued posteriorly by a narrow medial crest, which closely approaches the mandibular foramen. The mandibular foramen is large, oval, located in the posterior part of the ascending ramus anteroventral to the condyle and slightly anterodorsal to the angular process. The angular process is deflected somewhat medially, large, in the shape of a blade all edges of which are rounded or a blade with a tapering posterior side (Pl. 9, figs. 8, 9a).

The incisive region of the dentary is not preserved in available specimens; the number of incisors and even their presence or absence remain an open question. The canine has a long root and a relatively low crown. The crown is massive, curved, with a slightly inflated posterior base, without edges. The crown is inclined slightly labially relative to the long axis of the root. The wear facet is apical, descends posterolingually. The posterior margin of the floor of the alveolus of canine is located ahead of the anterior root of P_3. C_1 and P_2 are separated by a small space.

P_2 is small, reduced, with a low oval crown having a small protoconid and a small projection at the posterior base. Its alveolus is small, circular or oval. Posterior to P_2, the cheek teeth are positioned close to each other.

Table 33. Measurements of the upper cheek teeth of *Kennatherium shirense* Mellett et Szalay, 1968

Specimen PIN, no.	Tooth	Length	Width	Labial height
3107/347	P^3	1.75	1.25	1.35
	P^4	1.5	2.4	1.3
3107/348	P^3	1.55	1.3	–
	P^4	1.3	1.95	–
3107/349	P^4	1.45	2.4	–
	M^1	1.15	2.1	–
3107/365	M^2	1.0	2.1	0.9

P_3 is double-rooted, the posterior root is much more massive than the anterior root. The paraconid is absent (sometimes, its rudiment in the shape of a tiny enamel bulge is present). The protoconid is high, conical, with a slightly posteriorly curved apex. The talonid has a small cusp.

P_4 is clearly molarized. The paraconid is small, sometimes, hardly discernible, shows a trend towards fusion with the base of the metaconid. The metaconid and protoconid are approximately equal in height and massiveness, closely fused at the base. The talonid is long, slightly lower than the paraconid, open lingually. The cristid oblique is connected to the base of the protoconid. The entoconid is compressed strongly longitudinally, located posterior to the hypoconid. The hypoconulid is fused with the entoconid.

M_1 is substantially shorter than P_4. The trigonid is compressed strongly longitudinally, the protoconid is slightly higher than the metaconid. The paraconid is displaced lingually, highly elevated, and fused with the metaconid. At the anterior base of the protoconid, there is a more or less developed, short precingulid, which looks like a small tubercle rather than a cingulid. In a heavily worn tooth, the precingulid is united with the paraconid (Fig. 42n). The talonid is relatively wide and short, much lower than the paraconid, level with the precingulid. The cristid oblique is connected to the middle of the posterior base of the trigonid. The entoconid expands transversely, is displaced posterior in relation to the hypoconid, but to a lesser extent than that of P_4. The centrally located small hypoconulid is only slightly detached from the entoconid and separated from the hypoconid by a distinct posterolabial depression.

M_2 is similar in size and structure to M_1, but its talonid is narrower. The cristid oblique is median. The hypoconid and entoconid are equally massive; the entoconid is circular, occupies a posterolingual position in relation to the hypoconid. The hypoconulid is completely reduced. In contrast to P_3–M_1, the roots of M_2 are completely fused and their alveoli are connected; in fact, only one alveolus narrowed in the middle is present.

Table 34. Measurements of crowns and alveoli of lower cheek teeth of *Kennatherium shirense* Mellett et Szalay, 1968

Specimen PIN, no.	Measurements of crowns			
	tooth	length	width	
			trigonid	talonid
3107/353	P_2	0.7	0.55	
	P_3	1.5	0.85	
	P_4	1.55	0.95	0.85
	M_1	1.35	1.0	0.95
	M_2	1.35	–	0.7
3107/368	P_3	1.2	0.8	
3107/350	P_3	1.4	0.75	
3107/352	P_3	1.5	0.85	
3107/371	P_3	1.4	0.85	
	P_4	1.5	0.95	0.75
3107/367	P_3	1.45	0.8	
	P_4	1.5	0.95	0.95
	M_1	1.15	0.95	0.9
3107/369	P_3	1.5	0.9	
	P_4	1.8	1.0	1.0
	M_1	1.35	1.1	0.95
3107/368	P_4	1.5	–	–
3107/366	P_4	1.5	1.0	0.95
	M_1	1.3	1.05	0.9
3107/354	M_1	1.35	0.95	0.8
Specimen PIN, no.	**Measurements of alveoli**			
	tooth	length	width	
			anterior alveolus	posterior alveolus
3107/350	P_2	0.4	0.45	
	P_4	1.5	0.75	0.8
	M_1	1.2	0.8	0.8
	M_2	1.2	0.75	0.65
3107/367	P_2	0.55	0.6	
	M_2	1.25	0.75	0.7
3107/368	P_2	0.55	0.6	
	M_1	1.3	0.8	0.8
3107/353	P_2	0.8	0.65	
	M_2	1.25	0.8	0.75
3107/369	P_2	0.8	0.7	
3107/370	M_1	1.25	0.85	0.8
	M_2	1.2	0.8	0.75
3107/371	M_1	1.2	–	–
	M_2	1.2	–	–

Table 35. Measurements of the horizontal ramus of the lower jaw of *Kennatherium shirense* Mellett et Szalay, 1968

Parameter		Specimen PIN, no. 3107/								
		350	353	354	366	367	368	369	370	371
Height	under P_4	2.7	2.6	3.15	2.7	3.0	3.0	3.0	2.5	2.5
	under M_1	2.7	2.75	3.25	2.8	3.05	3.0	3.25	2.65	2.6
	under M_2	2.75	3.0	3.15	3.0	3.0	3.1	–	2.8	2.6
Thickness at M_2		1.5	1.55	1.65	1.6	1.5	1.65	–	1.35	–

The humerus is moderately broad (Pl. 10, fig. 6; Figs. 43a–43e). Its proximal region is massive. The head has a convex articular surface, which is turned dorsally to the same extent as posteriorly. The greater and lesser tubercles are moderately developed. The crest of the greater tubercle is strong, projects substantially laterally, closely approaches the middle of the diaphysis. The crest of the lesser tubercle is well developed, reaches the middle of the bone, forms a low projection overhanging the bone body. The crests of the greater and lesser tubercles are not fused distally, a slightly concave triangular area is located between them. A relatively large teres tubercle in the shape of a low, thick, and rough crest extending for about one-sixth of the total length of the humerus is located on the posteromedial side of the bone on a level with the distal portion of the crest of the lesser tubercle. A long, deep, and relatively wide longitudinal groove extends on the medial side of the bone and separates the projection of the crest of the lesser tubercle from the posteromedially located structures, including the lesser tubercle in the proximal region and the teres muscle in the distal region. The posterior surface of the proximal region of the bone is convex in the axial part and strongly deepened near the crest of the greater tubercle.

The diaphysis is distinct, composing about one-fifth or one-fourth of the total length of the bone, rounded triangular in section. The distal region is moderately widened (the medial half is well preserved). Judging from the small fragment preserved, the crest of the lateral epicondyle almost reaches proximally the middle of the diaphysis. The surface of the proximal portion of the posterior side of the crest of the lateral epicondyle and adjacent distal part of the diaphysis is slightly rugose. The medial epicondyle slightly curves. The entepicondylar foramen is large. The medial condyle is broad and flattened. The olecranon fossa is relatively small and rather shallow.

The ulna is narrow, concave laterally, flat medially, convex posteriorly, and keel-shaped anteriorly (Pl. 10, fig. 7; Figs. 43f–43h). The olecranon is approximately as long as the semilunar incisure, curves anteromedially. It is narrow, with a slightly concave medial surface and a tubercle weakly projecting anteriorly. The coronoid and anconeal processes clearly project, the semilunar incisure expands moderately distally, while the radial incisure and the supinator crest are relatively weak.

Measurements, mm. Measurements of the cheek teeth are in Tables 33 and 34, those of the horizontal ramus of the lower jaw are in Table 35.

Length of P^3–P^4, 3.0 (specimen PIN, no. 3107/347); 2.9 (PIN, no. 3107/348); length of P^4–M^1 (PIN, no. 3107/349), 2.65.

Lingual height of M^2, 1.25; together with the root, 2.2 (PIN, no. 3107/365).

Length of P_3–P_4, 3.0 (PIN, no. 3107/353); 3.25 (PIN, no. 3107/368); P_3–M_1, 4.35 (PIN, no. 3107/353); P_4–M_1, 2.8 (PIN, no. 3107/366) and 2.85 (PIN, no. 3107/353); P_4–M_2, 4.15; M_1–M_2, 2.65 (PIN, no. 3107/366).

Alveolar length of P_2–M_2, 6.35 (PIN, no. 3107/350) and 6.6 (PIN, no. 3107/353); P_2–M_1, 5.25 (PIN, no. 3107/368); P_3–P_4, 3.2; P_3–M_2, 5.8; P_4–M_2, 4.15 (PIN, no. 3107/350); M_1–M_2, 2.6 (PIN, no. 3107/370); 2.5 (PIN, nos. 3107/350, 371).

External length of the crown of C_1 along straight line, 2.3; length of the root, 3.45; diameters of the base, 1.25 × 1.1 (PIN, no. 3107/351); height of P_2 with the root, 1.95; width of the root, 0.55 (PIN, no. 3107/353).

Explanation of Plate 10

→

Figs. 1 and 2. *Didymoconus rostratus* (Gromova, 1960), holotype PIN, no. 478/332, incomplete skeleton, ×3: (1) right humerus: (1a) anterior and (1b) medial views; (2) left ulna: (2a) medial, (2b) anterior, and (2c) lateral views; Kazakhstan, Chelkar-Teniz, Kur-Say locality; Lower Oligocene, Chelkar-Nura Formation.

Figs. 3 and 4. *Ardynictis captor* Lopatin, 2003, ×3: (3) specimen PIN, no. 3107/390, fragment of the right humerus: (3a) anterior, (3b) posterior, (3c) lateral, (3d) medial, and (3e) distal views; (4) specimen PIN, no. 3107/391, fragment of the left ulna: (4a) medial, (4b) anterior, and (4c) lateral views; Khaychin-Ula 2 locality, Mongolia; Middle Eocene, Khaychin Formation.

Fig. 5. *Khaichinula lupula* sp. nov., specimen PIN, no. 3107/393, incomplete left ulna, ×3: (5a) medial, (5b) anterior, and (5c) lateral views; Khaychin-Ula 2 locality, Mongolia; Middle Eocene, Khaychin Formation.

Figs. 6 and 7. *Kennatherium shirense* Mellett et Szalay, 1968, ×3: (6) specimen PIN, no. 3107/388, left humerus: (6a) anterior, (6b) posterior, (6c) lateral, (6d) medial, and (6e) proximal views; (7) specimen PIN, no. 3107/389, fragment of the left ulna: (7a) medial, (7b) anterior, and (7c) lateral views; Khaychin-Ula 2 locality, Mongolia; Middle Eocene, Khaychin Formation.

Plate 10

Measurements of the ascending ramus of the lower jaw: distance from the posterior edge the condyle to the posterior edge of M_1, 8.7; to the posterior edge of the alveolus of M_2, 7.5; to the anterior base of the coronoid process, 7.0; to the anterior edge of the masseteric fossa, 7.75; thickness of the condyle, 1.5; width of the condylar head, 2.3; dorsal length of the neck with the head, 2.7 (1.8 + 0.9) (PIN, no. 3107/354); length of the angular process, 2.0 (PIN, nos. 3107/350, 354); height, 1.0 (PIN, no. 3107/350) and 1.2 (PIN, no. 3107/354).

Humerus (PIN, no. 3107/388): total length from the head to the distal edge in projection onto the bone axis, 18.2; anterior width of the proximal end, 4.9; thickness of the proximal end, 3.2; width of the diaphysis at the constriction, 2.0; thickness of the diaphysis, 1.8.

Ulna (PIN, no. 3107/389): length of the olecranon along the anterior surface, 3.0; length of the semilunar incisure, 2.8; width at the distal part of the semilunar incisure, 1.7; width at the anconeal process, 1.7; thickness at the anconeal process, 2.2.

Remarks. *Kennatherium shirense* was described based on a single lower jaw fragment, with the preserved coronoid region (without dorsal part of the coronoid process), heavily worn M_1, and alveoli of M_2 (Mellett and Szalay, 1968). The assignment of the specimens described from Khaychin-Ula to this species is supported by the identical structure and dimensions of the coronoid region in specimens PIN, nos. 3107/352 and 353 and the holotype of *K. shirense* and by clear similarity in the shape and dimensions of M_1. In the holotype, this tooth is heavily worn; however, the structures on its occlusal surface are undoubtedly formed on the basis of the same elements as observed, for example, in M_1 of specimens PIN, nos. 3107/353 and 354. The worn teeth represented in the collection of PIN (PIN, nos. 3107/366, 367, 369) are identical in structure to M_1 of the holotype (Fig. 42n).

The fragments of maxillae are referred to this species based on their dimensions and functional correspondence to mandibular specimens.

The humerus and ulna (specimens PIN, nos. 3107/388 and 389, respectively) of a small member of Didymoconidae are associated with other specimens of *Kennatherium shirense* based on their size. They could not belong to *Ardynictis captor*, because of considerable difference in size and structure. The bones are completely formed and undoubtedly belong to adults; therefore, they could not be referred to juveniles of the much larger species *Khaichinula lupula*, despite a high structural similarity to respective bones of the Didymoconinae (Pl. 10, figs. 1, 2; see also Gromova, 1960). *Erlikotherium edentatum* apparently also had substantially larger limb bones. The proportions of the humeri of *Kennatherium* and *Didymoconus* are very similar (Gromova, 1960, text-fig. 6). At the same time, in *Kennatherium*, the crest of the lesser tubercle, teres tubercle, and the groove for a tendon between them are substantially better developed, which suggest a more profound fossorial specialization of *Kennatherium*.

Occurrence. Middle Eocene (Irdinmanhan) of northern China and Mongolia.

Material. The collection of PIN contains the following specimens from the Khaychin Formation of the Khaychin-Ula 2 locality: three fragments of maxillae, with P^3 and P^4 (PIN, nos. 3107/347, 348) and with P^4 and M^1 (PIN, no. 3107/349); three isolated teeth: M^2 (PIN, no. 3107/365), C_1 (PIN, no. 3107/351), and P_3 (PIN, no. 3107/352); ten dentary fragments: with P_3 and P_4 (PIN, nos. 3107/368, 371), with P_2–M_1 (PIN, no. 3107/353), with P_3–M_1 (PIN, nos. 3107/367, 369), with P_4–M_2 (PIN, no. 3107/366), with M_1 and ascending ramus (PIN, no. 3107/354), three fragments without teeth (PIN, nos. 3107/350, 370, 386); and two incomplete forelimb bones, i.e., the left humerus (PIN, no. 3107/388) and the left ulna (PIN, no. 3107/389).

Genus *Erlikotherium* Lopatin, gen. nov.

Etymology. From the mythological Mongolian *Erlik* (host of the subterranean world) and the Greek *therion* (beast).

Type species. *Erlikotherium edentatum* sp. nov.

Diagnosis. Dental formula $I^?/_0C^1/_1P^?/_2M^2/_2$. P_2 absent, long diastema present between canine and P_3. P_3 with small paraconid. Cusps of trigonid of M_1 and M_2 massive. Paraconid of P_4 and M_1 large, wide, bilobed. M_2 with hypoconulid, roots not fused.

Species composition. Type species, Middle Eocene (Irdinmanhan) of Mongolia.

Comparison and remarks. The new genus differs from *Kennatherium* in the absence of P_2, the presence of the paraconid on P_3, the structure of trigonids of P_4–M_2, the presence of the hypoconulid and separate roots of M_2. The differences from *Zeuctherium* are uncertain, because this genus is only represented by the upper teeth.

Erlikotherium edentatum Lopatin, sp. nov.

Plate 11, figs. 1–10

Etymology. From the Latin *edentatus* (lacking teeth).

Holotype. PIN, no. 3107/358, left dentary fragment with M_1 and M_2; Mongolia, Khaychin-Ula 2 locality; Middle Eocene, Khaychin Formation.

Description (Fig. 44). A medium-sized representative of the Didymoconidae: the C_1–M_2 row is about 16 mm long, the P_3–M_2 row is about 9 mm long, the P_4–M_2 row is about 7 mm long, and the total length of the lower jaw is about 30 mm.

The lower jaw has a massive horizontal ramus and a long coronoid region. The symphysis reaches posteriorly the middle or the posterior part of P_3. A deep postsymphysial fossa is present. A long diastema is

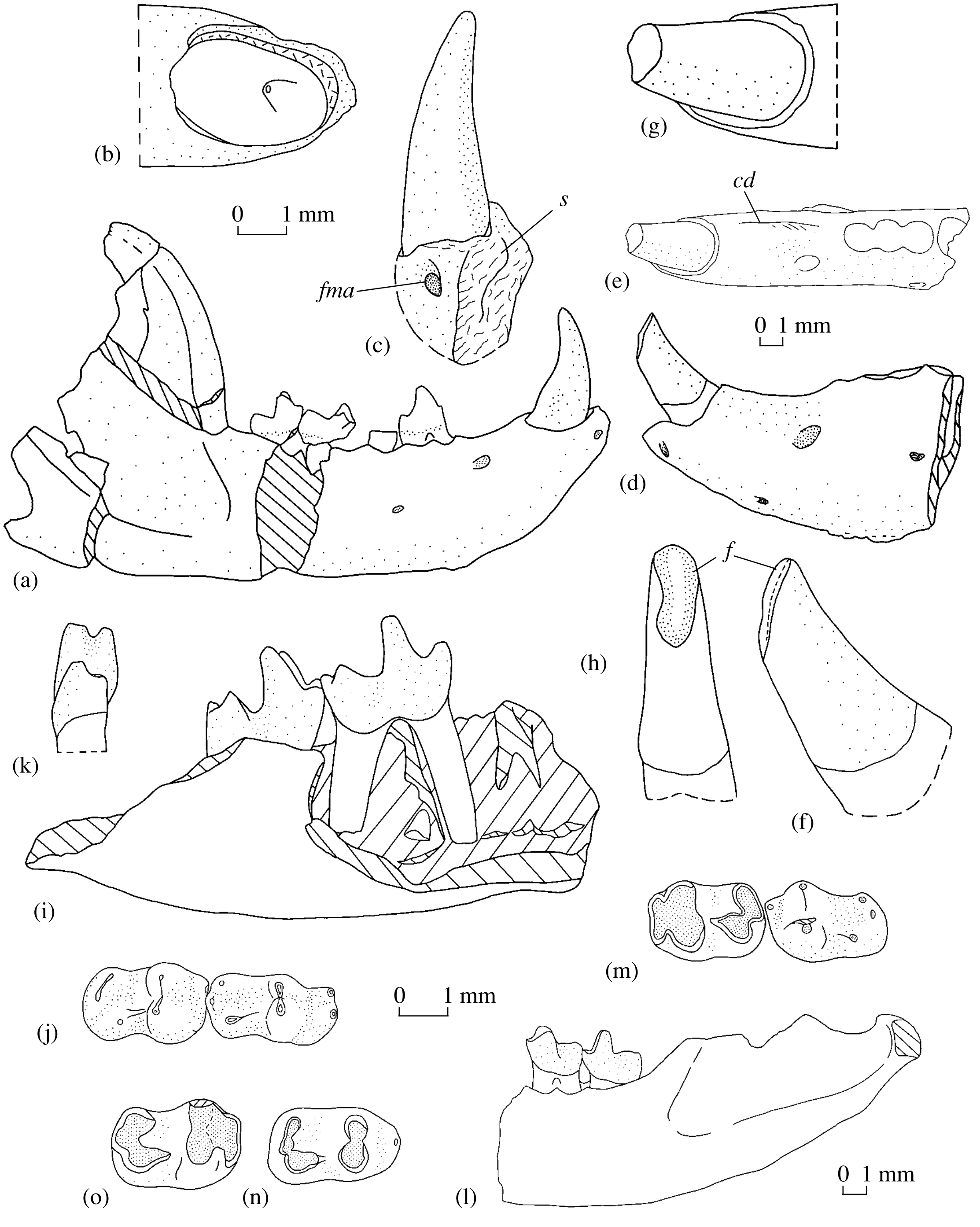


Fig. 44. *Erlikotherium edentatum* sp. nov.: (a–c) specimen PIN, no. 3107/383, right dentary fragment with complete C_1 and P_3, anterior root of P_4, and damaged M_1 and M_2: (a) general appearance, labial view, and (b, c) anterior region of the lower jaw with C_1: (b) occlusal and (c) anterior views; (d–h) specimen PIN, no. 3107/387, left dentary fragment with C_1: (d, e) general appearance: (d) labial and (e) occlusal views; (f–h) C_1: (f) labial, (g) occlusal, and (h) anterior views; (i–k) specimen PIN, no. 3107/356, right dentary fragment with DP_4–M_1: (i) general appearance, labial view, and (j) DP_4–M_1, occlusal view, (k) DP_4, anterior view; (l, m) holotype PIN, no. 3107/358, left dentary fragment with M_1 and M_2: (l) general appearance, labial view, and (m) M_1 and M_2, occlusal view; (n) specimen PIN, no. 3107/327, right P_4, occlusal view; and (o) specimen PIN, no. 3107/328, right M_1, occlusal view; Khaychin-Ula 2 locality, Mongolia; Khaychin Formation, Middle Eocene. Designations: (*cd*) diastematic ridge, (*f*) anterior wear facet of the canine, (*fma*) anterior mental foramen, and (*s*) symphysis.

Plate 11

located between the canine and P_3; within this diastema, the dorsal edge of dentary curves ventrally, abruptly narrows, and looks like a sharp diastematic ridge (Figs. 44d, 44e). The alveolar margin of the dentary in the cheek teeth region is frequently substantially higher than the region of the diastema. The anterior mental foramen is very large, funnel-shaped, located in line with the posterior part of the diastema, faces dorsolabially. The posterior mental foramen is relatively small, located under P_3 or the anterior part of P_4. Another foramen is located on the anterior side of the dentary under the canine.

The body of the dentary is gently arched from the symphysis to the angular process. The base of the coronoid process is relatively gently sloping (the angle between the ascending and horizontal rami is about 140°). The coronoid process is high, with a narrow triangular apex hooked posteriorly. The masseteric fossa is deep and clearly outlined, its anterior part reaches the line of the alveolus of the posterior root of M_2. The massive condylar crest bordering ventrally the masseteric fossa extends to the lateral side of the condyle. The condyle is massive, the articular surface covers a sector about 180°. The neck of the condyle deviates slightly dorsally, so that most of its articular surface faces posterodorsally, located on a level with the crowns of cheek teeth. The transverse axis of the condyle is inclined slightly posterolaterally.

The postalveolar projection is relatively small, with a fine-pitted surface; a narrow medial crest extends posteroventrally and terminates slightly anterodorsal to the mandibular foramen. The mandibular foramen is large, oval, located in the posteroventral part of the ascending ramus anteroventral to the condyle and slightly anterodorsal to the angular process. The angular process is large, in the shape of a posteriorly tapering blade; it curves somewhat medially, has a medial depression for the pterygoid muscle, a flat ventromedial area, and a rough lateral area for the posterior portion of the masseter.

The lower incisors were not developed, which is evident from the structure of the anterior region of the lower jaw clearly observed in specimen PIN, no. 3107/383 (Pl. 11, fig. 5; Figs. 44b, 44c). In connection with the absence of incisors, the lower canine occupies a terminal anterior position in the tooth row. The canine crown is massive, relatively low, flattened laterally at the base, with a blunt apex curving slightly posteriorly. A relatively sharp basal anterolingual edge is developed. In worn teeth, an intense wear facet descends from the apex onto the anterior or anterolabial side of the crown; this suggests that the lower canine rubbed against the upper canine posteriorly (Pl. 11, figs. 3a–3c; Figs. 44d–44h).

In the P_3–M_2 row, neighboring teeth are positioned closely. P_3 is double-rooted, the posterior root is much more massive than the anterior root. The paraconid is small; the protoconid is high, conical, with the apex curved slightly posteriorly; the talonid is massive, unicuspid.

P_4 is clearly molarized. The paraconid is small, basal. The metaconid and protoconid are fused, the protoconid is slightly more massive than the metaconid. The talonid is long, equal in height to the paraconid, widely open lingually. The cristid oblique is connected to the base of the protoconid. The talonid basin is slightly deepened. The hypoconid is massive, the entoconid is compressed strongly longitudinally, the hypoconulid is indiscernible.

DP_4 differs from P_4 in the narrower and elongated crown; the large bilobed paraconid; the long talonid with a sharp cristid oblique, a deepened talonid basin, and three well-developed cusps. The entoconid is circular; the hypoconulid is positioned centrally, removed substantially from the hypoconid closer to the entoconid, but is not fused with it and looks like a separate cusp.

M_1 has a very wide and short paraconid, the lingual part of which in the unworn condition is elevated in the shape of a conical cusp, while the central and labial parts are flat. The protoconid and metaconid are fused, separated only in the upper quarter of their total height. The protoconid is slightly more massive and higher than the metaconid. In a heavily worn tooth, the trigonid acquires a large facet expanding onto the paraconid and onto the gently sloping common anterior wall of the protoconid and metaconid (Fig. 44o). The talonid is relatively wide and long, equal in height to the paraconid. The cristid oblique is connected to the posterior wall of the trigonid in line with the protoconid portion of the protocristid. The talonid basin is deep in the unworn condition. The hypoconid is large; the entoconid and hypoconulid are twinned and the latter is distinguished by its greater height in only unworn teeth.

Explanation of Plate 11

Figs. 1–10. *Erlikotherium edentatum* sp. nov.: (1) holotype PIN, no. 3107/358, left dentary fragment with M_1 and M_2: (1a) labial view, ×3, (1b) occlusal view, ×3, (1c) lingual, ×3, and (1d) M_1 and M_2, occlusal view, ×8; (2) specimen PIN, no. 3107/356, right dentary fragment with DP_4–M_1: (2a) labial view, ×3, (2b) occlusal view, ×3, (2c) lingual view, ×3, and (2d) DP_4–M_1, occlusal view, ×8; (3) specimen PIN, no. 3107/387, left dentary fragment with C_1, ×3: (3a) labial, (3b) occlusal, and (3c) lingual views; (4) specimen PIN, no. 3107/376, right dentary fragment with C_1 and complete ascending ramus, ×3: (4a) labial and (4b) lingual views; (5) specimen PIN, no. 3107/383, right dentary fragment with C_1 and P_3–M_2, labial view, ×3; (6) specimen PIN, no. 3107/375, left dentary fragment with C_1 and incomplete ascending ramus: (6a) labial view, ×3, (6b) occlusal view, ×3, and (6c) M_1, occlusal view, ×8; (7) specimen PIN, no. 3107/327, right P_4, occlusal view, ×8; (8) specimen PIN, no. 3107/328, right M_1, occlusal view, ×8; (9) specimen PIN, no. 3107/373, right dentary fragment without teeth, labial view, ×3; (10) specimen PIN, no. 3107/374, right dentary fragment without teeth, labial view, ×3; Khaychin-Ula 2 locality, Mongolia; Middle Eocene, Khaychin Formation.

Table 36. Measurements of the lower cheek teeth of *Erlikotherium edentatum* sp. nov.

Specimen PIN, no.	Tooth	Length	Trigonid width	Talonid width
3107/356	DP_4	2.8	1.35	1.3
	M_1	2.6	1.6	1.5
3107/379	P_4	2.5	1.45	1.4
	M_1	2.25	1.5	1.4
	M_2	2.35	1.5	1.25
3107/383	P_3	2.2	1.05	1.1
	M_1	2.6	1.6	1.5
	M_2	2.5	1.5	1.25
3107/358 (holotype)	M_1	2.35	1.5	1.5
	M_2	2.55	1.4	1.3
3107/327	P_4	2.75	1.55	1.55
3107/382	P_4	2.5	1.5	1.45
3107/328	M_1	2.75	1.75	1.6
3107/357	M_1	2.5	1.75	1.6
3107/375	M_1	2.45	1.5	1.4
3107/384	M_1	–	1.3	–

M_2 is similar in size and structure to M_1, but has a shorter paraconid and a narrower talonid. The labial portion of the paraconid is considerably reduced.

Measurements, mm. The measurements of cheek teeth are given is Table 36, of the lower jaw, in Tables 37 and 38.

Length of tooth rows: specimen PIN, no. 3107/383: C_1–M_2, 16.0; P_3–M_2, 9.0; P_4–M_2, 6.7; M_1–M_2, 4.9; specimen PIN, no. 3107/379: P_4–M_2, 7.1; M_1–M_2, 4.6.

Alveolar length of tooth rows: specimen PIN, no. 3107/376: P_3–M_2, 11.5; P_4–M_2, 9.0; M_1–M_2, 5.7; specimen PIN, no. 3107/377: P_3–M_2, 10.6; P_4–M_2, 8.2; M_1–M_2, 5.2; specimen PIN, no. 3107/380: P_3–M_2, 10.5; P_4–M_2, 8.0; M_1–M_2, 5.2; specimen PIN, no. 3107/375: P_3–M_2, 10.1; P_4–M_2, 8.0; specimen PIN, no. 3107/381: P_3–M_2, 10.1; P_4–M_2, 7.8; M_1–M_2, 5.0; the holotype: M_1–M_2, 5.2.

Diameters of the base of C_1, 2.9 × 1.9 (PIN, no. 3107/387); 2.4 × 1.8 (PIN, no. 3107/383); 2.3 × 1.7 (PIN, no. 3107/376); 2.0 × 1.4 (PIN, no. 3107/375).

Length of the diastema between C_1 and P_3, 3.6 (PIN, no. 3107/375); 3.7 (PIN, no. 3107/383).

Angular process (length × height), 5.0 × 2.2 (PIN, no. 3107/380); 4.5 × 1.6 (PIN, no. 3107/376).

Variability. Specimen PIN, no. 3107/356, with unworn DP_4, not formed P_4, and incompletely erupted M_1, represents the juvenile stage (see Fig. 44i; an apex of a cusp that is broken off and found near the posterior side of the tip of the anterior root of DP_4 is interpreted as remains of incompletely mineralized crown of P_4). The horizontal ramus of the lower jaw of this specimen is 60–76% as deep as that of adults (see Table 37). At

Table 37. Measurements of the horizontal ramus of the lower jaw of *Erlikotherium edentatum* sp. nov.

Parameter		Specimen PIN, no. 3107/										
		356	holotype	374	375	376	377	379	380	381	383	387
Height	under P_4	3.7	–	–	4.7	5.5	5.0	5.5	5.1	4.0	6.0	7.5
	under M_1	3.6	4.7	–	5.0	5.5	–	5.8	5.6	4.3	6.0	–
	under M_2	–	5.0	4.0	5.2	5.8	5.0	6.0	5.9	4.4	6.5	–
Thickness at M_2		–	2.5	2.8	2.5	2.8	2.5	2.8	2.8	2.7	2.8	–

Table 38. Measurements of the ascending ramus of the lower jaw of *Erlikotherium edentatum* sp. nov.

Parameter	Specimen PIN, no.	
	3107/375	3107/376
Height of coronoid region	14.0	18.0
Distance from posterior edge of condyle to posterior edge of M_2	12.0	14.0
Distance from posterior edge of condyle to anterior base of coronoid process	10.5	13.0
Distance from posterior edge of condyle to anterior edge of masseteric fossa	11.5	13.0
Thickness of condyle	2.1	2.2
Width of articular head	4.1	4.0
Dorsal length of neck with head	3.0 (1.5 + 1.5)	3.0 (1.5 + 1.5)

the senescent stage (specimen PIN, no. 3107/387), which is characterized by heavily worn teeth, including canine (Pl. 11, figs. 3a–3c; Figs. 44d–44h), the horizontal ramus is twice as deep as that of juveniles and 1.25–1.5 times as deep as that of adults.

Material. In addition to the holotype, the collection of PIN contains the following specimens from the type locality: 12 dentary fragments, with C_1 and P_3–M_2 (PIN, no. 3107/383); with C_1, M_1, and incomplete ascending ramus (PIN, no. 3107/375); with C_1 and complete ascending ramus (PIN, no. 3107/376); with C_1 (PIN, no. 3107/387); with DP_4–M_1 (PIN, no. 3107/356); with P_4–M_2 (PIN, no. 3107/379); and without teeth (PIN, nos. 3107/373, 374, 377, 378, 380, 381); and five isolated teeth: two P_4 (PIN, nos. 3107/327, 382) and three M_1 (PIN, nos. 3107/328, 357, 384).

SUPERORDER FERAE LINNAEUS, 1758

Ferae: Linnaeus, 1758, p. 37.

Diagnosis. Predominantly carnivorous and omnivorous small and large epitherian mammals adapted to terrestrial, semiaquatic, aquatic, or semiarboreal mode of life. General habitus ranging from light and slender to heavy. Head usually small relative to body. Limbs varying in length; pentadactyl or tetradactyl; plantigrade, semiplantigrade, or digitigrade; with claws; transformed into flippers in aquatic forms.

Skull with large orbits, well-developed zygomatic arches, and relatively large braincase. Jugal large. Lacrimal small, with facial process, which sometimes absent. Tympanic bulla either absent or formed by ectotympanic or entotympanic bones.

Dentition characterized by teeth with roots and moderately or considerably developed adaptations to vertical cutting. Dental formula $I^{3-1}/_{3-0}C^{1}/_{1}P^{4-1}/_{4-1}M^{3-0}/_{3-0}$ (in exceptional cases, four or five molars present), with trend towards reduction of posterior molars and anterior premolars. Incisors usually small, canines from small and moderately increased to very strong. Cheek teeth tuberculosectorial and sectorial, usually, with pointed cusps and bladelike crests. In omnivorous–phytophagous forms, cusps blunt; sometimes, crowns of cheek teeth considerably reduced. Diphyodonty of dentition clearly pronounced.

Composition. Three orders: Cimolesta McKenna, 1975, Upper Cretaceous–Upper Oligocene of North America, Upper Cretaceous–Lower Oligocene of Europe, Lower Paleocene–Lower Oligocene of Asia, Lower Paleocene of South America, Upper Paleocene–Lower Oligocene of Africa; Creodonta Cope, 1875, Upper Paleocene–Oligocene of North America, Eocene–Miocene of Eurasia and Africa; and Carnivora Bowdich, 1821, Paleocene–Recent of Northern Hemisphere, Miocene–Recent of Africa, Pliocene–Recent of South America, Pleistocene–Recent of Australia.

Comparison and remarks. The differences from insectivores in dental structure are listed above (see diagnosis of the superorder Insectivora). The differences from other placentals are basically evident from the diagnosis. It should be noted that the extremely wide morphological diversity of groups assigned recently to the superorder Ferae substantially decreases the accuracy of its definition. The composition accepted here for the superorder Ferae approximately corresponds to Carnivora sensu Averianov (2003). In contrast to the concept of McKenna (McKenna, 1975a; McKenna and Bell, 1997), it does not contain Pholidota Weber, 1904, Tillodontia Marsh, 1875, and Pantodonta Cope, 1873 (see also Novacek, 1986; Novacek et al., 1988; Archibald and Rose, 2005) as distinct orders or taxa of the order Cimolesta. In contrast to the system proposed by Averianov and according to the system of McKenna, Cimolesta comprises Palaeoryctida, Pantolesta, and Taeniodonta (see also Eberle, 1999).

ORDER CIMOLESTA MCKENNA, 1975

Cimolesta: McKenna, 1975a, p. 41.

Diagnosis (only dental characters). Small and medium-sized members of Ferae with dental formula $I^{3-2}/_{3-1}C^{1-0}/_{1-0}P^{4-2}/_{4-2}M^{3}/_{3}$. Incisors small or excessively developed. Canines from relatively small to strong, usually, with blunted apices. Cheek teeth tuberculosectorial, bunodont, or cylindrical, with flat dentin surface. Carnassial pair not distinguished.

Composition. Five suborders: Didelphodonta McKenna, 1975, Upper Cretaceous–Middle Eocene of North America, Upper Cretaceous–Middle Eocene of Europe, Lower Paleocene of South America, Upper Paleocene of North Africa, and Lower Eocene of Asia; Palaeoryctida Averianov, 2003, Paleocene–Lower Eocene of North America, Upper Paleocene–Lower Eocene of North Africa, Upper Paleocene–Middle Eocene of Asia; Pantolesta McKenna, 1975, Lower Paleocene–Lower Oligocene of North America, Upper Paleocene–Lower Oligocene of Europe, Asia, and Africa; Apatotheria Scott et Jepsen, 1936, Paleocene–Upper Oligocene of North America, Paleocene–Upper Eocene of Europe; and Taeniodonta Cope, 1876, Paleocene–Middle Eocene of North America.

Comparison. Regarding the dentition, Cimolesta differ from Carnivora and Creodonta in the absence of pronounced adaptation for predation, primarily, the absence of strong pointed canines or a pair of opposed sectorial carnassials. In turn, structural variants of the dentition characteristic of Cimolesta (see below) are not observed in Carnivora or Creodonta.

Remarks. Within the order Cimolesta, the affinity of Didelphodonta and Taeniodonta has been demonstrated with certainty (Eberle, 1999). The position of other groups remains problematic, they are often ranked as distinct orders (see Carroll, 1988), but usually retained in the nearest (or next to nearest) higher taxon, for example, Ferungulata (Averianov, 2003).

SUBORDER DIDELPHODONTA MCKENNA, 1975

Didelphodonta: McKenna, 1975a, p. 41.

Diagnosis (only dental characters). Primitive insectivore-like cimolestans. Dental formula $I^{3-2}/_3C^1/_1P^4/_4M^3/_3$. Cheek teeth tuberculosectorial. Upper premolars without paracrista, with strong shearing postcrista. Upper molars trituberculate or protodilambdomorph, expanded considerably transversely and shortened longitudinally. Paracone substantially higher than metacone. Protocone compressed longitudinally. Precingulum and postcingulum usually weak or absent. P_1–P_3 relatively small, showing trend towards reduction; P_1 single-rooted, P_2 single- or double-rooted. P_4 premolariform, semimolariform, or submolariform. Paraconid absent in P_1–P_3 and developed to varying extent in P_4. Lower molars with high and wide trigonids and low, relatively narrow talonids with three clearly differentiated cusps.

Composition. One family, Cimolestidae Marsh, 1889, Upper Cretaceous–Middle Eocene of North America, Upper Cretaceous–Middle Eocene of Europe, Lower Paleocene of South America, Upper Paleocene of North Africa, and Lower Eocene of Asia.

Comparison. In the dentition, the Didelphodonta differ from the Palaeoryctida in the type of molar structure, the structure of incisors, and the presence of P^1 and P_1. They differ from the Pantolesta in the more pointed cheek teeth and the absence of large canines; from the Apatotheria and Taeniodonta, in the absence of specializations characteristic of these groups (excessively developed, soricid-like incisors; reduced apatotherian-like antemolars; or cylindrical cheek teeth typical for taeniodonts) and in the more pronounced tuberculosectorial structure of premolars and molars.

FAMILY CIMOLESTIDAE MARSH, 1889

Cimolestidae: Marsh, 1889, p. 89.

Didelphodontinae: Matthew in Matthew and Granger, 1918, p. 571.

Procerberinae: Sloan and Van Valen, 1965, p. 225.

Type genus. *Cimolestes* Marsh, 1889, Upper Cretaceous–Lower Paleocene of North America, Upper Paleocene of North Africa.

Diagnosis. The same as the diagnosis of the suborder.

Generic composition. *Cimolestes* Marsh, 1889 (= *Nyssodon* Simpson, 1927), Upper Cretaceous–Lower Paleocene of North America, Upper Paleocene of North Africa; *Acmeodon* Matthew et Granger, 1921, *Gelastops* Simpson, 1935 (= *Emperodon* Simpson, 1935), *Pararyctes* Van Valen, 1966, Paleocene of North America; *Procerberus* Sloan et Van Valen, 1965, *Alveugena* Eberle, 1999, Lower Paleocene of North America; *Avunculus* Van Valen, 1966, Upper Paleocene of North America; *Didelphodus* Cope, 1882 (= *Phenacops* Matthew, 1909, = *Didelphyodus* Winge, 1923), Lower–Middle Eocene of North America and Europe; *Tinerhodon* Gheerbrant, 1995, Upper Paleocene of Africa; *Aboletylestes* Russell, 1964, Upper Paleocene of Europe and North Africa; *Ilerdoryctes* Marandat, 1989, Lower Eocene of Europe; and *Naranius* Russell et Dashzeveg, 1986, *Tsaganius* Russell et Dashzeveg, 1986, and *Bagalestes* gen. nov., Lower Eocene of Asia.

Comparison and remarks. In addition to the genera listed above, the family apparently includes certain taxa represented by fragmentary remains from the Upper Cretaceous (Campanian) of France, Lower Paleocene of South America, and Lower Eocene of Morocco (see McKenna and Bell, 1997) presumably belong to the Cimolestidae.

Genus *Naranius* Russell et Dashzeveg, 1986

Naranius: Russell and Dashzeveg, 1986, p. 280.

Type species. *Naranius infrequens* Russell et Dashzeveg, 1986, Lower Eocene of Mongolia.

Diagnosis. P^4 without metacone, with large protocone projection. Upper molars broad, with large stylar shelf. Postparaconule and premetaconule crests absent or very weak. Precingulum and postcingulum well developed. P_2 and P_3 considerably reduced, double-rooted, identical in size. P_4 premolariform, with small basal paraconid, high protoconid, and shearing talonid; without precingulid. Lower molars with moderately high and slender cusps, paraconid closely adjoining metaconid, trigonid basin poorly pronounced, precingulid narrow; in M_1 and M_2 talonid short, talonid cusps aligned along posterior margin of tooth crown, entoconid considerably reduced. Talonid of M_3 elongated, with large hypoconulid.

Species composition. Type species.

Comparison. *Naranius* differs from *Cimolestes* and *Didelphodus* in the weakly developed postparaconule and premetaconule crests, the better pronounced precingulum and postcingulum of the upper molars, and in the considerably reduced P_2 and P_3. It differs from *Procerberus* and *Alveugena* in the greater transverse expansion of the less massive upper molars; it differs from *Gelastops* and *Pararyctes* in the large projection of the protocone of P^4; from *Procerberus, Gelastops*, and *Acmeodon*, in the absence of metacone on P^4. In addition, *Naranius* differs from *Procerberus* in the well-developed lingual cingula of upper molars, reduced P_3, premolariform P_4, and reduced entoconid of M_1–M_3. *Naranius* differs from *Tsaganius* in the considerably reduced P_2 and P_3, premolariform P_4, narrow precingulid of lower molars, and more elongated talonid of M_3. The most prominent characters distinguishing *Naranius* from the majority of genera of the Cimolestidae are the well-developed lingual cingula of M^1–M^3 and the considerably reduced P_2 and P_3.

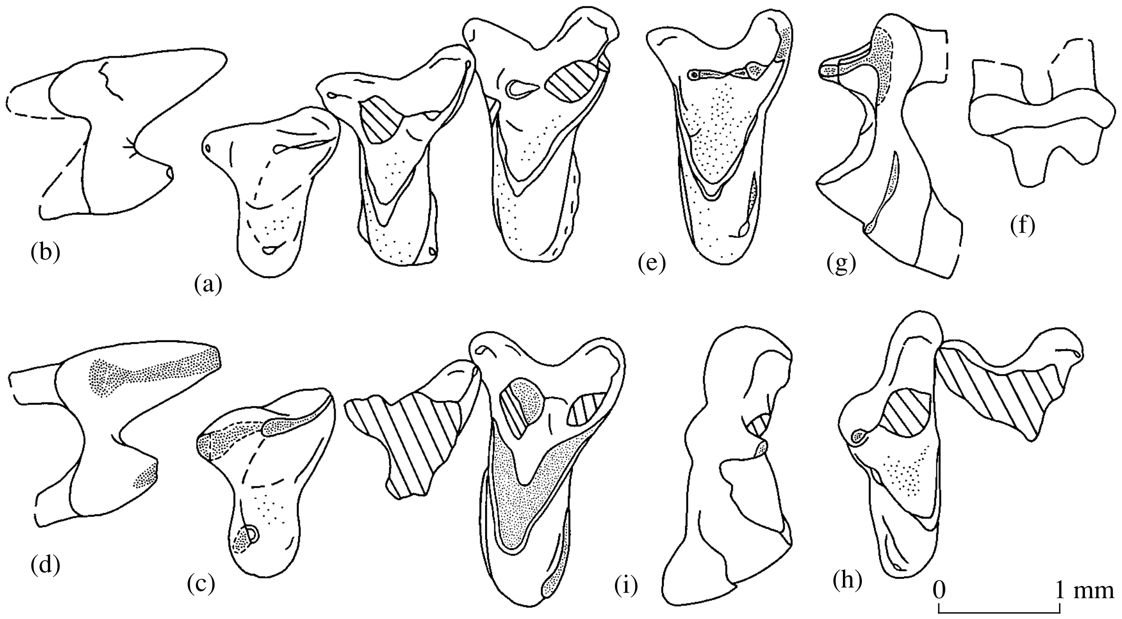


Fig. 45. *Naranius infrequens* Russell et Dashzeveg, 1986: (a, b) specimen PIN, no. 3104/1001, left P^4–M^2: (a) occlusal view and (b) P^4, anterior view; (c, d) specimen PIN, no. 3104/1002, left P^4, fragmentary M^1 and M^2: (c) occlusal view, (d) P^4, anterior view; (e–g) specimen PIN, no. 3104/1010, left M^2: (e) occlusal, (f) labial, and (g) posterior views; (h, i) specimen PIN, no. 3104/1007, right M^2 and M^3: (h) occlusal view and (i) M^3, posterior view; Tsagan-Khushu locality, Mongolia; Bumban Member, Naran-Bulak Formation, Lower Eocene.

Naranius infrequens Russell et Dashzeveg, 1986

Plate 12, figs. 1–13

Naranius infrequens: Russell and Dashzeveg, 1986, p. 280, text-fig. 7.

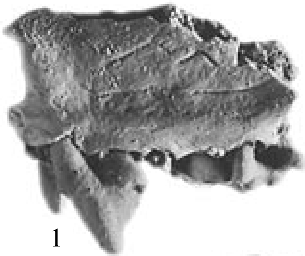
Holotype. PSS, no. 20-73, left dentary fragment with P_3–M_1 and alveoli of P_1–P_2; Mongolia, Tsagan-Khushu locality; Lower Eocene, Naran-Bulak Formation, Bumban Member.

Description (Figs. 45, 46). The maxilla has a narrow zygomatic process, with its base located in line with M^2/M^3. The infraorbital canal is short and narrow; its anterior foramen is above the space between P^3 and P^4, the posterior foramen is above the anterior part of M^1.

P^4 is triangular, with a large projection of the protocone. The labial side of the tooth crown is straight, the styles are relatively small, the ectocingulum is weak. The paracone is high, with a pointed apex and a sharp postcrista extending to the metastyle (Fig. 45a). This crest substantially rises near the middle. The labial and lingual lobes of the tooth are clearly separated by a noticeable anteroposterior compression in the middle part of the tooth crown. The protocone is moderately high, the projection of the protocone has a small basin, the postprotocrista is better developed than the preprotocrista; in line with the posterolingual corner of the paracone, the postprotocrista becomes the postcingulum, which extends to the metastyle. In a considerably worn tooth, large wear facets are formed on the anterior side of the paracone and on the parastyle (caused by occlusion with the protoconid of P_4). A small wear facet is also present on the anterior side of the protocone (Figs. 45c, 45d).

M^1 and M^2 are widened considerably transversely and compressed longitudinally in the middle part, directly lingual to the paracone and metacone. The paracone and metacone are moderately high, slender; their bases are positioned closely, but the apices are widely spaced. In M^1, the parastyle projects anteriorly, while that of M^2 forms a large, anterolabially directed parastylar lobe. The paracrista is absent; a weak and short parastylar crest, which terminates at the base of the paracone, is sometimes present. A large metastylar lobe projects posterolabially. The metacrista is high, strong, and particularly long in M^1. The metacrista of M^2 is directed more labially; distally, it is connected to the postmetaconule crest. The ectoflexus is relatively shallow in M^1, but very deep in M^2. The ectocingulum is narrow. The paraconule is small, ridgelike, rises only slightly more than the preprotocrista. A short and narrow postparaconule crest, which reaches the lingual base of the paracone is sometimes present (Fig. 45e). The metaconule is larger than the paraconule, also ridgelike, forms an elongated thickening of the postprotocrista. A distinct premetaconule crest is absent; in one specimen, a weak eminence is present in its place (Fig. 45e). The long postmetaconule crest reaches the metastyle at the point of connection with the metacrista (in M^2) or slightly more dorsally (in M^1). In this region, an extensive wear facet is formed on the posterior side

Plate 12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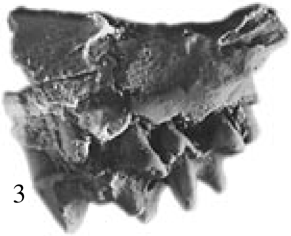
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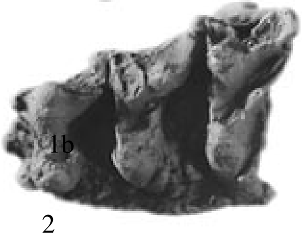

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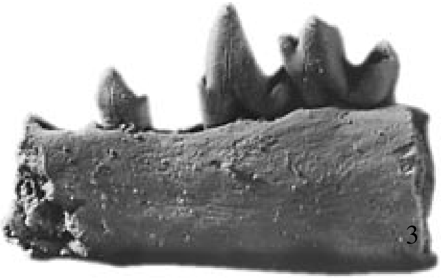

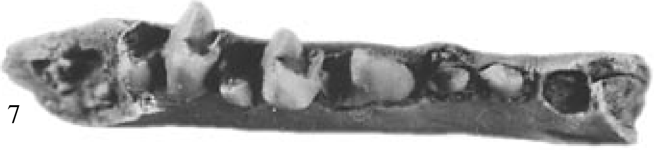
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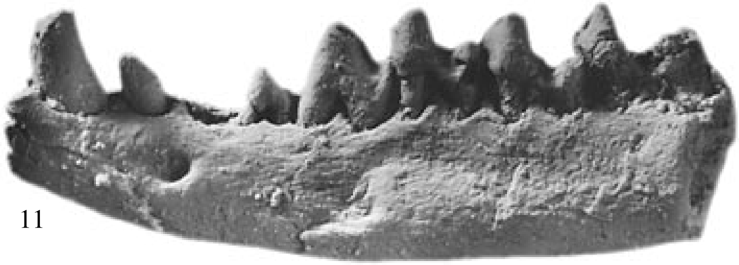
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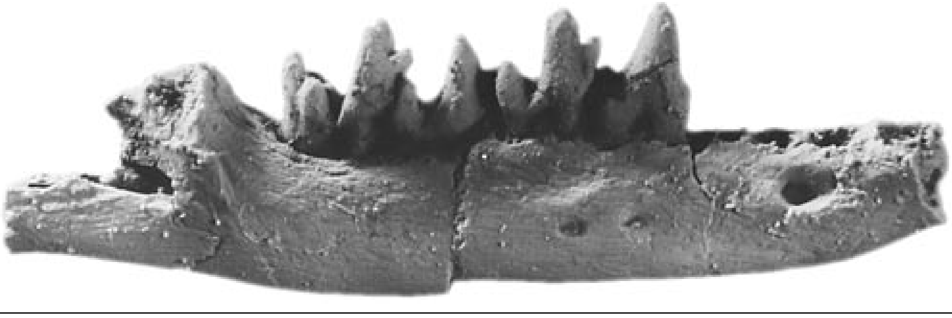
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of the crown (Fig. 45g). In a significantly worn tooth, the conules disappear without leaving a trace; however, strong preparaconule and postmetaconule crests are retained (Fig. 45c). The protocone is approximately equal in height to the paracone, has an almost vertical lingual slope. The precingulum is narrow, long. The postcingulum is relatively wide, long, forms a small hypoconal shelf, the posterolingual corner of which sometimes has a small cusp of the hypocone (it is usually better developed in M^1). Sometimes, several small cuspules are formed along the entire extent of the postcingulum (Fig. 45a). As a tooth is worn, a narrow facet is formed on the postcingulum (Figs. 45c, 45g).

M^3 expanded transversely, has a strong parastylar lobe, which projects considerably labially (Fig. 45h). The paracrista is narrow, but complete, reaching the apex of the paracone. The metastyle and metacrista are absent, the posterior projection of the crown is formed by the metacone, which is substantially lower and less massive than the paracone. The ectocingulum is weak. The paraconule is ridgelike, the metaconule is circular, the postmetaconule crest is short, and the postparaconule and premetaconule crests are absent. In all other respects, the lingual lobe of M^3 is similar to that of M^2.

The horizontal ramus of the lower jaw is long and low, substantially curved opposite the molars (Fig. 46a). The anterior mental foramen is located under P_1–P_2 (usually under the space between these teeth); the posterior mental foramen is under P_4 or the trigonid of M_1 (usually under the talonid of P_4). As a rule, the anterior foramen is much larger than the posterior foramen, and the posterior foramen frequently closely approaches the ventral edge of the jaw. The symphysis reaches posteriorly the line of the anterior part of P_2.

The ascending ramus is relatively long, the distance between the anterior base of the coronoid process and the incisure between the articular and angular processes is approximately half as long as the horizontal ramus. The ventral edge of the ascending ramus is substantially elevated relative to that of the horizontal ramus and curves dorsally (Fig. 46a). The mandibular foramen is narrow, located in line with the talonids of molars. The coronoid process is high (the ascending ramus is three times as high as the horizontal ramus), relatively long, rectangular in shape; its anterior edge gently slopes (the angle is about 120°). The masseteric fossa is deep. A moderately developed postalveolar tubercle, medial crest, and distinct medial depression, which occupies a large area dorsal to the medial crest, are present.

Judging from the alveoli, incisors are small, similar in size, with I_2 somewhat larger than the others (Figs. 46c, 46d). The canine is relatively large, gently curved; the lingual side of its crown is flattened, the apex is slightly pointed (Figs. 46d–46f).

The crowns of premolars are positioned vertically, the crowns of molars are inclined slightly lingually. P_1 is single-rooted, much larger than P_2 or P_3, and approximately half as long as the canine; its crown is simple conical, flattened slightly transversely (Figs. 46g, 46h). P_2 and P_3 are double-rooted, small, less than half as long and half as high as P_4, separated from one another by a small diastema. The tooth crown is simple in structure, with a low protoconid and a small posterior cuspule, which is substantially better developed in P_3 than in P_2 (Figs. 46i–46k).

P_4 is large, at least as long and as wide as M_1. The paraconid is rudimentary, basal, frequently completely absent. The protoconid is high, conical, curved slightly posteriorly. The posterolingual rib of the protoconid only approaches ventrally the talonid and the anterior end of the cristid oblique and has a distinct thickening in basal part (Figs. 46j, 46m, 46n). The talonid is short, with a small terminal cusp, a sharp cristid oblique (directed posterolabially), and a distinct posterolingual cingulid.

The lower molars have a moderately high trigonid and half as high talonid. The trigonid is columnar, compressed considerably longitudinally. The paraconid occupies a high position, but is relatively small and projects slightly anteriorly. The trigonid basin is poorly pronounced. The precingulid is narrow. The protoconid and metaconid are approximately equal in size, fused for two-thirds (in M_2 and M_3) or three-fourths (in M_1) of their height. The protocristid notch is broad. The

Explanation of Plate 12

Figs. 1–12. *Naranius infrequens* Russell et Dashzeveg, 1986, ×10: (1) specimen PIN, no. 3104/1002, left maxillary fragment with P^4, damaged M^1 and M^2, labial view; (2) specimen PIN, no. 3104/1001, left maxillary fragment with P^4–M^2, occlusal view; (3) specimen PIN, no. 3104/1003, left maxillary fragment with M^1–M^3, labial view; (4) specimen PIN, no. 3104/1010, left maxillary fragment with M^2, occlusal view; (5) specimen PIN, no. 3104/1007, right maxillary fragment with M^2–M^3, occlusal view; (6) specimen PIN, no. 3104/1046, left dentary fragment with C_1 and alveoli of I_1–I_3, labial view; (7) specimen PIN, no. 3104/1022, right dentary fragment with P_2–M_2 and alveoli of C_1–P_1, occlusal view; (8) specimen PIN, no. 3104/1023, right dentary fragment with P_2 and P_4–M_1, lingual view; (9) specimen PIN, no. 3104/1040, left dentary fragment with the talonid of M_2 and complete M_3, lingual view; (10) specimen PIN, no. 3104/1014, right dentary fragment with P_4–M_3, alveoli of I_1–P_3, and incomplete ascending ramus, labial view; (11) specimen PIN, no. 3104/1016, left dentary fragment with C_1–P_1 and P_3–M_3 and alveoli of P_2, labial view; (12) specimen PIN, no. 3104/1017, right dentary fragment with P_4–M_3 and alveoli of C_1–P_3, labial view; (13) specimen PIN, no. 3104/1057, left dentary fragment with M_3, occlusal view; Tsagan-Khushu locality, Mongolia; Lower Eocene, Naran-Bulak Formation, Bumban Member.

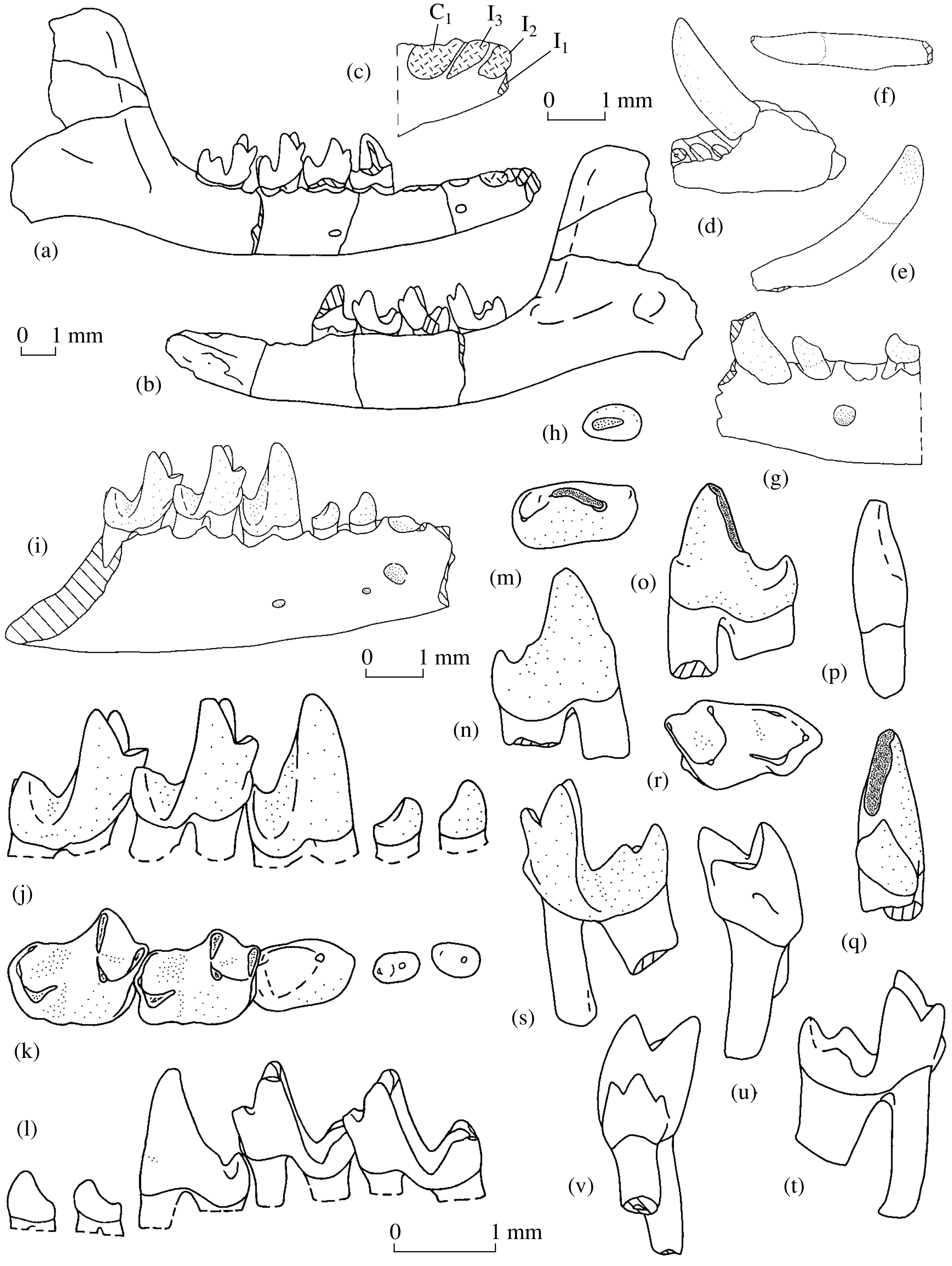


Fig. 46. *Naranius infrequens* Russell et Dashzeveg, 1986: (a, b) specimen PIN, no. 3104/1014, right dentary fragment with P_4–M_3, alveoli of I_1–P_3, and incomplete ascending ramus: (a) labial and (b) lingual views; (c) specimen PIN, no. 3104/1020, right dentary fragment, anterior region with alveoli of I_1–C_1, labial view; (d) specimen PIN, no. 3104/1046, left dentary fragment with C_1 and alveoli of I_1–I_3, labial view; (e, f) specimen PIN, no. 3104/1074, left C_1: (e) lingual and (f) posterior views; (g, h) specimen PIN, no. 3104/1016, left dentary fragment, anterior region with C_1–P_1 and P_3: (g) labial view and (h) P_1, occlusal view; (i–l) specimen PIN, no. 3104/1022, right dentary fragment with P_2–M_2 and alveoli of C_1–P_1: (i) general appearance, labial view, (j) P_2–M_2, labial view, (k) P_2–M_2, occlusal view, and (l) P_2–M_2, lingual view; (m–q) specimen PIN, no. 3104/1077, right P_4: (m) occlusal, (n) labial, (o) lingual, (p) anterior, and (q) posterior views; (r–v) specimen PIN, no. 3104/1080, left M_3: (r) occlusal, (s) labial, (t) lingual, (u) anterior, and (v) posterior views; Tsagan-Khushu locality, Mongolia; Bumban Member, Naran-Bulak Formation, Lower Eocene.

Table 39. Measurements of the upper cheek teeth of *Naranius infrequens* Russell et Dashzeveg, 1986

Specimen PIN, no.	Tooth	Length on labial side	Width	
			parastyle–protocone	metastyle–protocone
3104/1001	P^4	1.3	–	1.45
	M^1	1.45	1.75	1.9
	M^2	1.3	2.1	2.2
3104/1002	P^4	1.25	–	1.5
	M^2	1.35	2.25	2.25
3104/1008	P^4	1.25	–	–
3104/1012	P^4	1.2	–	–
3104/1009	M^1	1.45	1.9	2.0
3104/1003	M^1	1.4	1.75	1.9
	M^2	–	–	2.1
	M^3	0.8	2.25	–
3104/1004	M^1	–	–	2.0
	M^2	1.2	2.0	2.1
3104/1010	M^2	1.25	2.1	2.1
3104/1007	M^2	1.25	–	–
	M^3	0.95	2.2	–
3104/1013	M^3	0.9	–	–

Table 40. Measurements of the lower teeth of the best preserved specimens of *Naranius infrequens* Russell et Dashzeveg, 1986

Specimen PIN, no.	Tooth	Length	Width	
			trigonid	talonid
3104/1016	C_1	0.9	0.6	
	P_1	0.5	0.4	
	P_3	0.6	0.35	
	P_4	1.1	0.5	0.45
	M_1	1.2	0.7	0.7
	M_2	1.15	0.75	0.65
	M_3	1.5	0.9	0.6
3104/1023	P_2	0.6	0.4	
	P_4	1.15	0.7	0.6
	M_1	1.4	0.85	0.85
3104/1022	P_2	0.5	0.3	
	P_3	0.5	0.3	
	P_4	1.0	0.6	0.6
	M_1	1.3	0.8	0.7
	M_2	1.4	0.9	0.8
3104/1024	P_3	0.5	0.35	
	P_4	1.0	–	–
	M_1	1.5	0.9	0.8
	M_2	1.5	1.0	–
3104/1014	P_4	1.2	0.7	0.55
	M_1	1.5	0.85	0.8
	M_2	1.5	1.1	–
	M_3	1.65	1.1	0.7
3104/1017	P_4	1.25	0.6	0.5
	M_1	1.35	0.85	0.75
	M_2	1.5	1.0	0.75
	M_3	1.75	1.0	0.6
3104/1019	P_4	1.1	0.7	–
	M_1	1.4	0.9	0.75
	M_2	1.5	1.0	–
	M_3	1.7	1.0	0.7
3104/1025	M_1	1.3	0.95	0.75
	M_2	1.5	0.95	0.8
	M_3	1.55	1.0	0.7

Table 41. Measurements of C_1 and P_1–P_3 of *Naranius infrequens* Russell et Dashzeveg, 1986 (collection of PIN)

Tooth	N	Length		N	Width	
		limits	Δ		limits	Δ
C_1	5	0.65–0.9	0.78	5	0.5–0.7	0.61
P_1	1	0.5	–	1	0.4	–
P_2	3	0.5–0.6	0.55	3	0.3–0.4	0.33
P_3	8	0.5–0.7	0.56	8	0.3–0.4	0.34

metaconid is displaced slightly anteriorly in relation to the protoconid. The posterior wall of the trigonid is vertical. The talonid is slightly narrower than the trigonid. The hypoflexid is deep. A small prominence is frequently present at the base of the crown under the hypoflexid (Figs. 46i, 46j). The small widely lingually open talonid basin is clearly deepened in the lingual part. The cristid oblique is connected to the base of the posterior wall of the trigonid approximately under the protocristid notch. Sometimes, the anterior end of the cristid oblique terminates short of the trigonid base, so that the hypoflexid and talonid basin communicate. The talonid cusps of M_1 and M_2 are aligned along the posterior edge of the tooth crown and form an integral columnar structure. The hypoconid is relatively large and high; the hypoconulid is substantially smaller and somewhat lower (in an unworn tooth, slightly higher), occupies a median position, extends transversely. The entoconid is small, longitudinally elongated, displaced slightly posteriorly in relation to the hypoconid. M_3 is characterized by a long and narrow talonid with an increased hypoconulid projecting considerably posteriorly and a very small ridgelike entoconid (Figs. 46r–46v).

Measurements, mm. For measurements of the upper and lower teeth and the horizontal ramus of the lower jaw, see Tables 39–43.

Length of the upper tooth row: P^4–M^2, 4.55 (specimen PIN, no. 3104/1001) and 4.75 (PIN, no. 3104/1002);

Table 42. Measurements of P_4 and M_1–M_3 of *Naranius infrequens* Russell et Dashzeveg, 1986 (collection of PIN)

Tooth	*N*	Length		Width					
				trigonid			talonid		
		limits	Δ	*N*	limits	Δ	*N*	limits	Δ
P_4	18	1.0–1.3	1.19	15	0.5–0.7	0.62	12	0.45–0.7	0.57
M_1	17	1.2–1.5	1.35	17	0.7–0.95	0.85	17	0.7–0.9	0.77
M_2	13	1.15–1.5	1.41	13	0.75–1.1	0.95	12	0.65–0.85	0.78
M_3	20	1.5–1.85	1.61	18	0.85–1.1	0.98	19	0.6–0.8	0.69

M^1–M^2, 2.9 (PIN, no. 3104/1003); and M^2–M^3, 2.15 (PIN, no. 3104/1001).

Length of the lower tooth row: C_1–M_3, 8.3 (PIN, no. 3104/1016); P_4–M_3, 5.7 (PIN, no. 3104/1014), 5.55 (PIN, no. 3104/1019), 5.4 (PIN, no. 3104/1017), 5.3 (PIN, no. 3104/1015), and 4.8 (PIN, no. 3104/1016); M_1–M_3, 4.45 (PIN, no. 3104/1019), 4.4 (PIN, no. 3104/1014), 4.3 (PIN, no. 3104/1017), 4.15 (PIN, no. 3104/1025), 4.1 (PIN, no. 3104/1015), and 3.75 (PIN, no. 3104/1016).

Depth of the lower jaw at the coronoid process, 6.15; length of the ascending ramus, 5.0 (PIN, no. 3104/1014).

Remarks. The structure of P^4, M^3, C_1, and ascending ramus of the lower jaw of *Naranius infrequens* are described for the first time.

Occurrence. Lower Eocene (Bumbanian) of Mongolia.

Material. The collection of PIN contains 80 specimens from the type locality, including 11 fragments of maxillae: with P^4–M^2 (PIN, no. 3104/1001), with P^4 and M^2 (PIN, no. 3104/1002), with M^1–M^3 (PIN, no. 3104/1003), three specimens with M^1 and M^2 (PIN, nos. 3104/1004–1006), with M^2–M^3 (PIN, no. 3104/1007), with P^4 (PIN, no. 3104/1008), with M^1 (PIN, no. 3104/1009), and two specimens with M^2 (PIN, nos. 3104/1010, 1011); two isolated fragmentary upper teeth: P^4 (PIN, no. 3104/1012) and M^3 (PIN, no. 3104/1013); 60 dentary fragments: two with P_4–M_3, alveoli of I_1–P_3, and incomplete ascending ramus (PIN, nos. 3104/1014, 1015); one with C_1–P_1 and P_3–M_3 and alveoli of P_2 (PIN, no. 3104/1016); with P_4–M_3 and alveoli of C_1–P_3 (PIN, no. 3104/1017); with P_3–M_2 and alveoli of I_2–C_1 (PIN, no. 3104/1018); with P_4–M_3 (PIN, no. 3104/1019); with P_3 and M_3, fragmentary P_4–M_2, and alveoli of I_1–P_2 (PIN, no. 3104/1020); with P_2, fragmentary P_4–M_3, and alveoli of P_1 and P_3 (PIN, no. 3104/1021); with P_2–M_2 and alveoli of C_1–P_1 (PIN, no. 3104/1022); with P_2, P_4, M_1, and alveoli of P_1 and P_3 (PIN, no. 3104/1023); with P_3–M_2 (PIN, no. 3104/1024); with M_1–M_3 and fragmentary P_4 (PIN, no. 3104/1025); five specimens with P_4–M_1 (PIN, nos. 3104/1026–1030); four with M_1–M_3 (PIN, nos. 3104/1031–1034); three with M_1 and M_2 (PIN, nos. 3104/1035–1037); eight with M_2 and M_3 (PIN, nos. 3104/1038–1045); one with C_1 and alveoli of I_1–I_3 (PIN, no. 3104/1046); three with P_3 (PIN, nos. 3104/1047–1049); five with P_4 (PIN, nos. 3104/1050–1054); two with M_1 (PIN, nos. 3104/1055, 1056); 13 with M_3 (PIN, nos. 3104/1057–1069); and four without teeth (PIN, nos. 3104/1070–1073); seven isolated lower teeth: three C_1 (PIN, nos. 3104/1074–1076), three P_4 (PIN, nos. 3104/1077–1079), and one M_3 (PIN, no. 3104/1080).

Table 43. Depth of the horizontal ramus of the lower jaw of *Naranius infrequens* Russell et Dashzeveg, 1986 (collection PIN)

Level	*N*	Limits	Δ
under P_3	20	1.55–1.9	1.67
under P_4	17	1.7–2.2	1.95
under M_1	19	1.75–2.7	2.12
under M_2	18	1.7–2.5	2.11
under M_3	19	1.7–2.4	2.01

Genus *Tsaganius* Russell et Dashzeveg, 1986

Tsaganius: Russell and Dashzeveg, 1986, p. 284.

Type species. *Tsaganius ambiguus* Russell et Dashzeveg, 1986, Lower Eocene of Mongolia.

Diagnosis. P_2 small. P_3 large, only slightly smaller than P_4. P_4 semimolarized, with relatively high paraconid, distinct precingulid, high protoconid, well-developed metaconid, and simple talonid (with shearing longitudinal crest and terminal cusp). Lower molars with high and slender cusps; paraconid closely adjoining metaconid, trigonid basin poorly pronounced, precingulid strong; in M_1 and M_2, talonid short and low; talonid cusps aligned along posterior margin of tooth crown; entoconid considerably reduced. Talonid of M_3 elongated only slightly.

Species composition. Type species.

Comparison. *Tsaganius* differs from *Cimolestes* and *Didelphodus* in the reduced P_2 and semimolariform P_4; from *Procerberus*, in the less molarized P_4 and reduced entoconid of M_1–M_3; from *Naranius*, in the less reduced P_2 and nonreduced P_3, semimolariform

P_4, the strong precingulid of the lower molars, and less elongated talonid of M_3. *Tsaganius* differs from the majority of other genera of the Cimolestidae in the distinctive structure of P_4.

Remarks. Russell and Dashzeveg (Russell and Dashzeveg, 1986) indicated that *Tsaganius ambiguus* is similar to *Batodon tenuis* (which was assigned to palaeoryctids). They referred *Tsaganius* to the Cimolestidae (Didelphodontinae) and noted that the ancestor of *Tsaganius* was probably related to *Batodon*; however, intermediate Paleocene taxa remained unknown (Russell and Dashzeveg, 1986, p. 286). *Tsaganius* differs from the Geolabididae (including *Batodon*) in the large P_3, the ridgelike paraconid of P_4, more differentiated metaconid and protoconid of P_4–M_3, the shortened talonid of M_1 and M_2, and in the better developed hypoconulid of M_1–M_3.

Tsaganius ambiguus **Russell et Dashzeveg, 1986**

Plate 13, figs. 1–7

Tsaganius ambiguus: Russell and Dashzeveg, 1986, p. 284, text-fig. 8.

Holotype. PSS, no. 20-89, left dentary fragment with P_4–M_3; Mongolia, Tsagan-Khushu locality; Lower Eocene, Naran-Bulak Formation, Bumban Member.

Description (Fig. 47). The horizontal ramus of the lower jaw is low and long. The mental foramina are under the posterior part of P_2 and under the talonid of P_4 or the trigonid of M_1. Judging from the alveoli, P_2 is double-rooted, substantially smaller than P_3, its anterior end is frequently turned somewhat externally relative to the tooth row axis.

P_3 is almost as large as P_4, has a very small paraconid, a high protoconid inclined anteriorly with a sharp posterolingual edge, and a short talonid with a sharp longitudinal crest, which extends obliquely from the base of the posterolingual edge of the protoconid to the terminal talonid cusp.

The trigonid of P_4 and molars is high, columnar, compressed considerably longitudinally. P_4 has a well-developed trigonid with a shearing paraconid and a high detached metaconid. The paraconid is approximately as high as the talonid. The precingulid is short, but distinct, located directly under the paraconid. The protoconid is slightly higher and more massive than the metaconid. The talonid is short, its terminal cusp is large and high. It enters the fold between the precingulid and paraconid of M_1. The longitudinal shearing crest extends in the middle of the talonid and is connected to the base of the metaconid.

In the molars, the high trigonid and low talonid are widely separated by a very deep and large hypoflexid and a well-developed lingual fold. The paraconid is moderately high, relatively small, deviates slightly anteriorly. The angle between the paracristid and protocristid is acute. The precingulid is strong. The protoconid and metaconid are approximately equal in size, positioned opposite each other. The talonid is short, very low, equal in width to the trigonid of M_1, and slightly narrower than that of M_2. The cristid oblique is connected to the base of the protoconid. In M_1 and M_2, the talonid cusps are arranged in a row on the posterior margin of the crown. The hypoconid is relatively small, but more massive than the other talonid cusps. The hypoconulid is slightly higher than the hypoconid, median. The entoconid is very small and low, extends longitudinally, connected at the base to the hypoconulid. In M_3, the talonid is narrow, slightly more elongated than in M_1 and M_2 because of a larger and more projecting hypoconulid. The entoconid is small, ridgelike, positioned apart from the hypoconulid and connected to it by a fine crest.

Table 44. Measurements of the lower cheek teeth of *Tsaganius ambiguus* Russell et Dashzeveg, 1986

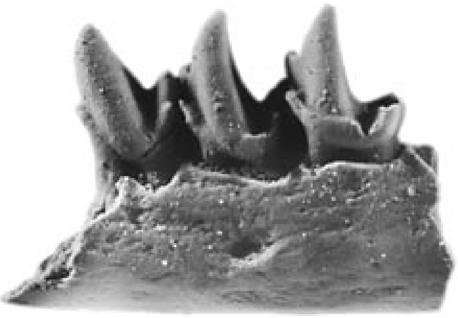
Specimen PIN, no.	Tooth	Length	Width	
			trigonid	talonid
3104/961	P_3	0.85	0.5	0.4
	P_4	0.9	0.65	0.6
	M_1	1.0	0.75	0.65
3104/962	P_4	1.0	0.6	0.55
	M_1	–	–	0.65
	M_2	1.05	0.7	0.6
3104/964	P_4	0.95	0.65	0.55
	M_1	1.0	0.7	0.6
3104/980	P_4	1.0	0.65	0.6
3104/975	P_4	0.95	0.6	0.5
3104/981	M_1	0.95	0.75	0.6
3104/963	M_1	–	–	0.6
	M_2	0.95	0.7	0.6
3104/967	M_1	1.0	0.75	0.65
	M_2	0.9	0.7	0.6
3104/970	M_2	0.95	0.75	0.6
	M_3	–	0.6	0.45
3104/965	M_3	1.0	0.65	0.45

Measurements, mm. For measurements of the teeth and the horizontal ramus of the lower jaw, see Tables 44 and 45, respectively.

Length of the tooth row: P_3–M_1, 2.25 (specimen PIN, no. 3104/961); P_4–M_2, 2.8 (PIN, no. 3104/962); P_4–M_1, 1.8 (PIN, no. 3104/964); M_1–M_2, 2.7 (PIN, no. 3104/967); and M_2–M_3, 1.75 (PIN, no. 3104/971).

Alveoli of premolars (total length of two alveoli × width of anterior alveolus–width of posterior alveolus): P_2: 0.55 × 0.3–0.3 (PIN, no. 3104/975), 0.6 × 0.3–0.35 (PIN, no. 3104/969), and 0.65 × 0.3–0.3 (PIN, no. 3104/976); P_3: 0.85 × 0.4–0.45 (PIN, no. 3104/976), 0.9 × 0.4–0.45 (PIN, no. 3104/975), and 0.9 × 0.4–0.5 (PIN, no. 3104/969).

Plate 13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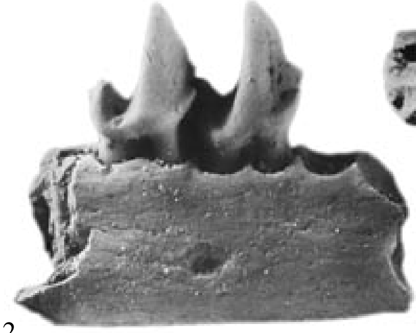
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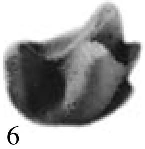
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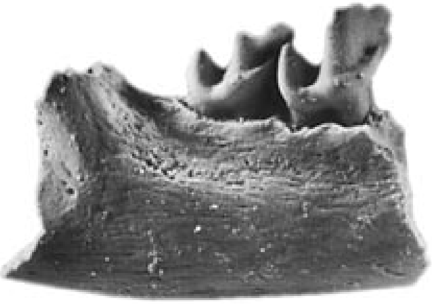
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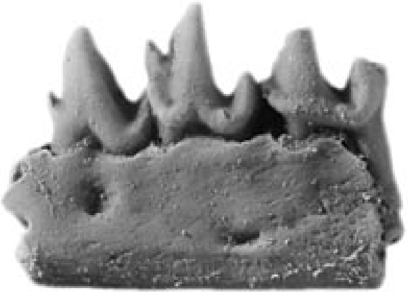
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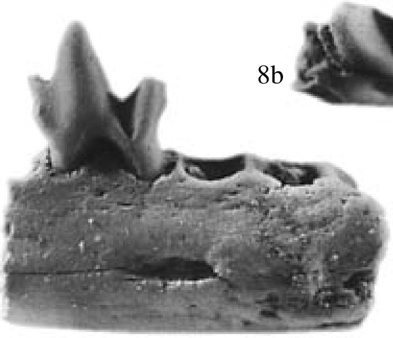
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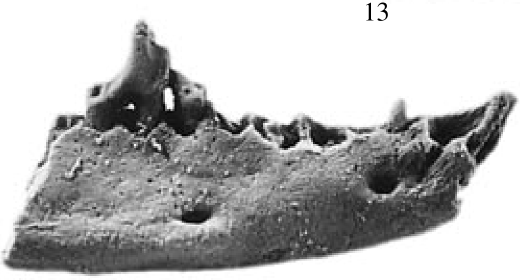
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Table 45. Depth of the horizontal ramus of the lower jaw of *Tsaganius ambiguus* Russell et Dashzeveg, 1986 (collection PIN)

Height	Specimen PIN, no. 3104/											
	961	962	963	964	965	966	967	969	970	971	975	976
under P_4	1.3	1.5	1.45	1.45	–	–	–	1.4	–	–	1.4	1.4
under M_1	1.4	1.45	1.5	1.5	–	1.45	1.5	1.4	–	–	–	1.5
under M_2	–	1.4	1.6	–	1.5	1.4	1.45	–	1.5	1.5	–	–
under M_3	–	–	–	–	1.45	1.4	–	–	1.6	1.45	–	–

Height at the protoconid: P_3, 1.1 (PIN, no. 3104/961); P_4: 1.25 (PIN, no. 3104/961), 1.2 (PIN, no. 3104/964), and 1.1 (PIN, no. 3104/980); M_1: 1.2 (PIN, no. 3104/961), 1.15 (PIN, no. 3104/981), and 1.1 (PIN, no. 3104/964); M_2, 1.1 (PIN, no. 3104/967).

Occurrence. Lower Eocene (Bumbanian) of Mongolia.

Material. The collection of PIN contains 20 specimens from the type locality, including 18 dentary fragments: with P_3–M_1 (PIN, no. 3104/961); two specimens with P_4–M_2 (PIN, nos. 3104/962, 963); with P_4 and M_1 (PIN, no. 3104/964); two specimens with M_1–M_3 (PIN, nos. 3104/965, 982); with M_1 and M_3 (PIN, no. 3104/966); three specimens with M_1 and M_2 (PIN, nos. 3104/967–969); five with M_2 and M_3 (PIN, nos. 3104/970–974); two with P_4 (PIN, nos. 3104/975, 976); with M_1 (PIN, no. 3104/977); and two with M_3 (PIN, nos. 3104/978, 979); and two isolated teeth, P_4 (PIN, no. 3104/980) and M_1 (PIN, no. 3104/981).

Genus *Bagalestes* Lopatin, gen. nov.

Etymology. From the Mongolian *baga* (small) and the Greek *lestes* (robber).

Type species. *Bagalestes trofimovi* sp. nov.

Diagnosis. P_3 large. P_4 premolariform, compressed transversely, with basal paraconid, high protoconid, and short widened talonid. Lower molars with high and slender cusps, detached paraconid, well-pronounced trigonid basin, and strong precingulid; in M_1 and M_2, talonid short and low, talonid cusps aligned along posterior margin of tooth crown, entoconid ridge-like. Mental foramina displaced far posteriorly, located under P_4 and under M_1/M_2.

Species composition. Type species, Lower Eocene (Bumbanian) of Mongolia.

Comparison. *Bagalestes* differs from other cimolestid genera in the unusual posterior position of the mental foramina. In addition, it differs from *Cimolestes* in the transversely compressed protoconid of P_4; from *Procerberus* in the premolariform P_4 and reduced entoconid of M_1 and M_2; from *Naranius* in the nonreduced P_3, transversely compressed protoconid of P_4, strong precingulid, and the structure of the paraconid region and entoconid of M_1 and M_2; from *Tsaganius* in the premolariform P_4 and the structure of M_1 and M_2.

Bagalestes trofimovi Lopatin, sp. nov.

Plate 13, figs. 8 and 9

Etymology. The species is named in memory of the Russian paleotheriologist B.A. Trofimov.

Holotype. PIN, no. 3104/960, left dentary fragment with P_4–M_2; Mongolia, Tsagan-Khushu locality; Lower Eocene, Naran-Bulak Formation, Bumban Member.

Explanation of Plate 13

Figs. 1–7. *Tsaganius ambiguus* Russell et Dashzeveg, 1986: (1) specimen PIN, no. 3104/961, left dentary fragment with P_3–M_1, labial view, ×15; (2) specimen PIN, no. 3104/964, right dentary fragment with P_4–M_1, labial view, ×15; (3) specimen PIN, no. 3104/967, right dentary fragment with M_1 and M_2, labial view, ×15; (4) specimen PIN, no. 3104/970, right dentary fragment with M_2 and M_3, labial view, ×15; (5) specimen PIN, no. 3104/962, right dentary fragment with P_4–M_2, occlusal view, ×15; (6) specimen PIN, no. 3104/980, right P_4, occlusal view, ×20; (7) specimen PIN, no. 3104/981, left M_1, occlusal view, ×20; Tsagan-Khushu locality, Mongolia; Lower Eocene, Naran-Bulak Formation, Bumban Member.

Figs. 8 and 9. *Bagalestes trofimovi* sp. nov., ×15: (8) holotype PIN, no. 3104/960, left dentary fragment with P_4–M_2: (8a) labial and (8b) occlusal views; (9) specimen PIN, no. 3104/959, left dentary fragment with M_1, labial view; Tsagan-Khushu locality, Mongolia; Lower Eocene, Naran-Bulak Formation, Bumban Member.

Figs. 10 and 11. *Nuryctes alayensis* Lopatin et Averianov, 2004, ×10: (10) specimen PIN, no. 3486/110, left maxillary fragment with heavily worn P^4–M^1 and alveoli of P^3 and M^2, occlusal view; (11) holotype ZIN, no. 86145, right dentary fragment with I_3 and P_4–M_1 and alveoli of I_1, I_2, C_1, and P_3, labial view; Andarak 2 locality, Kyrgyzstan; uppermost Lower Eocene, lower part of the Alai Beds.

Figs. 12–14. *Nuryctes gobiensis* Lopatin et Averianov, 2004, ×10: (12) holotype PIN, no. 3107/414, right dentary fragment with P_4–M_3, labial view; (13) specimen PIN, no. 3107/415, left dentary fragment with M_2 and alveoli of M_1 and M_3, labial view; (14) specimen PIN, no. 3107/416, left dentary fragment with M_2, alveoli of M_1 and M_3, and the base of the ascending ramus, labial view; Khaychin-Ula 2 locality, Mongolia; Middle Eocene, Khaychin Formation.

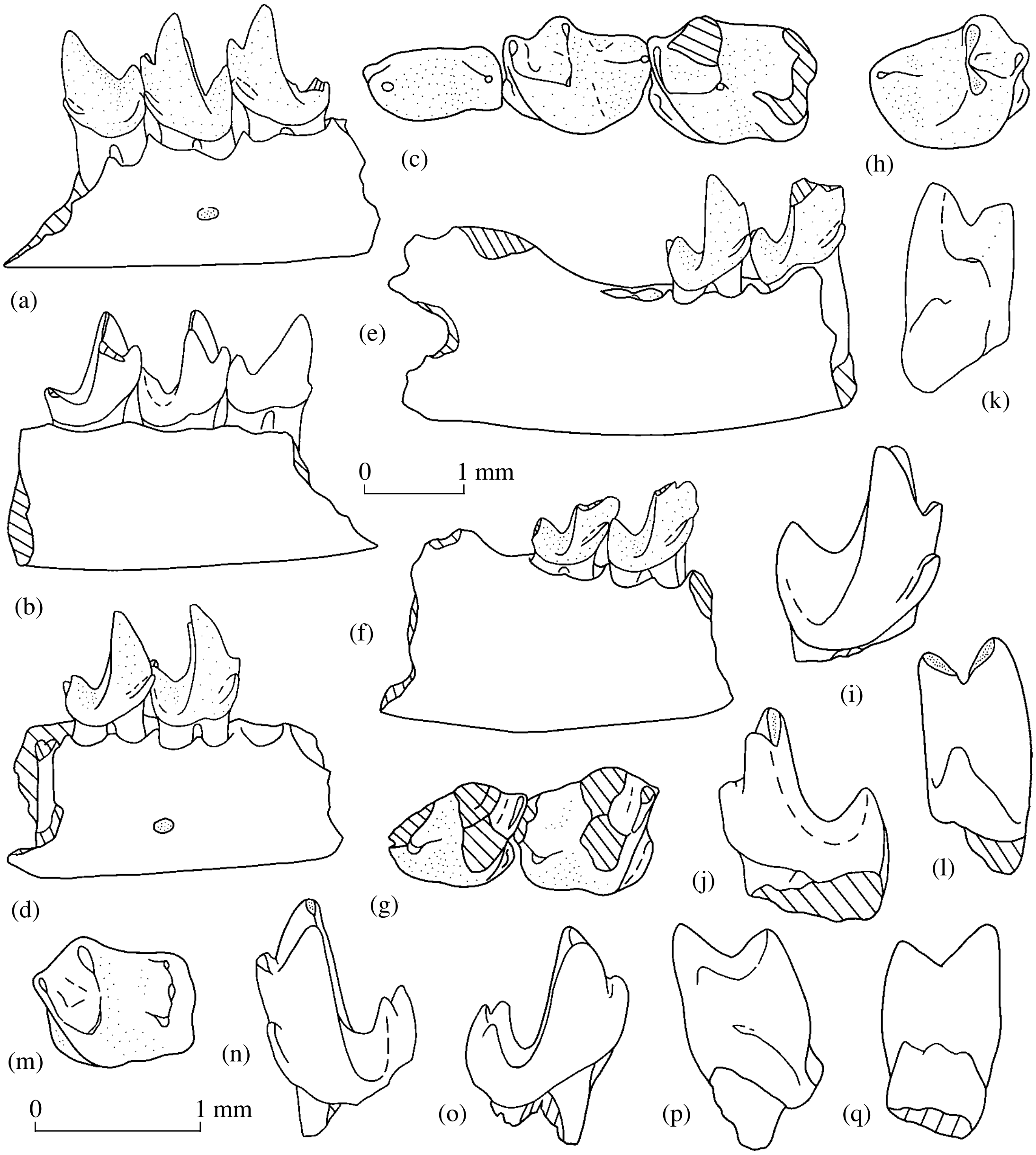


Fig. 47. *Tsaganius ambiguus* Russell et Dashzeveg, 1986: (a–c) specimen PIN, no. 3104/961, left dentary fragment with P_3–M_1: (a) general appearance, labial view, (b) general appearance, lingual view, and (c) P_3–M_1, occlusal view; (d) specimen PIN, no. 3104/964, right dentary fragment with P_4–M_1, labial view; (e) specimen PIN, no. 3104/967, right dentary fragment with M_1 and M_2, labial view; (f, g) specimen PIN, no. 3104/970, right dentary fragment with M_2 and M_3: (f) general appearance, labial view, and (g) M_2 and M_3, occlusal view; (h–l) specimen PIN, no. 3104/980, right P_4: (h) occlusal, (i) labial, (j) lingual, (k) anterior, and (l) posterior views; (m–q) specimen PIN, no. 3104/981, left M_1: (m) occlusal, (n) labial, (o) lingual, (p) anterior, and (q) posterior views; Tsagan-Khushu locality, Mongolia; Bumban Member, Naran-Bulak Formation, Lower Eocene.

Description (Fig. 48). The horizontal ramus of the lower jaw is slender and low. The mental foramina are displaced far posteriorly; the anterior foramen is under the middle of P_4, while the posterior foramen is under the talonid of M_1 or the paraconid of M_2. Judging from the preserved posterior alveolus, P_3 is relatively large.

P_4 is premolariform, transversely compressed. The paraconid is well-developed, but relatively small, positioned basally. The protoconid is high, pointed, with a straight subvertical posterior wall and a distinct posterolingual rib, which reaches ventrally the talonid. The talonid is short, but relatively wide, with a small terminal cusp and a weak longitudinal crest near the lingual margin.

M_1 is slightly longer than P_4. The paraconid is detached from the metaconid, has a short crest. The trigonid basin is small, but distinct. The precingulid is relatively strong. The protoconid and metaconid are fused for three-fourths of their height. The metaconid is slightly lower than the protoconid and is displaced somewhat anteriorly in relation to it. The posterior wall of the trigonid is vertical. The talonid is slightly narrower than the trigonid. The hypoflexid is shallow. The talonid basin is very deep, open only near the metaconid. The cristid oblique is connected to the base of the posterior wall of the trigonid in line with the apex of the protoconid. The talonid cusps are aligned along the posterior edge of the tooth crown and form an integral columnar structure. The hypoconid is relatively large and high; the hypoconulid and entoconid are small and low, fused, sometimes, form an integral ridgelike eminence. M_2 differs from M_1 in the structure of the talonid, the deeper hypoflexid, and better developed hypoconulid and entoconid.

Measurements, mm. Holotype: length of P_4–M_2, 2.8; P_4: length, 0.9; trigonid width, 0.45; talonid width, 0.4; height at the protoconid, 1.0; M_1: length, 1.0; trigonid width, 0.65; talonid width, 0.6; height at the protoconid, 1.05; M_2: length, 1.0; talonid width, 0.7; depth of the horizontal ramus of the lower jaw under M_1, 1.4.

Specimen PIN, no. 3104/959: M_1: length, 1.15; trigonid width, 0.65; talonid width, 0.6; height at the protoconid, 1.1; depth of the horizontal ramus of the lower jaw under M_1, 1.6.

Material. In addition to the holotype, the collection of PIN contains a dentary fragment with M_1 (PIN, no. 3104/959) from the type locality.

SUBORDER PALAEORYCTIDA AVERIANOV, 2003

Palaeoryctida: Averianov, 2003, p. 18.

Diagnosis (only dental characters). Small zalambdodont insectivore-like cimolestans with dental formula $I^3/_3C^1/_1P^{3-2}/_{3-2}M^3/_3$. Cheek teeth tuberculosectorial. Upper incisors vertical; I^1 small, I^2 and I^3 increased. C^1 large. P^1 absent. P^2 small, single-rooted. Protocone of P^3 reduced or absent. P^4 semimolariform, with large protocone. Molars of protozalambdomorph type. M^1–M^3 with large styles, reduced metacone, well-developed protocone; precingulum and postcingulum absent or very weak. Lower incisors procumbent, I_2 increased, I_3 considerably reduced. C_1 usually large. P_1 absent. P_2 small, single-rooted or absent. P_3 and P_4 premolariform, relatively large. M_1–M_3 with high and wide trigonids and low, narrow talonids with reduced cusps and without entocristid.

Composition. One family, Palaeoryctidae Winge, 1917, Paleocene–Lower Eocene of North America, Upper Paleocene–Middle Eocene of Asia, Upper Paleocene–Lower Eocene of North Africa.

Comparison. In the structure of the dental system, the Palaeoryctida differ from all other members of the Cimolesta in the protozalambdomorph type of molar structure. In addition, the Palaeoryctida differ from the Didelphodonta in the structure of incisors and the absence of P^1 and P_1, and from the Apatotheria and Taeniodonta in the absence of specializations characteristic of these groups.

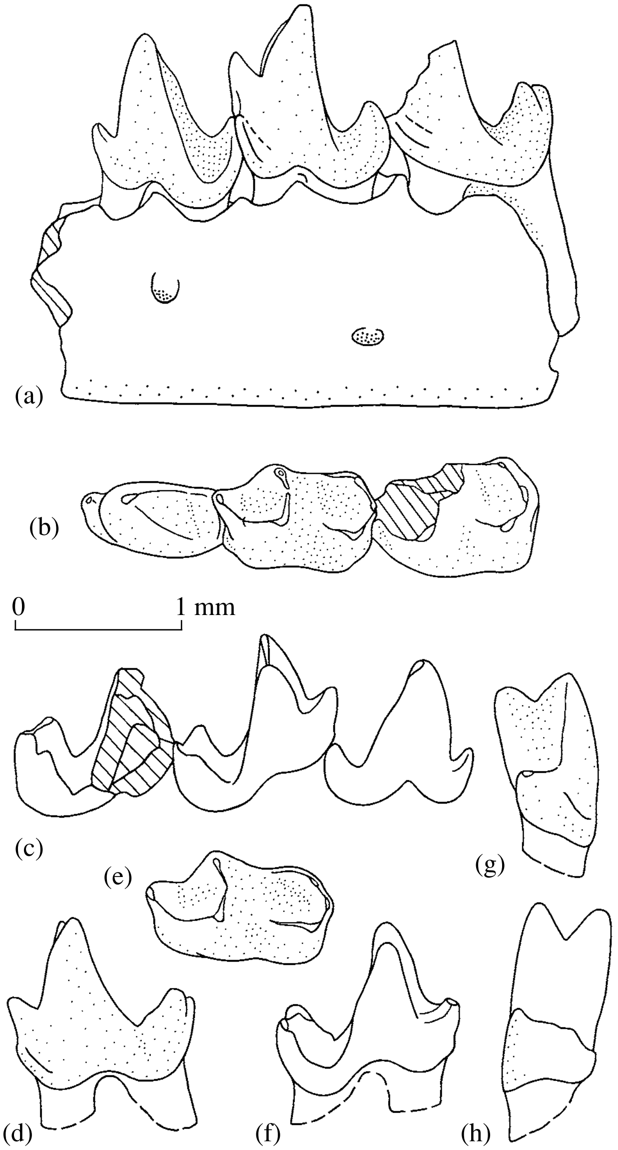


Fig. 48. *Bagalestes trofimovi* sp. nov.: (a–c) holotype PIN, no. 3104/960, left dentary fragment with P_4–M_2: (a) labial view, (b) P_4–M_2, occlusal view, and (c) P_4–M_2, lingual view; (d–h) specimen PIN, no. 3104/959, left M_1: (d) labial, (e) occlusal, (f) lingual, (g) anterior, and (h) posterior views; Tsagan-Khushu locality, Mongolia; Bumban Member, Naran-Bulak Formation, Lower Eocene.

FAMILY PALAEORYCTIDAE WINGE, 1917

Palaeoryctae: Winge, 1917, p. 161.

Palaeoryctidae: Simpson, 1931, p. 268.

Type genus. *Palaeoryctes* Matthew, 1913, Paleocene–Lower Eocene of North America and North Africa.

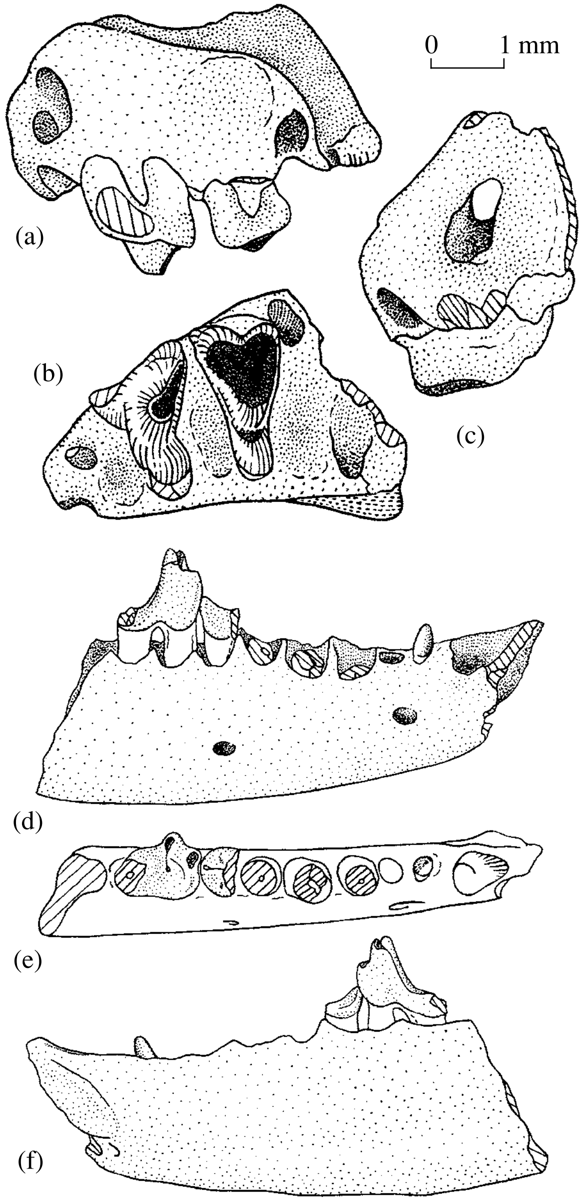


Fig. 49. *Nuryctes alayensis* Lopatin et Averianov, 2004: (a–c) specimen PIN, no. 3486/110, left maxillary fragment with P^4–M^1: (a) labial, (b) occlusal, and (c) posterior views; (d–f) holotype ZIN, no. 86145, right dentary fragment with I_3 and P_4–M_1: (d) labial, (e) occlusal, and (f) lingual views; Andarak 2 locality, Kyrgyzstan; lower part of the Alai Beds, uppermost Lower Eocene.

Diagnosis. The same as the diagnosis of the suborder.

Generic composition. *Palaeoryctes* Matthew, 1913, Paleocene (Torrejonian–Clarkforkian)–Lower Eocene (Wasatchian) of North America, Upper Paleocene–Lower Eocene of North Africa; *Aaptoryctes* Gingerich, 1982, Upper Paleocene (Upper Tiffanian) of North America; *Lainoryctes* Fox, 2004, Upper Paleocene (Upper Tiffanian) of North America; *Eoryctes* Thewissen et Gingerich, 1989, Lower Eocene (Lower Wasatchian) of North America; *Ottoryctes* Bloch, Secord et Gingerich, 2004, Lower Eocene (Middle Wasatchian) of North America; *Nuryctes* Tong, 2003, uppermost Lower Eocene–Middle Eocene (Irdinmanhan) of Asia; and *Pinoryctes* gen. nov., Upper Paleocene (Gashatan) of Asia.

Remarks. In addition to the Paleocene of North America, *Palaeoryctes* was recorded in the Upper Paleocene–Lower Eocene of North Africa (Gheerbrant, 1992, 1993; McKenna and Bell, 1997). Fox (2004) believes that the assignment of these specimens to this genus or even the family Palaeoryctidae is questionable.

Genus *Nuryctes* Tong, 2003

Neoryctes (non Arrow, 1908): Tong, 1997, p. 29.

Nuryctes: Tong, 2003, p. 88; Lopatin and Averianov, 2004b, p. 88.

Type species. *Neoryctes qinlingensis* Tong, 1997, Middle Eocene of China.

Diagnosis. Anterior foramen of infraorbital canal located above P^3, posterior foramen above P^4. Upper molars with rudimentary metacone, without conules, considerably lingually displaced paracone, and small protocone. P_2 absent. P_3 double-rooted, relatively large. P_4 nonmolarized, without paraconid, with well-developed unicuspid talonid. Trigonid of lower molars moderately high. Entoconid of M_1–M_3 absent. Talonid of M_1 and M_2 short, with small hypoconid and hypoconulid; talonid of M_3 elongated, with moderately developed hypoconid and high terminal hypoconulid.

Species composition. *N. qinlingensis* (Tong, 1997), Middle Eocene (Irdinmanhan) of China; *N. alayensis* Lopatin et Averianov, 2004, uppermost Lower Eocene (Irdinmanhan) of Kyrgyzstan; *N. gobiensis* Lopatin et Averianov, 2004, Middle Eocene (Irdinmanhan) of Mongolia.

Comparison. *Nuryctes* differs from *Palaeoryctes, Aaptoryctes, Eoryctes, Ottoryctes*, and *Lainoryctes* in the considerably lingually displaced paracone, the small protocone, and rudimentary metacone of the upper molars. In addition it differs from these genera, except for *Lainoryctes*, in the absence of P_2, the lower crowns, and the absence of entoconid of M_1–M_3 (lower teeth of *Lainoryctes* have not been described). It differs from *Palaeoryctes, Aaptoryctes*, and *Lainoryctes* in the absence of conules, from *Palaeoryctes* in the elongated talonid of M_3, from *Aaptoryctes* in the structure of the talonid of P_4, and from *Eoryctes* and *Ottoryctes* in the absence of paraconid and better developed talonid of P_4.

Nuryctes alayensis Lopatin et Averianov, 2004

Plate 13, figs. 10 and 11

Proteutheria or Lipotyphla genus and species indet.: Averianov and Godinot, 1998, p. 212.

Nuryctes alayensis: Lopatin and Averianov, 2004b, p. 88, text-figs. 1a, 1b, 2–4.

Holotype. ZIN, no. 86145, right dentary fragment with I_3, P_4, M_1 and alveoli of I_1, I_2, C_1, and P_3;

Kyrgyzstan, Andarak 2 locality; uppermost Lower Eocene, lower part of the Alai Beds.

Description (Figs. 49, 50). The infraorbital canal extends from the line of the posterior labial root of P^3 to the line of the posterior root of P^4. The anterior foramen of the infraorbital canal is circular (1.0 × 0.8 mm). In the most anterior region, the infraorbital canal has an internal foramen for the posterior labial root of P^3. The posterior foramen of the infraorbital canal is oval, compressed laterally (Fig. 49c). In rear view, the posterior region of the medial wall of the infraorbital canal has a prominence, which divides longitudinally the canal into two parts.

The zygomatic arch is absent: above the anterior labial root of M^2, the lateral wall of the anterior part of the orbit terminates in a steep slope (the alveolus of the posterior labial root of M^2 is located much more lingually, within the palatal process of the maxilla). On the dorsal side, this region of the maxilla has a relatively sharp ridge becoming posteriorly a massive thickening. In line with M^1, the lateral surface of the maxilla has a small rounded area, which was probably the origin of the maxillonasalis muscle.

P^4 is relatively wide, has a large lingual projection. The parastylar lobe is relatively small, projects anteriorly, the metastylar lobe is large, projects considerably posterolabially. The ectocingulum is weak. The massive paracone and small metastyle are connected by a strong postcrista. The postcingulum is well-developed at the level of the paracone and postcrista. The protocone is relatively large, but low.

M^1 is symmetrical, narrow triangular, with a deep ectoflexus. The parastylar lobe is better developed than the metastylar lobe. The parastyle is in the shape of a small cingular cuspule at the anterolabial end of the parastylar lobe, it is connected lingually to the preprotocrista and, posteriorly, to the base of the stylocone (Fig. 50). Most of the parastylar lobe is occupied by a relatively large and massive stylocone, which is connected lingually to the preparacrista. The anterior projection of the stylocone is in the shape of a small cuspule adjoining a short, lingually directed supplementary crest, which is connected to the preprotocrista. The ectocingulum is weak. The metastylar lobe is extended posterolabially. The stylar shelf is large. The paracone is massive, with a conical apex, occupies a central position on the tooth crown. Just posterolabial to the apex of the paracone, the posterior crest has a small thickening, which is certainly a rudiment of the metacone. Crests of the preparacrista and postmetacrista are sharp. The protocone is relatively small and low (in slightly worn teeth, it is half as high as the paracone), with a conical apex located in line with the apex of the paracone. The crests of the preprotocrista and postprotocrista are relatively long, extending labially to the parastyle and metastyle, respectively.

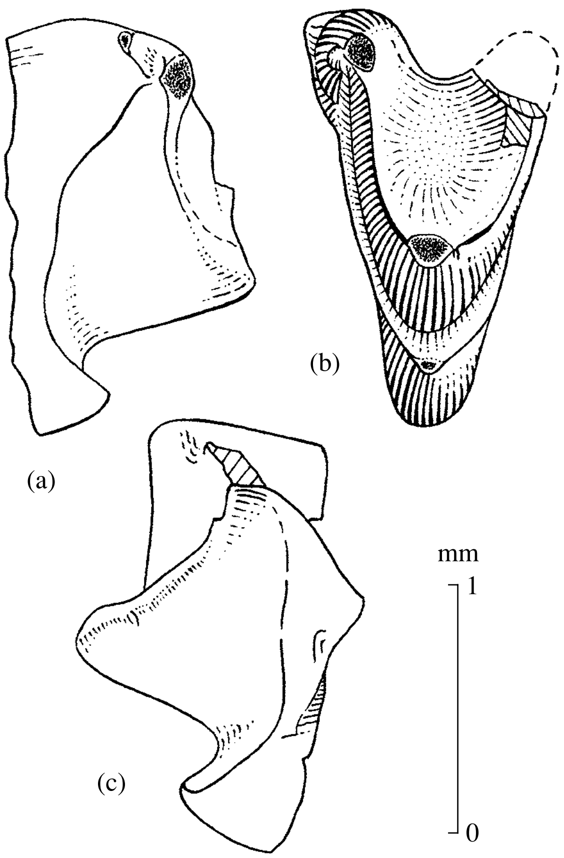


Fig. 50. *Nuryctes alayensis* Lopatin et Averianov, 2004, specimen PIN, no. 3486/207, left M^1: (a) anterior, (b) occlusal, and (c) posterior views; Andarak 2 locality, Kyrgyzstan; lower part of the Alai Beds, terminal Lower Eocene.

Judging from the alveoli, M^2 was substantially wider than M^1. M^3 or its alveoli are not preserved. In the spaces between the teeth, the maxilla has deep, oval vascularized depressions.

The horizontal ramus of the lower jaw (Figs. 49d–49f) is relatively high and slender, the lingual margin in higher than the labial margin. The mental foramina are large: the anterior foramen is located under I_3/C_1 at the mid-depth of the horizontal ramus, while the posterior foramen is in line with the talonid of P_4, close to the ventral edge of the jaw. The symphysis reaches posteriorly the line of the space between I_2 and I_3.

$I_3 < C_1 < I_1 < I_2$. Alveoli of I_1 and I_2 are large (particularly in I_2), extended longitudinally. I_3 is considerably reduced, very small, peglike. C_1 is slightly larger than I_3. Judging from the alveoli, P_3 is double-rooted, relatively large, approximately as long as P_4. P_4 is relatively large, double-rooted, with a low, moderately developed talonid, which has a small terminal cusp and a short longitudinal crest. In M_1, the precingulid is weak, the paraconid is relatively large and massive. The protoconid and metaconid are high, slender, inclined strongly anteriorly; the protocristid has a deep notch. The talonid is narrow (its posterior part is broken off, so that structural details remain uncertain).

Measurements, mm. Holotype: length of alveolus of I_2, ca. 0.85; I_3: length, 0.27; width, 0.25; alveolus of C_1: length, 0.35; width, 0.35; length of P_3 along alveoli, 1.2; length of P_4, ca. 1.15; M_1: total length, ca. 1.1; talonid length, ca. 0.5; trigonid width, 0.75; talonid width, 0.65; height on the protoconid, 1.1; depth of the horizontal ramus of the lower jaw under M_1/M_2 on lingual side, 2.1; on labial side, 2.0.

Specimen PIN, no. 3486/110: length from the anterior root of P^4 to the posterior wall of the alveolus of the lingual root of M^2, 3.6; length × width: P^4, 1.4 × 1.6; M^1, 1.15 × 2.05; width of M^2 along alveoli of the anterior labial and lingual roots, 2.3.

Specimen PIN, no. 3486/207, M^1: length, >1.05; width, 1.8; height posteriorly: paracone, 1.1; protocone, 0.55.

Comparison. *Nuryctes alayensis* differs from *N. qinlingensis* in the less reduced P_3, which is approximately equal in length to P_4 (in *N. qinlingensis*, P_3 is almost half as long as P_4), in the weak precingulid of M_1, and in the more anterior position of the posterior mental foramen (under P_4 instead of under M_1). *N. alayensis* differs from *N. gobiensis* in the less reduced talonid of P_4, less massive cusps of the trigonid, less developed precingulid of M_1, and in the more anterior position of the posterior mental foramen (under P_4 instead of M_1).

Occurrence. Uppermost Lower Eocene (Irdinmanhan) of Kyrgyzstan.

Material. In addition to the holotype, the type locality has yielded a maxillary fragment with heavily worn P^4 and M^1 and alveoli of P^3 and M^2 (PIN, no. 3486/110) and a slightly worn isolated M^1 (PIN, no. 3486/207).

Nuryctes gobiensis Lopatin et Averianov, 2004

Plate 13, figs. 12–14

Nuryctes gobiensis: Lopatin and Averianov, 2004b, p. 91, text-figs. 1c–1e and 5.

Holotype. PIN, no. 3107/414, right dentary fragment with P_4–M_3; Mongolia, Khaychin-Ula 2 locality; Middle Eocene, Khaychin Formation.

Description (Fig. 51). The horizontal ramus of the lower jaw is low in young individuals (with unworn molars, Pl. 13, figs. 13, 14; Figs. 51d–51f) and relatively high in older animals (Pl. 13, fig. 12; a fig. 51a-51c). The lingual margin is substantially higher than the labial margin. The posterior mental foramen is relatively small, located in line with the anterior root of M_1 close to the ventral margin of the jaw (sometimes, it coincides with a short groove, see Fig. 51a). The talonid of P_4 a short and low, the longitudinal crest is weak, the terminal cusp is undeveloped.

M_1 and M_2 are similar in size and structure, M_1 is distinguished by the narrower and wider open lingually trigonid. The precingulid is well-pronounced, but small, projects only slightly. The anterior side of the crown has a vertical reentrant fold formed by the precingulid and the anterolingual projection of the crown, which contains the posterior projection of the talonid of the preceding tooth. The paraconid is small, ridgelike, highly elevated above the level of the precingulid. The paracristid is at an angle of approximately 45° to the long axis of the jaw. The protoconid and metaconid are approximately equal in height, massive at the base. The transverse protocristid has a deep and wide notch. The trigonid basin is shallow. The talonid is relatively narrow. The cristid oblique is weak, directed longitudinally. The hypoconid and hypoconulid are very small, closely adjoin each other. In an unworn or slightly worn condition, the hypoconid is slightly higher than the hypoconulid. The entoconid is absent. In a considerably worn tooth, the trigonid basin disappears and two large facets appear; the first is on the paraconid and anterior walls of the protoconid and metaconid, the second is in the region of the protocristid. On the talonid, the undivided wear facet expands on the hypoconid and hypoconulid and descends along the posterolingual wall.

M_3 is longer than other molars. The talonid of M_3 is low, very narrow, and strongly elongated; its hypoconid and hypoconulid are on the same longitudinal line. The hypoconulid is terminal, elevated above the level of the hypoconid. The entoconid is absent.

Measurements, mm. Holotype: length of M_1–M_3, 3.5; M_1: total length, 1.1; talonid length, 0.4; trigonid width, 0.7; talonid width, 0.6; M_2: total length, 1.15; talonid length, 0.45; trigonid width, 0.85; talonid width, 0.65; length of M_3 along alveoli, 1.25; depth of the horizontal ramus of the lower jaw under M_1/M_2: on the lingual side, 2.25, and on the labial side, 2.0.

Specimen PIN, no. 3107/415: M_2: total length, 1.2; talonid length, 0.6; trigonid width, 0.9; talonid width, 0.6; height of the trigonid along the protoconid, 1.2; height of the talonid along the hypoconid, 0.7; depth of the horizontal ramus of the lower jaw under M_1/M_2 on the lingual side, 1.5; on the labial side, 1.45.

Specimen PIN, no. 3107/416: length of alveoli of M_1, 1.1; M_2: total length, 1.2; talonid length, 0.5; trigonid width, 0.8; talonid width, 0.5; height of the trigonid along the protoconid, 1.25; height of the talonid along the hypoconid, 0.7; length of alveoli of M_3, 1.25; depth of the horizontal ramus of the lower jaw under M_1/M_2 on the lingual side, 2.0; on the labial side, 1.75.

Comparison. *Nuryctes gobiensis* differs from *N. alayensis* in the more reduced talonid of P_4, more massive cusps of the trigonid, better developed precingulid of M_1, and in the more posterior position of the posterior mental foramen (under M_1 instead of P_4). It differs from *N. qinlingensis* in the more reduced talonid of P_4 and relatively smaller paraconid and precingulid of M_2.

Remarks. Regarding the dental structure, *Nuryctes* differs from other known palaeoryctids in the better pronounced zalambdomorphy of the upper

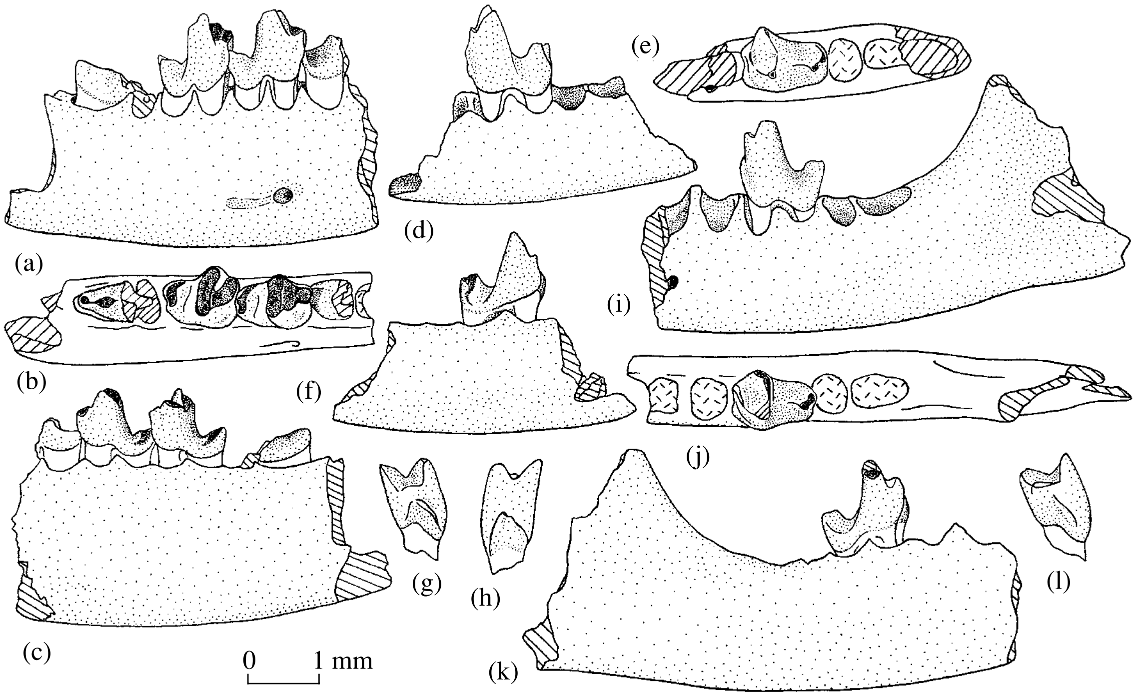


Fig. 51. *Nuryctes gobiensis* Lopatin et Averianov, 2004: (a–c) holotype PIN, no. 3107/414, right dentary fragment with P_4–M_3: (a) labial, (b) occlusal, and (c) lingual views; (d–h) specimen PIN, no. 3107/415, left dentary fragment with M_2: (d) labial, (e) occlusal, and (f) lingual views, (g) M_2, anterior view, and (h) M_2, posterior view; (i–l) specimen PIN, no. 3107/416, left dentary fragment with M_2: (i) labial, (j) occlusal, and (k) lingual views, and (l) M_2, anterior view; Khaychin-Ula 2 locality, Mongolia; Khaychin Formation, Middle Eocene.

molars, the absence of P_2, the absence of entoconid on M_1–M_3, and in the elongated talonid of M_3. All of these characters correspond to the general evolutionary trend realized in members of the family during the Paleocene and Early Eocene; advanced conditions of these characters agree with relatively late time of existence of the genus considered.

In the earliest species *N. alayensis*, P_3 is substantially larger than in *N. qinlingensis*, while the posterior mental foramen occupies a more anterior position than in *N. qinlingensis* and *N. gobiensis*. In *N. gobiensis*, the talonid of P_4 and the paraconid of M_2 are reduced to a greater extent than in *N. alayensis* and *N. qinlingensis*. Thus, the evolutionary trends in the morphology of the lower jaw and teeth of *Nuryctes* include (1) the displacement of the posterior mental foramen from the line of P_4 to the line of M_1, (2) directional reduction of P_3, (3) decrease in the length of talonid of P_4, and (4) reduction of the paraconid of M_2.

A decrease in length of the talonid of P_4 and the paraconid of molars probably reflects the development of specialization of the zalambdomorph dental apparatus. Based on the tooth wear pattern, Butler (1972) proposed that palaeoryctids performed food treatment mostly by primitive vertical cutting, in contrast to the zalambdodont Lipotyphla, which predominantly used transverse masticatory movements. In *Nuryctes*, the interaction of high and long subtransverse crests of the preparacrista, postprotocrista, and protocristid probably had the major cutting effect (double prevallum/postvallid shearing, see Fox, 1970). The paracristid occluded with the postmetacrista and postprotocrista, while the talonid occluded with the protocone. Thus, the longitudinal shortening of the paraconid was associated with a more transverse orientation of the paracristid, which was connected functionally with appropriate modification of the postmetacrista caused by reduction of the metacone and directional expansion of molars. The reduction of the talonid is connected with the reduction of the protocone, which also promotes development of the cutting function of the main crests. The exception is the elongated crest of the talonid of M_3, which probably occluded with the long, posteriorly oblique postmetacrista of M^3.

Based on the above, *N. gobiensis* may be regarded as a more advanced species than *N. qinlingensis*; this, in turn, suggests that the Shipigou locality (Sichuan, Henan, China) is older than the Khaychin-Ula 2 locality (within the Irdinmanhan and Middle Eocene). The sequence of Eocene faunas containing *Nuryctes* should be as follows (from earlier to later): Andarak 2, Shipigou, and Khaychin-Ula 2.

Occurrence. Middle Eocene (Irdinmanhan) of Mongolia.

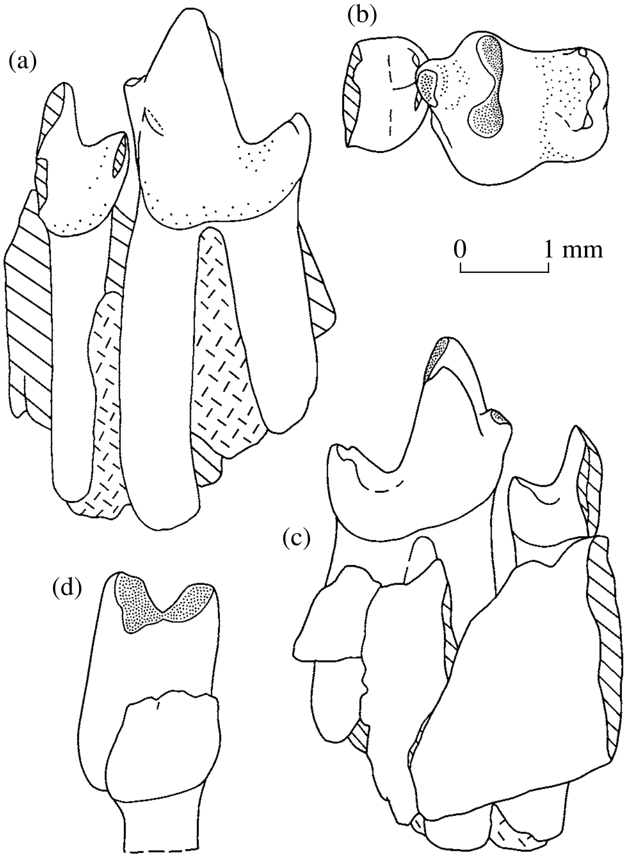


Fig. 52. *Pinoryctes collector* sp. nov., holotype PIN, no. 3104/830, left dentary fragment with the talonid of P_4 and complete M_1: (a) general appearance, labial view, (b) P_4 and M_1, occlusal view, (c) general appearance, lingual view, and (d) M_1, posterior view; Tsagan-Khushu locality, Mongolia; Zhigden Member, Naran-Bulak Formation, Upper Paleocene.

Material. In addition to the holotype, the type locality has yielded two dentary fragments: with M_2 and alveoli of M_1 and M_3 (specimen PIN, no. 3107/415) and with M_2, alveoli of M_1 and M_3, and the base of the ascending ramus (PIN, no. 3107/416).

Genus *Pinoryctes* Lopatin, gen. nov.

Etymology. From the abbreviation *PIN* (Paleontological Institute of the Russian Academy of Sciences) and the Greek *oryctes* (digger).

Type species. *Pinoryctes collector* sp. nov.

Diagnosis. Trigonid of lower molars moderately high, approximately twice as high as talonid, compressed slightly longitudinally; paraconid small, conical; precingulid weak; talonid narrow, tricuspid; cristid oblique considerably reduced.

Species composition. Type species, Upper Paleocene (Gashatan) of Mongolia.

Comparison. *Pinoryctes* differs from *Palaeoryctes, Aaptoryctes, Eoryctes*, and *Ottoryctes* in the lower trigonid of lower molars, which is less compressed longitudinally; the conical (rather than ridge-like) paraconid; and in the considerably reduced cristid oblique. In addition, it differs from *Palaeoryctes, Eoryctes,* and *Ottoryctes* in the weak precingulid and from *Aaptoryctes* in the narrower talonid. *Pinoryctes* differs from *Nuryctes* in the presence of the entoconid, greater reduction of the cristid oblique, and in the conical paraconid.

Pinoryctes collector Lopatin, sp. nov.

Plate 14, fig. 1

Etymology. From the Latin *collector* (gatherer).

Holotype. PIN, no. 3104/830, left dentary fragment with talonid of P_4 and complete M_1; Mongolia, Tsagan-Khushu locality; Upper Paleocene, Naran-Bulak Formation, Zhigden Member.

Description (Fig. 52). P_4 has a relatively short and wide unicuspid talonid. The shearing longitudinal crest is small. A short and relatively low supplementary ridge extends on the posterolingual side of the talonid cusp.

M_1 has long, widely spaced roots and relatively massive crown with a moderately high trigonid and a relatively low talonid. The trigonid is approximately twice as high as the talonid. The paraconid is in the shape of a small circular cusp, located close to the mid-height of the anterior side of the crown in line with the protocristid notch. The precingulid is weak. The protoconid and metaconid are fused for four-fifth of their height; the protoconid is slightly higher than the metaconid and much more massive, particularly, at the base. The massive integral wear facet descends posteroventrally along the protoconid and metaconid. The hypoflexid is small. The talonid is much narrower that the trigonid. The cristid oblique is indistinct, very short, terminates short of the base of the posterior wall of the trigonid, so that the hypoflexid communicates with the shallow talonid basin. The hypoconid, hypoconulid, and entoconid are small and low, but clearly outlined, arranged in a single longitudinal row on the posterior margin of the tooth.

Measurements**,** mm. Holotype: length of the talonid of P_4, 0.5; talonid width, 1.1; total length of M_1, 2.2; trigonid length, 1.4; trigonid width, 1.65; and talonid width, 1.3.

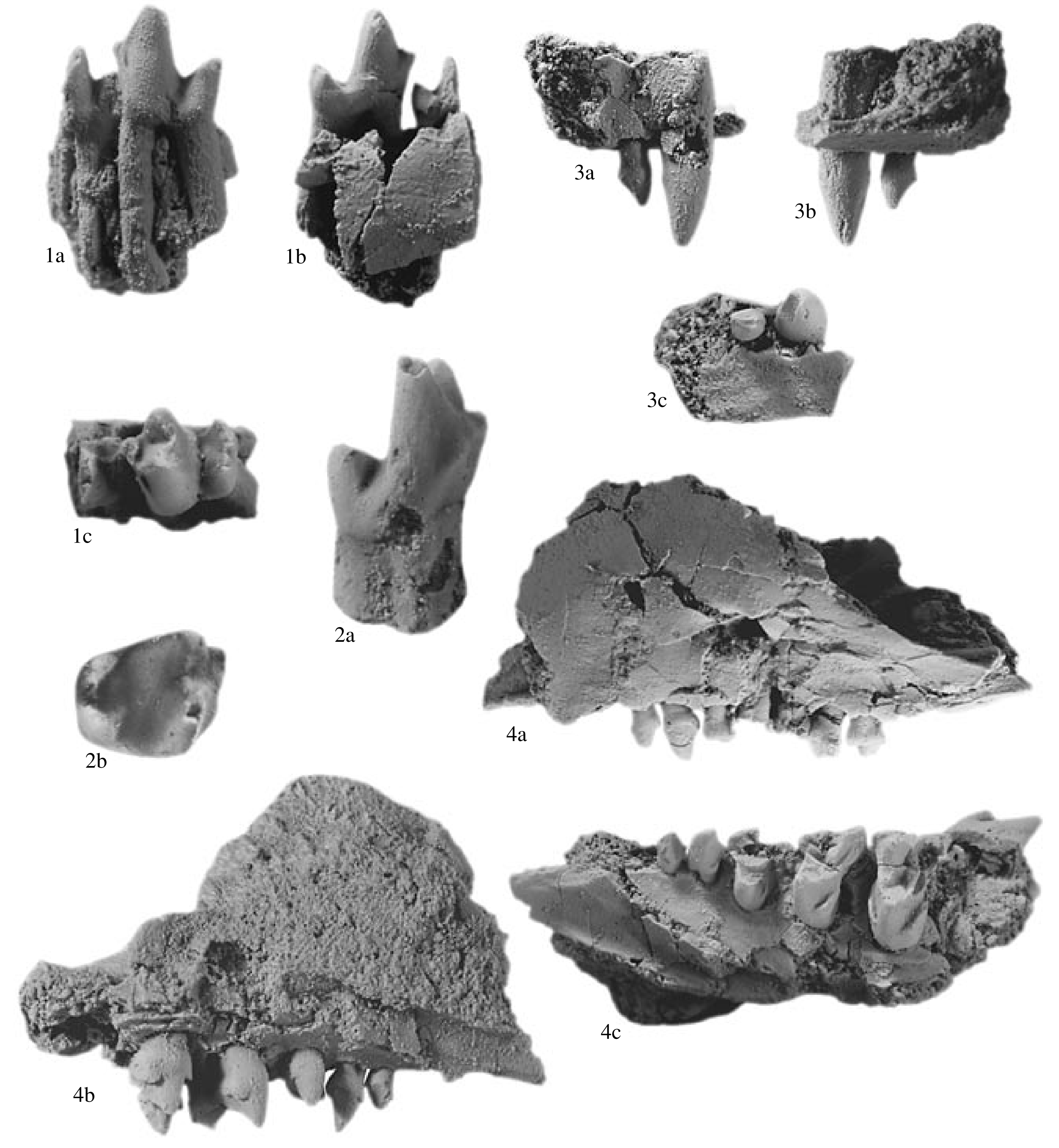
Material. Holotype.

Palaeoryctidae gen. et sp. indet.

Plate 14, fig. 2

Description (Fig. 53). The horizontal ramus of the lower jaw is relatively massive and high. M_1 and M_2 have separate roots, the roots of M_3 are fused. The crown of M_3 is short, with a broad trigonid and short talonid. The trigonid is approximately twice as high as

Plate 14



Explanation of Plate 14

Fig. 1. *Pinoryctes collector* sp. nov., holotype PIN, no. 3104/830, left dentary fragment with partially preserved P_4 and complete M_1, ×8: (1a) labial, (1b) lingual, and (1c) occlusal views; Tsagan-Khushu locality, Mongolia; Upper Paleocene, Naran-Bulak Formation, Zhigden Member.

Fig. 2. Palaeoryctidae gen. et sp. indet., specimen ZIN, no. 89275, right M_3, ×20: (2a) labial and (2b) occlusal views; Andarak 2 locality, Kyrgyzstan; uppermost Lower Eocene, lower part of the Alai Beds.

Figs. 3 and 4. *Zhigdenia nemegetica* sp. nov., ×5: (3) specimen PIN, no. 3104/799, right maxillary fragment with C^1–P^2: (3a) labial, (3b) lingual, and (3c) occlusal views; (4) holotype PIN, no. 3104/431, left maxillary fragment with P^2–M^2, roots of M^3, and alveolus of C^1: (4a) labial, (4b) lingual, and (4c) occlusal views; Tsagan-Khushu locality, Mongolia; Upper Paleocene, Naran-Bulak Formation, Zhigden Member.

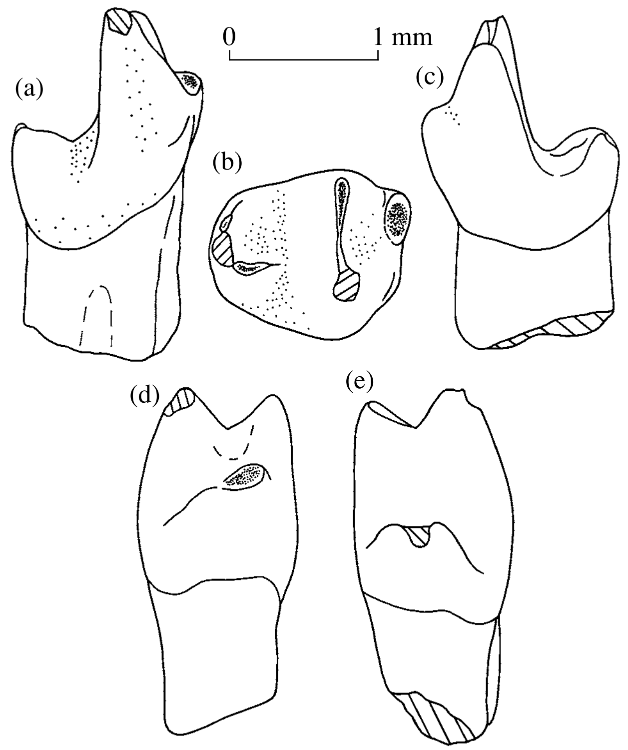


Fig. 53. Palaeoryctidae gen. et sp. indet., specimen ZIN, no. 89275, right M_3: (a) labial, (b) occlusal, (c) lingual, (d) anterior, and (e) posterior views; Andarak 2 locality, Kyrgyzstan; lower part of the Alai Beds, uppermost Lower Eocene.

the talonid, compressed considerably longitudinally. The paraconid is located close to the midheight of the anterior side of the crown, looks like a small, heavily worn circular cusps, displaced lingually relative to the paracristid notch and is fused with the metaconid. The precingulid is weak. The protoconid and metaconid are fused for four-fifths of the height of the posterior side of the trigonid; at the apices, they are separated by a broad protocristid notch. The protoconid is slightly more massive and higher than the metaconid. The hypoflexid is weak. The talonid narrows posteriorly; has a weak cristid oblique, distinct low hypoconid, and only slightly differentiated entoconid and hypoconulid (the hypoconulid is broken off) arranged in a line along the posterior margin of the tooth.

Measurements, mm. Specimen ZIN, no. 89275, M_3: total length, 1.3; talonid length, 0.5; trigonid width, 1.15; talonid width, 0.8.

Specimen PIN, no. 3486/109: depth of the horizontal ramus of the lower jaw under M_2, 2.7; length of M_2 along roots, 1.1; alveolar length of M_2, 1.25; alveolar length of M_3, 1.25.

Comparison and remarks. Regarding the structure of M_3, the form described differs from *Palaeoryctes, Eoryctes*, and *Ottoryctes* in the smaller difference in height between the trigonid and talonid and in the weak precingulid. It differs from *Aaptoryctes* in the paraconid displaced far lingually, the wider talonid, and less developed talonid cusps; from *Nuryctes* in the shortened tricuspid talonid. Available material is insufficient for intentional comparison with *Pinoryctes*, although it is possible to state that the taxon from Andarak is similar to *P. collector* in the extent to which the trigonid is higher than the talonid and in the shape of the paraconid; however, it differs in the greater longitudinal compression of the trigonid, the lingual displacement of the paraconid, better developed cristid oblique, and less distinct talonid cusps. At the same time, all the characters listed widely vary within any palaeoryctid genus (see Bloch et al., 2004), the more so, in comparisons between different teeth of the tooth row (M_1 of *P. collector* and M_3 from the Andarak locality were compared). *P. collector* is 1.7 times as large as the form from Andarak. Thus, it is clear that we deal with a new species; however, its generic status remains uncertain and, hence, I refrain from the establishment of a new taxon.

The currently known Asian palaeoryctids (*Pinoryctes*, Palaeoryctidae gen. et sp. indet. from Andarak, and *Nuryctes*) are similar in the equally small difference in height between the trigonid and talonid of the lower molars. The trigonid of these taxa is approximately twice as high as the talonid, whereas North American palaeoryctids show a much greater difference (usually, by 2.5 times or a little more). Since this similarity is clearly plesiomorphic, it cannot support close relationships between Asian taxa; however, it suggests approximately equal and early isolation from the lineage of *Palaeoryctes*. This genus is placed at the base of the Late Paleocene–Early Eocene adaptive radiation of North American palaeoryctids (Bloch et al., 2004). Thus, it seems plausible that Asian genera are derivatives of a local adaptive radiation of the Palaeoryctidae.

Material. The Andarak 2 locality has yielded isolated M_3 (specimen ZIN, no. 89275; collected by A.O. Averianov in 1995) and a dentary fragment with a broken M_2 and alveoli of M_1 and M_3 (specimen PIN, no. 3486/109; collected by N.S. Shevyreva in 1975).

SUBORDER PANTOLESTA MCKENNA, 1975

Pantolesta: McKenna, 1975a, p. 41.

Diagnosis (only dental characters). Small and medium-sized cimolestans of insectivore-like appearance, with dental formula $I^{3-2}/_{3}C^{1}/_{1}P^{4-2}/_{4-2}M^{3}/_{3}$. Cheek teeth ranging from low-crowned to high-crowned, tuberculosectorial or bunodont. Incisors small. Canines usually large, vertical or curved. Anterior premolars small, with trend towards reduction; $P^3/_3$ and $P^4/_4$ large, with trend towards increase in size and massiveness. P_4 submolariform, semimolariform, or premolariform. Upper molars moderately widened transversely. Styles and cingula of M^1–M^3 weak or absent. In M_1–M_3, paraconid with trend towards fusion with metaconid.

Composition. Three families: Pantolestidae Cope, 1884, Paleocene–Lower Oligocene of North America, Upper Paleocene–Oligocene of Eurasia, Upper Paleocene–Lower Eocene of North Africa; Paroxyclaenidae Weitzel, 1933, Eocene of Eurasia; and Ptolemaiidae Osborn, 1908, Upper Eocene–Lower Oligocene of North Africa.

Comparison. In the structure of the dentition, Pantolesta differs from Palaeoryctida in the structural pattern of molars, from Didelphodonta in the presence of large canines and in the less pointed cusps of the cheek teeth, and from Apatotheria and Taeniodonta in the absence of specializations characteristic of these groups.

FAMILY PANTOLESTIDAE COPE, 1884

Pantolestidae: Cope, 1884, p. 719.

Dyspternidae: Kretzoi, 1943, p. 195.

Cymaprimadontidae: Clark, 1968, p. 242.

Todralestidae: Gheerbrant, 1991, p. 1249.

Type genus. *Pantolestes* Cope, 1872, Lower Eocene of Europe, Middle Eocene of North America.

Diagnosis. Pantolestans with dental formula $I^{3-2}/_3C^1/_1P^{4-3}/_{4-3}M^3/_3$. Incisors small; canines large, massive; C_1 frequently semiprocumbent. $P^1/_1$–$P^3/_3$ premolariform. P^4 semimolariform. M^1–M^3 with small styles, narrow stylar shelf, and widely spaced conical paracone and metacone. Conules, lingual cingula, and hypocone developed to varying degree. P_4 premolariform or semimolariform. M_1–M_3 with large massive cusps of trigonid, well-developed cusps of talonid, and distinct crests. Facial region of skull short, middle region elongated, skull base widened. Posterior mental foramen in line with P_4–M_2.

Composition. Three subfamilies: Pentacodontinae Simpson, 1937, Paleocene–Lower Eocene of North America; Pantolestinae Cope, 1884, Paleocene–Eocene of North America, Upper Paleocene–Lower Eocene of North Africa, Upper Paleocene–Eocene of Europe and Asia; and Dyspterninae Kretzoi, 1943, Lower Eocene–Lower Oligocene of Europe, Lower Oligocene of Asia.

Comparison. The Pantolestidae differ from the Paroxyclaenidae in the better differentiated cuspate structure of upper and lower molars, less reduced anterior premolars, and less massive posterior premolars, the presence of the hypocone and styles, and in the better developed lingual cingula on the upper molars. The Pantolestidae differ from the Ptolemaiidae in the skull shape, usually more complete dental formula, larger C_1, less reduced anterior premolars, less molarized P_4, in the absence of pronounced specialization of posterior premolars and molars manifested in high crowns and excessively developed $P^3/_3$–$P^4/_4$, in the presence of a stylar shelf and cingula on the upper molars, and in the more posterior position of the mental foramen.

SUBFAMILY PANTOLESTINAE COPE, 1884

Pantolestidae: Cope, 1884, p. 719

Pantolestinae: Simpson, 1937, p. 121.

Type genus. *Pantolestes* Cope, 1872, Lower Eocene of Europe, Middle Eocene of North America.

Diagnosis. $P^4/_4$ moderately large. P^4 lacking metacone and having well-developed styles and small protocone without distinct lingual cingula. Cusps of molars well differentiated; paracone, metacone, protocone, protoconid, and metaconid usually rather high, whereas crown base relatively low. Upper molars relatively short and broad. $M^3/_3$ relatively large. P_4 premolariform, without metaconid; its talonid unicuspid, without basin. Lower molars with clearly detached paraconid projecting anterolingually or closely adjoining metaconid. Posterior mental foramen in line M_1/M_2.

Generic composition. *Propalaeosinopa* Simpson, 1927 (= *Bessoecetor* Simpson, 1936), Paleocene of North America, Upper Paleocene of Europe; *Palaeosinopa* Matthew, 1901 (= *Niphredil* Van Valen, 1978), Upper Paleocene–Lower Eocene of North America, Lower Eocene of Europe; *Thelysia* Gingerich, 1982, Upper Paleocene of North America; *Pagonomus* Russell, 1964, Upper Paleocene of Europe; *Todralestes* Gheerbrant, 1991, Upper Paleocene–Lower Eocene of North Africa; *Pantolestes* Cope, 1872 (= *Passalacodon* Marsh, 1872; = *Anisacodon* Marsh, 1872), Lower Eocene of Europe, Middle Eocene of North America; *Premontrelestes* Smith, 2001, Lower Eocene of Europe; *Buxolestes* Jaeger, 1970, Middle Eocene of Europe; *Chadronia* Cook, 1954 (= *Cymaprimadon* Clark, 1968), Upper Eocene of North America; *Galethylax* Gervais, 1850, *Bouffinomus* Mathis, 1989, Upper Eocene of Europe; *Oboia* Gabunia, 1989, Upper Eocene of Asia; and *Zhigdenia* gen. nov., Upper Paleocene of Asia.

Comparison. The Pantolestinae differ from the Pentacodontinae and Dyspterninae in the more differentiated cusps of molars, smaller $P^4/_4$, relatively shorter and wider upper molars, relatively long lower molars, better detached paraconid of M_1–M_3, nonreduced $M^3/_3$, and in the more posterior position of the posterior mental foramen. In addition, the Pantolestinae differ from the Pentacodontinae in the nonmolarized structure of $P^4/_4$.

Genus *Zhigdenia* Lopatin, gen. nov.

Etymology. From the Zhigden Member of the Naran-Bulak Formation.

Type species. *Zhigdenia nemegetica* sp. nov.

Diagnosis. P^1 absent. P^2–P^3 considerably reduced, without protocone and parastyle. P^4 substantially narrower than M^1. M^1 and M^2 without distinct ectoflexus, parastylar lobe relatively large, conules well-developed, hypocone small. M^3 wider than M^2.

Species composition. Type species, Upper Paleocene (Gashatan) of Mongolia.

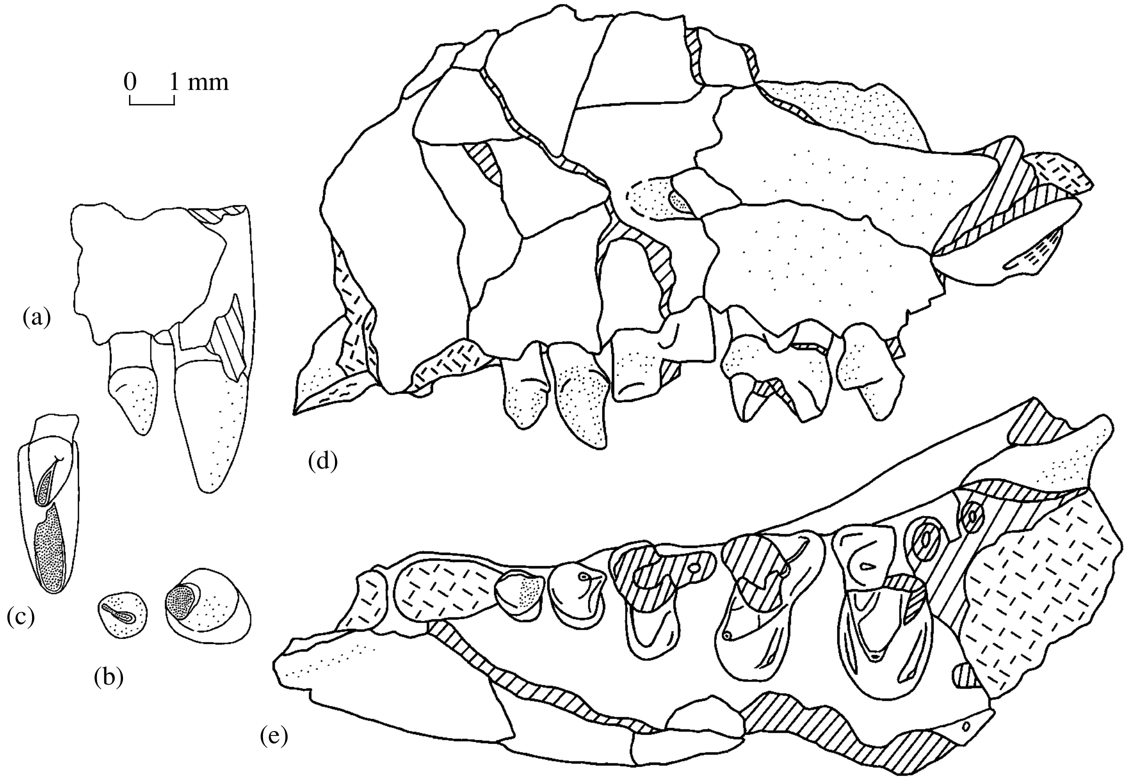


Fig. 54. *Zhigdenia nemegetica* sp. nov.: (a–c) specimen PIN, no. 3107/799, right maxillary fragment with C^1 and P^2: (a) general appearance, labial view, (b) C^1–P^2, occlusal view, and (c) C^1–P^2, posterior view; (d, e) holotype PIN, no. 3107/431, left maxillary fragment with P^2–M^2: (d) labial and (e) occlusal views; Tsagan-Khushu locality, Mongolia; Zhigden Member, Naran-Bulak Formation, Upper Paleocene.

Comparison and remarks. *Zhigdenia* differs from other genera of the Pantolestinae in the more reduced upper premolars. It is most similar to *Premontrelestes*, which is represented by *P. duchaussoisi* Smith, 2001 and cf. *Premontrelestes* sp. from the Early Eocene Prémontré locality in France (Smith, 2001). *Zhigdenia* differs from this genus in the absence of P^1, more reduced P^2–P^3, the absence of distinct ectoflexus and less pronounced hypocone of M^1 and M^2, the better developed conules and parastylar lobe of M^1 and M^2, and in the relatively wider M^3.

Zhigdenia nemegetica Lopatin, sp. nov.

Plate 14, figs. 3 and 4

Etymology. From the Nemegt Depression.

Holotype. PIN, no. 3107/431, left maxillary fragment with P^2–M^2; Mongolia, Tsagan-Khushu locality; Upper Paleocene, Naran-Bulak Formation, Zhigden Member.

Description (Fig. 54). The infraorbital foramen is small, located above the posterior region of P^4. The anterior base of the zygomatic arch is in line with the middle of M^2, while the posterior base is displaced substantially more distally than M^3.

C^1 is large, vertical, with a massive crown slightly pointed at the apex. A large oval wear facet is located on the posterolingual side of the crown.

P^2 is small, single-rooted, with a low, short, simple conical crown having a relatively small paracone, a weak metastyle, and a short postcrista connecting them. In a slightly worn tooth, the wear facet is restricted to the postcrista, but expands onto the whole of the posterolingual side of the paracone with wear.

P^3 is somewhat larger than P^2, double-rooted, with one labial and one lingual roots. Its paracone is high, pointed conical; the postcrista is short, the metastyle is distinct. The posterolingual projection is rudimentary, without a cusp. A weak precingulum and a better developed postcingulum are present.

P^4 has a large lingual projection, a weak parastylar projection, and a strong metastylar lobe. The protocone is relatively large, but low. The postcingulum is weak, in the shape of a short and narrow cingulum located distal to the apex of the protocone.

M^1 is much wider than P^4. The ectoflexus is undeveloped. The parastylar and metastylar lobes project only slightly. The metacrista is short, high, and sharp. The ectocingulum is distinct. The protocone is low, with a conical apex located at the same transverse line as the parastyle. The preprotocrista and postprotocrista are massive and long, reach conules. The paraconule and metaconule are small, but distinct, bifurcating. The precingulum is short and slender. The postcingulum is relatively narrow, with a small hypocone. M^2 is substantially more massive and wider than M^1, symmetrical (the apex of the protocone is at the same transverse line as the paracone), its structural elements (particularly, the postcingulum in the shape of a hypoconal shelf) are better pronounced. Judging from the alveoli, M^3 was wider than M^2.

Measurements, mm. Holotype: length × width P^2, 1.0 × 0.9; P^3, 1.2 × 1.2; P^4, 2.3 × 2.4; M^1, 2.3 × 3.2; M^2, ? × 3.95; length of the lingual lobe of P^4, 1.1; M^1, 1.4; M^2, 1.9; labial height of the crown of P^2, 1.3; and that of P^3, 1.9.

Specimen PIN, no. 3107/799, length × width of C^1, 1.6 × 1.3; P^2, 1.05 × 1.0; labial height of the crown of C^1, 2.8; and that of P^2, 1.4.

Remarks. *Zhigdenia* differs from other known pantolestines in the considerably reduced anterior upper premolars. The reduction of the posterolingual cusp of P^3 and in general small dimensions of P^1–P^3 are characteristic to the genera *Premontrelestes* and *Buxolestes* (Jaeger, 1970; Koenigswald, 1980; Pfretzschner, 1989; Smith, 2001) and some species of *Palaeosinopa* (such as *P. dorri*, see Dorr, 1977; Gingerich, 1980); however, in *Zhigdenia*, the upper premolars are reduced to a much greater extent. Thus, the upper cheek teeth of *Zhigdenia* combine primitive for Pantolestinae characters of molars (small hypocone, large conules, relatively well-developed parastylar lobe) with advanced specialization of anterior premolars (disappearance of P^1 and significant reduction and simplification of P^2 and P^3), which are connected with a shortening of the snout. The reduced P^1 and P^2 are characteristic of some Pantolesta that do not belong to Pantolestinae, for example, *Simidectes*, Paroxyclaenidae, and Ptolemaiidae (see Van Valen, 1965a; Crusafont-Pairo and Russell, 1967; Coombs, 1971; Simons and Bown, 1995); however, all the taxa listed have large P^3.

Material. In addition to the holotype, a right maxillary fragment with C^1 and P^2 (specimen PIN, no. 3107/799) from the type locality.

CHAPTER 4. ECOLOGICAL STRUCTURE OF EARLY PALEOGENE COMMUNITIES OF INSECTIVORE MAMMALS OF ASIA

Due to the high population number and relative accessibility, insects are a rich food source for land vertebrates, including mammals. Specialized consumers of this resource are commonly named entomophages. In mammals, they comprise taxa adapted to feeding predominantly or exclusively on insects and other land invertebrates. Members of the majority of mammal orders are facultative entomophages, except for specialized herbivores. Obligatory entomophages comprise insectivores, elephant shrews, tree shrews, many bats, and edentates, some rodents and carnivores, many marsupials and all strictly specialized taxa of various taxonomic position that feed on colonial insects.

Extant lipotyphlan insectivores are the second most efficient consumers of insect after birds. Insectivores occupy a special position in the biota as a unique group of carnivorous (zoophagous, faunivorous) vertebrates adapted for feeding on both overground and subterranean invertebrates. From the trophic point of view, they are carnivorous generalists, which easily change preferred prey type and, consequently, do not demonstrate tendencies to the change of population number or reproductive strategy depending on the density of particular species of food resources. Recent insectivore communities are arranged ecologically with reference to size and adaptive characteristics of species composing them.

Insectivores feed basically on animals. They consume various invertebrates, including earth worms, gastropods, wood lice, millepedes, spiders, ants, termites, various beetles, and other adult and larval insects. Semiaquatic insectivores hunt crustaceans, gastropods, bivalves, and aquatic insects as well as small fish. In addition, many insectivores consume small vertebrates and carrion, some use a greater or lesser proportion of plant food. The primary feeding type (omnivorous, entomophagous, malacophagous, worm-eating, flesh-eating) is usually clearly manifested in the structure of the dentition and, hence, can be reconstructed more or less reliability in extinct taxa.

Regarding the adaptive zone, insectivores are divided into terrestrial (overground), mostly aquatic, semiaquatic, aquatic–fossorial, fossorial, and arboreal (see Symonds, 2005). In diggers, it is possible to recognize semifossorial taxa, which get food from the upper layer of soil, and true fossorial (subterranean) taxa, which obtain food in underground burrows (see, e.g., Contreras and McNab, 1990; Nevo, 1995; Lacey et al., 2000; Borghi et al., 2002). These adaptations are clearly manifested in the structure of limbs, skull, and lower jaw. According to the principle of actualism, functional relationships between the locomotion and feeding type enable the mode of life of extinct insectivores to be reconstructed based on the structure of the dentition.

The interest in the community structure of insectivore mammals of the Early Paleogene of Asia is imposed by the necessity of paleoecological analysis of evolutionary factors of the groups under consideration. To date, three associations can be subject to ecological analysis (all in Mongolia): (1) Late Paleocene association from the Zhigden Member of the Naran-Bulak Formation of the Tsagan-Khushu locality, (2) Early Eocene association from the Bumban Member of the Naran-Bulak Formation of the same locality, and (3) Middle Eocene association from the Khaychin Formation from the Khaychin-Ula 2 locality. For short,

Table 46. Body mass of Paleogene Asian insectivores and insectivore-like mammals estimated based on the skull length according to the formula $Y = 3.68X - 3.83$, where Y is log of the body mass in g, X is log of the skull length in mm (Thewissen and Gingerich, 1989) or based on dimensions of M_1 according to the formula $Y = 1.628X + 1.726$, where Y is Ln of the body mass in g, X is Ln of product of L and W, L is length of M_1 in mm, W is width of M_1 in mm (Bloch et al., 1998). Extant analogues after Strel'nikov (1970) and Gureev (1979), body mass categories: 2–25 g (body mass category 1: *Sorex*, *Blarina*, and *Urotrichus*), 25–50 g (body mass category 2: *Crocidura* and *Scapanulus*), 50–100 g (body mass category 3: *Hylomys*, *Podogymnura*, and *Talpa*), 100–500 g (body mass category 4: *Desmana* and *Scapanus*), 500–1000 g (body mass category 5: *Erinaceus*), 1000–2000 (body mass category 6: *Potamogale*, *Solenodon*, and *Echinosorex*), >2000 (body mass category 7: no living analogues)

Species	Primary data	Estimated body mass, g	Extant analogues, body mass, g
1	2	3	4
Early Paleocene, Shanghuanian			
Carnilestes palaeoasiaticus	1 M_1: Wang and Zhai, 1995	35.1	25–50
Carnilestes major	2 M_1: Wang and Zhai, 1995	127.3–144.5 ($\Delta = 136$)	100–500
Prosarcodon lonanensis	1 M_1: McKenna et al., 1984	47.4	25–50
Late Paleocene, Nongshanian			
Archaeoryctes notialis	1 M_1: Zheng, 1979	451.1	100–500
Late Paleocene, Gashatan			
Sarcodon pygmaeus	1 M_1: Szalay and McKenna, 1971	73.3	50–100
Hyracolestes ermineus	1 M_1: original data	35.5	25–50
	1 M_1: Szalay and McKenna, 1971	38.1	
	1 M_1: Meng et al., 1998	26.8	
Gobigeolabis verigranum	1 M_1: original data	2.25	2–25
Jarveia minuscula	1 M_1: Averianov, 1995	5.3	2–25
	1 M_1: original data	5.6	
Praolestes nanus	3 M_1: original data	19.2–22.4 ($\Delta = 20.7$)	2–25
Praolestes maximus	3 M_1: original data	40.7–65.0 ($\Delta = 56.4$)	50–100
Voltaia minuta	1 M_1: original data	22.8	2–25
Asionyctia guoi	16 M_1: Missiaen and Smith, 2005	4.7–10.0 ($\Delta = 7.4$)	2–25
Archaeoryctes euryalis	skull: original data	~3650	>2000
Wanolestes lii	1 M_1: Huang and Zheng, 2002	34.3	25–50
Pinoryctes collector	1 M_1: original data	48.5	25–50
Early Eocene, Bumbanian			
Prosarcodon maturus	3 M_1: original data	177.0–238.5 ($\Delta = 200.0$)	100–500
Bumbanius rarus	1 M_1: Russell and Dashzeveg, 1986	21.5	2–25
	4 M_1: original data	19.2–26.0 ($\Delta = 21.7$)	
Oedolius perexiguus	2 M_1: Russell and Dashzeveg, 1986	4.1–8.2 ($\Delta = 6.2$)	2–25
	7 M_1: original data	5.1–8.7 ($\Delta = 6.9$)	
Edzenius lus	2 M_1: original data	6.6–11.1 ($\Delta = 8.9$)	2–25
Eosoricodon terrigena	2 M_1: original data	~4.5–5.0	2–25
Ordolestes ordinatus	1 M_1: Russell and Dashzeveg, 1986	51.5	50–100
	3 M_1: original data	48.3–60.8 ($\Delta = 53.0$)	
Changlelestes dissetiformis	4 M_1: Tong and Wang, 1993	12.7–17.6 ($\Delta = 15.5$)	2–25
Naranius infrequens	4 M_1: Russell and Dashzeveg, 1986	5.3–7.9 ($\Delta = 7.0$)	2–25
	18 M_1: original data	4.2–9.2 ($\Delta = 7.2$)	
Tsaganius ambiguus	1 M_1: Russell, Dashzeveg, 1986	3.1	2–25
	4 M_1: original data	3.1–4.1 ($\Delta = 3.6$)	
Bagalestes trofimovi	2 M_1: original data	2.8–3.5 ($\Delta = 3.15$)	2–25
Early Eocene, Arshantan			
Archaeoryctes borealis	1 M_1: Meng, 1990	144.5	100–500

Table 46. (Contd.)

1	2	3	4
Middle Eocene, Irdinmanhan			
Metasarcodon reshetovi	3 M_1: original data	776.7–798.3 (Δ = 785.8)	500–1000
Soricolestes soricavus	2 M_1: original data	8.73–9.15 (Δ = 8.9)	2–25
Pakilestes lathrius	1 M_1: Russell and Gingerich, 1981	7.25	2–25
Ernosorex jilinensis	1 M_1: Wang and Li, 1990	39.8	25–50
Zaraalestes russelli	1 M_1: Storch and Dashzeveg, 1997	34.8	25–50
Eogalericius butleri	10 M_1: original data	22.4–29.0 (Δ = 25.0)	25–50
Microgalericulus esuriens	1 M_1: original data	21.4	2–25
Eochenus sinensis	8 M_1: Wang and Li, 1990	52.5–85.5 (Δ = 66.5)	50–100
Ardynictis captor	2 M_1: original data	37.8–60.1 (Δ = 49.0)	25–50
Kennatherium shirense	5 M_1: original data	6.5–10.7 (Δ = 8.8)	2–25
Erlikotherium edentatum	7 M_1: original data	40.7–72.5 (Δ = 54.3)	50–100
Nuryctes gobiensis	1 M_1: original data	3.67	2–25
Late Eocene, Ergilian			
Ictopidium lechei	1 M_1: Sulimski, 1970	~40	25–50
	1 M_1: Tong, 1990	37.3	
Oligochenus grandis	1 M_1: Lopatin, 2005a	230.0	100–500
Ardynictis furunculus	1 M_1: PIN, no. 3109/246	287.0	100–500
Ergilictis reshetovi	1 M_1: Lopatin, 1997	193.7	100–500
Early Oligocene, Shandgolian			
Gobisorex kingae	2 M_1: Sulimski, 1970	~30	25–50
Zaraalestes minutus	5 M_1: Sulimski, 1970	23.4–30.0 (Δ = 26.6)	25–50
Neurogymnurus indricotherii	1 M_1: Lopatin, 1999	70.0	50–100
Exallerix hsandagolensis	1 M_1: McKenna and Holton, 1967	365.7	100–500
Exallerix manahan	1 M_1: Lopatin and Zazhigin, 2003	1049.3	500–1000
Palaeoscaptor acridens	8 M_1: Sulimski, 1970	57.2–60.8 (Δ = 59.5)	50–100
	1 M_1: Huang, 1984	46.9	
Amphechinus cf. *minimus*	1 M_1: Sulimski, 1970	~30	25–50
Amphechinus aff. *kansuensis*	1 M_1: PIN, no. 4567/13	87.5	50–100
Amphechinus rectus	1 M_1: Trofimov, 1960	193.7	100–500
	13 M_1: Huang, 1984	112.1–209.7 (Δ = 148.3)	
	1 M_1: PIN, no. 4567/12	373.0	
Amphechinus gigas	1 M_1: Lopatin, 2002c	620.0	500–1000
	1 M_1: Huang, 1984	705.8	
Scymnerix tartareus	skull: Lopatin, 2003e	~45–50	100–500
	1 M_1: Lopatin, 2003e	205.3*	
Didymoconus colgatei	3 M_1: Gromova, 1960	327.5	100–500
Didymoconus berkeyi	skull: Wang et al., 2001	1085	1000–2000
Didymoconus gromovae	3 M_1: Lopatin, 1997	120.1–145.1 (Δ = 136.8)	100–500
Didymoconus rostratus	3 M_1: Gromova, 1960	103.8–133.5 (Δ = 113.7)	100–500
Archaeomangus ulanhureensis	1 M_1: Lopatin, 1997	446.7	100–500
Late Oligocene, Tabenbulukian			
Exallerix gaolanshanensis	skull: Qiu and Gu, 1988	~270*	500–1000
	1 M_1: Qiu and Gu, 1988	805.7	
Tshotgoria shineusensis	1 M_1: Lopatin, 1997	388.8	100–500

* In *Scymnerix* and *Exallerix*, the skull is considerably shortened comparison to the majority of insectivores; therefore, it is better to make estimates based on dimensions of M_1 (although these may be overestimates because of the special elongated shape of the trigonid of M_1 in these hedgehogs).

Table 47. Quantitative distribution of insectivore mammal specimens from the Upper Paleocene Zhigden Member of the Naran-Bulak Formation of the Tsagan-Khushu locality (Mongolia)

Taxon	Number of specimens	Proportion, %
Sarcodon pygmaeus	1	4.35
Hyracolestes ermineus	1	4.35
Total number of Micropternodontidae (2 species)	2	8.7
Gobigeolabis verigranum	2	8.7
Total number of Geolabididae (1 species)	2	8.7
Praolestes nanus	5	21.7
Praolestes maximus	8	34.8
Total number of Praolestinae (2 species)	13	56.5
Jarveia erronea	2	8.7
Total number of Asionyctiinae (1 species)	2	8.7
Total number of Nyctitheriidae (3 species)	15	65.2
Total number of Soricomorpha (6 species)	19	82.6
Archaeoryctes euryalis	1	4.35
Total number of Didymoconidae (1 species)	1	4.35
Pinoryctes collector gen. et sp. nov.	1	4.35
Total number of Palaeoryctidae (1 species)	1	4.35
Zhigdenia nemegetica gen. et sp. nov.	2	8.7
Total number of Pantolestidae (1 species)	2	8.7
Sum (9 species)	23	100

they are designated below as the Zhigden, Bumban, and Khaychin associations.

The ecological structure of these associations is characterized through the analysis of their taxonomic structure, recognition of dominant groups, estimations of the size structure of communities (see Table 46), and morphoecological analysis of characters of particular species.

The reconstruction of the ecological structure of each association indicated above is given below.

4.1. Late Paleocene Zhigden Association

Table 47 shows the taxonomic composition and abundance of insectivores and insectivore-like mammals in the Zhigden Member of the Naran-Bulak Formation of the Tsagan-Khushu locality. The total number of specimens is 23, which does not allow for statistically valid analysis; it is only possible to indicate rare taxa represented by one to three specimens (such as Micropternodontidae, Geolabididae, Didymoconidae, Pantolestidae, and *Jarveia* from nyctitheriids) and more abundant taxa (the nyctitheriid genus *Praolestes*). The Soricomorpha prevail in both taxonomic diversity (6 species out of 9) and number of specimens (19 of 23, i.e., more than 80%) looks. Taking into account the data on nyctitheriids in the Upper Paleocene of Kazakhstan and China, it is possible to conclude that they dominated the adaptive zone of small insect-eaters of the Late Paleocene mammal fauna of Asia.

Members of the Zhigden Association are rather various in size (Table 46); body mass category 1 (with a body mass of 2–25 g) includes the geolabidid *Gobigeolabis verigranum* (ca. 2 g of body mass) and the nyctitheriids *Jarveia erronea* (ca. 10 g) and *Praolestes nanus* (ca. 20 g); body mass category 2 (25–50 g) includes the micropternodontid *Hyracolestes ermineus* (ca. 30 g); body mass category 3 (50–100 g) includes the micropternodontid *Sarcodon pygmaeus* (ca. 70 g) and the nyctitheriid *Praolestes maximus* (ca. 55 g). The didymoconid *Archaeoryctes euryalis* weighed more than 3500 g (among extant insectivores, *Tenrec ecaudatus* can reach about 3 kg in captivity, see Eisenberg and Gould, 1970). Judging from the tooth dimensions, *Pinoryctes collector* (ca. 50 g) and *Zhigdenia nemegetica* belong to body mass categories 2 and 3, respectively. Thus, Zhigden insectivore mammals show clear size differentiation, which is well-pronounced in both the entire group and particular families and genera. Actually, two micropternodontid species and nyctitheriids of the genus *Praolestes* belong to different body mass categories, while the nyctitheriids *Jarveia erronea* and *Praolestes nanus* that belong to the same body mass category differ in body mass by a factor of approximately two.

Gobigeolabis verigranum is one of the smallest Paleogene insectivores (Table 46). Its body mass is estimated as approximately 2.25 g. The smallest mammal known in the geological history is the Early Eocene geolabidid *Batodonoides vanhouteni* Bloch et al., 1998 (USA, Wyoming, dated ca. 53 Ma). Based on the size of M_1, the mass of adult *B. vanhouteni* was estimated as 1.3–2.04 g (Bloch et al., 1998; Holroyd and Strait, 2005). The body mass of Early Jurassic *Hadrocodium wui* from China is estimated based on the skull length (12 mm long) as approximately 2 g (Luo et al., 2001); however, this is probably a juvenile skull. Late Cretaceous *Batodon tenuis* weighed about 5 g (Wood and Clemens, 2001). The smallest living land mammals are shrews. The mean mass of *Suncus etruscus* is about 1.8–2.5 g (ranging from 1.2 to 2.7 g, the body length is 35–53 mm), *Sorex minutissimus* is 1.5–4.0 g of mass, and *Microsorex hoyi* is 2–4 g (Nowak, 1991; Fons et al., 1997; Smith et al., 2004). Newborn shrews weigh a little less than 1 g (Fons et al., 1997; Langer, 2002).

The small size is in general characteristic of Lipotyphla (especially of Soricomorpha) during the entire history of this group. Bloch et al. (1998) have shown that, at the Paleocene–Eocene boundary, lipotyphlans (with the body mass 1.3–53 g) were the smallest insectivorous placentals of North America, while the adaptive zone of larger entomophages was occupied by numerous "proteutherians." According to Holroyd and Strait (2005), the body mass of most of the Early Eocene (Wasatchian) North American Lipotyphla ranged from 7 to 20 g (i.e., was the same as in Recent insectivore associations), and small nyctitheriids with 7–10 g of body mass dominated, while the geolabidids *Batodonoides* spp. were the smallest. The data on the Early Paleogene of Asia are rather incomplete; however, the finds of *Gobigeolabis verigranum* and small Nyctitheriidae (Table 46) suggest that, at the Paleocene–Eocene boundary, geolabidids and nyctitheriids were also the smallest insectivores of this region.

The distribution of insectivores and insectivore-like mammals of the Zhigden Association over the adaptive zones was apparently as follows. *Gobigeolabis* and *Jarveia* were small specialized insect-eaters, like small extant shrews. The adaptive zone of large extant shrews was occupied by nyctitheriids of the genus *Praolestes*. The micropternodontids, with their predatory specialization in the structure of canines and molars, should probably be regarded as small carnivorous–insectivorous taxa, analogues of living erinaceids. The Didymoconidae were probably semifossorial carnivorous–insectivorous animals, which dug out most of the food consumed in loose upper layers of soil, using the snout and forelimbs (see Section 4.3). Based on the structure of the humerus and skull, palaeoryctids are usually regarded as highly specialized fossorial animals (Van Valen, 1966; Thewissen and Gingerich, 1989). Pantolestids are thought to have been semiaquatic animals feeding on mollusks and other aquatic invertebrates (Matthew, 1909; Van Valen, 1967; Dorr, 1977; Koenigswald, 1980). Certain structural features of canines suggest that some pantolestids could probably kill or immobilize their prey using venomous saliva, as does extant *Solenodon* (Clark, 1968; Fox and Scott, 2005). The cheek teeth structure in other taxa suggests the omnivorous adaptation (Coombs, 1971). Taking into account the prevalence of nyctitheriids and their adaptations, it is possible to conclude that the Zhigden Insectivore Association showed a normal distribution of adaptive zones, i.e., small terrestrial entomophages dominated, while accompanying small and large terrestrial carnivorous–insectivorous, semifossorial, fossorial, and semiaquatic taxa were less frequent.

Based on the structure of isolated astragali and calcanei from the Upper Eocene of England that were tentatively referred to the Nyctitheriidae, Hooker (2001) proposed that nyctitheriids included some arboreal taxa resembling the tree shrew. The arboreal mode of life is in general atypical for extant insectivores, except for the tenrecs *Echinops telfairi* and *Microgale longicaudata* (Symonds, 2005). Therefore, this statement requires additional evidence; at present, it seems inexpedient to regard any (or, the more so, all) nyctitheres as arboreal animals. Gingerich (1987) described elongated metatarsals tentatively referred to *Leptacodon rosei* Gingerich, 1987 from the Upper Paleocene of Wyoming (USA) which suggest the digitigrade and, possibly, saltatorial locomotion of this nyctitheriid.

Table 48. Quantitative distribution of insectivore mammal specimens from the Lower Eocene Bumban Member of the Naran-Bulak Formation of the Tsagan-Khushu locality (Mongolia)

Taxon	Number of specimens	Proportion, %
Prosarcodon maturus	11	5.8
Total number of Micropternodontidae (1 species)	11	5.8
Bumbanius rarus	23	12.1
Total number of Praolestinae (1 species)	23	12.1
Oedolius perexiguus	23	12.1
Edzenius lus	5	2.65
Total number of Asionyctiinae (2 species)	28	14.75
Eosoricodon terrigena	21	11
Total number of Eosoricodontinae (1 species)	21	11
Total number of Nyctitheriidae (4 species)	72	37.85
Ordolestes ordinatus	5	2.65
Total number of Plesiosoricidae (1 species)	5	2.65
Total number of Soricomorpha (6 species)	88	46.3
Naranius infrequens	80	42.1
Tsaganius ambiguus	20	10.5
Bagalestes trofimovi	2	1.1
Total number of Cimolestidae (3 species)	102	53.7
Sum (9 species)	190	100

4.2. Early Eocene Bumban Association

The Bumban Association is similar in taxonomic diversity to the Zhigden Association; however, it is represented in the collection by an eight times larger sample (190 specimens, see Table 48), which provides the possibility of statistical analysis. Taxonomically, it is dominated by soricomorphs (6 species out of 9), but cimolestids are most abundant (almost 54% of the specimens identified), particularly, *Naranius infrequens* (more than 42%).

Table 49. Quantitative distribution of insectivore mammal specimens from the Middle Eocene Khaychin Formation of the Khaychin-Ula 2 locality (Mongolia)

Taxon	Number of specimens	Proportion, %
Metasarcodon reshetovi	5	4.7
Total number of Micropternodontidae (1 species)	5	4.7
Asiapternodus mackennai	3	2.9
Total number of Apternodontinae (1 species)	3	2.9
Soricolestes soricavus	6	5.8
Total number of Soricidae (1 species)	6	5.8
Total number of Soricomorpha (3 species)	14	13.4
Eogalericius butleri	20	19
Total number of Erinaceidae (1 species)	20	19
Total number of Erinaceomorpha (1 species)	20	19
Ardynictis captor	24	22.9
Total number of Ardynictinae (1 species)	24	22.9
Khaichinula lupula	8	7.6
Total number of Didymoconinae (1 species)	8	7.6
Kennatherium shirense	18	17.1
Erlikotherium edentatum	18	17.1
Total number of Kennatheriinae (2 species)	36	34.2
Total number of Didymoconidae (4 species)	68	64.7
Nuryctes gobiensis	3	2.9
Total number of Palaeoryctidae (1 species)	3	2.9
Sum (9 species)	105	100

The proportions of body mass categories considerably differ from those of the Zhigden Association (Table 46). Body mass category 1 comprises the majority of taxa, including the cimolestids *Bagalestes trofimovi, Tsaganius ambiguus*, and *Naranius infrequens* and the nyctitheriids *Eosoricodon terrigena, Oedolius perexiguus, Edzenius lus*, and *Bumbanius rarus*. This group is clearly differentiated; *Bagalestes* (ca. 3 g), *Tsaganius* (ca. 3.5 g), and *Eosoricodon* (ca. 4.5–5 g) are close to the lower limit of the group; *Oedolius* (ca. 6–7 g), *Naranius* (ca. 7 g), and *Edzenius* (ca. 9 g) are slightly larger, whereas *Bumbanius* is substantially larger (ca. 20 g). Body mass category 2 (25–50 g) is absent from the sample; however, this is compensated by the presence of *Bumbanius rarus* (ca. 19–26 g) and *Ordolestes ordinatus* (ca. 48–61 g, body mass category 3), the mass ranges of which partially overlap the values included in group 2. Body mass category 4 includes the micropternodontid *Prosarcodon maturus* (ca. 200 g).

Apparently, *Eosoricodon, Oedolius*, and *Edzenius* occupied the adaptive zone of small shrews, while *Bumbanius* corresponds to the zone of large shrews. The adaptive zone of carnivorous–insectivorous taxa showing tendency to predation was occupied by *Ordolestes* and *Prosarcodon* in the smaller and larger size classes, respectively. The adaptations of cimolestids are not completely clear; judging from the structure and wear pattern of teeth, they were small, unspecialized predatory or carnivorous–insectivorous animals (Lillegraven, 1969; Kielan-Jaworowska et al., 1979); relatively large taxa were likely omnivorous (Eberle, 1999); some were probably adapted for arboreal mode of life (see Szalay and Decker, 1974; Szalay, 1977; Kielan-Jaworowska et al., 2004). In addition, there were large, probably semiaquatic, pantolestids (see Russell and Dashzeveg, 1986).

Thus, the Bumban Insectivore Association was also dominated by small terrestrial entomophages supplemented by relatively large terrestrial carnivorous–insectivorous, small predatory, and large semiaquatic species.

A relatively high taxonomic diversity and large number of specimens of endemic genera of Cimolestidae in the basal Eocene of Mongolia are distinctive faunal characteristics of the Bumbanian Asian Land Mammal Age.

4.3. Middle Eocene Khaychin Association

The Khaychin Association shows the same taxonomic diversity as the Zhigden or Bumban associations, and available sample is quite representative statistically (105 specimens, see Table 49). The taxonomic composition considerably differs from those of earlier associations, it is dominated by the Didymoconidae (4 species of 9) rather than soricomorphs (3 species); however, the Erinaceidae, Soricidae, and Apternodontidae are also recorded. The Plesiosoricidae, Cimolestidae, and Pantolestidae are absent, while the Micropternodontidae and Palaeoryctidae are present. The Didymoconidae prevail (composing ca. 65% of specimens), and the most abundant species is *Ardynictis captor* (ca. 23%); however, the hedgehog *Eogalericius butleri* shows an only slightly lower abundance (19%) and exceeds in number the didymoconids *Kennatherium shirense* and *Erlikotherium edentatum* (ca. 17% each).

The analysis of distribution of taxa over body mass categories (Table 46) shows a relatively small proportion of group 1, represented by *Nuryctes gobiensis* (ca. 3.5 g), *Soricolestes soricavus* (ca. 9 g), and *Kennatherium shirense* (ca. 9 g). The body mass categories 2 and 3 include *Eogalericius butleri* (ca. 25 g), *Asiapternodus mackennai* (presumably ca. 25 g), *Ardynictis captor* (ca. 50 g), *Erlikotherium edentatum* (ca. 40–70 g), and *Khaichinula lupula* (presumably ca. 100 g). The large *Metasarcodon reshetovi* probably weighed about 800 g (body mass category 5).

Soricolestes was similar in size to extant *Sorex araneus* L. and probably occupied a similar ecological niche of a small entomophage. Apparently, *Soricolestes* acquired a primitive variant of the unique masticatory mechanism characteristic of extant Soricidae, which Zaitsev (2005) named horizontal cutting (or grating); this mechanism allows shrews to hunt relatively large and mobile prey.

The heavily worn zalambdomorph teeth of *Asiapternodus* are evidence for feeding on soil invertebrates and, hence, a semifossorial mode of life. The large size of the infraorbital canal indicates that *Asiapternodus* had a sensitive proboscis (see Thewissen and Gingerich, 1989; Lopatin, 2003b), which is usually well-developed in semifossorial, fossorial, and semiaquatic insectivores. Judging from the structure of the jaws and teeth, *Eogalericius* was probably an ecological analogue to the extant shrew-hedgehog *Hylomys*. *Metasarcodon reshetovi* is the latest sarcodontine, which reached the peak of predatory specialization of teeth and relatively large size. The structure of anterior teeth of *Nuryctes* (and probably some other palaeoryctids) suggests the semiaquatic–fossorial mode of life, resembling that of extant desmans.

Certain characters of the postcranial skeleton of the Didymoconinae (such as the short, massive forelimbs combined with relatively weak hind limbs, massive clavicle, elongated olecranon, long and massive ungual phalanges of the manus) suggest digging (Gromova, 1960) or even a specialized fossorial adaptation of these animals (Wang et al., 2001). The strongly developed crests and tubercles of the humerus of *Kennatherium* are probably evidence of well-pronounced fossorial specialization, as is characteristic of some extant Insectivora (Gureev, 1979; Özkan, 2004; Salton, 2005). The short and widened humerus of *Ardynictis captor* (Figs. 38a–38e) is even better adapted for digging than in Didymoconinae and Kennatheriinae. The cranial structure, which is known in both the Oligocene Didymoconinae and Paleocene–Eocene Ardynictinae, shows a number of characters presumably related to the fossorial mode of life (Gromova, 1960; Meng et al., 1994a; Lopatin, 2001a; Wang et al., 2001). This primarily concerns the general skull pattern, with a broad, massive snout and widened and flattened posterior region. The particular structure of the middle ear region, with increased epitympanic sinuses (Meng et al., 1994a), is probably associated with the sensitivity to low-frequency sounds which is characteristic of subterranean animals (Wang et al., 2001).

The cheek teeth of the Didymoconidae are functionally similar to the teeth of some zalambdodont insectivores, which feed on worms and insects. The pair of the upper and lower tooth rows forms a system of massive transverse crests and blunt cusps, which perform the crushing–cutting function (thus, the effect on a food object resembles chopping). The heavy wear of the cheek teeth, which is usually seen in the Didymoconidae, is probably attributable to soil particles inevitably getting into the mouth along with food objects extracted from the ground.

On the other hand, the features marked in the structure of forelimb bones of Didymoconidae are less pronounced than in highly specialized burrowers leading a subterranean mode of life (Gromova, 1960, p. 72). The humerus of Didymoconidae is similar in structure to that of digging mammals that are so-called terrier-type burrowers or scratch-diggers (see Campbell, 1938; Reed, 1954; Lessa, 1990). The humeri of this type actually retain the same structural pattern of the proximal region as in surface dwelling animals, having a rounded section of the diaphysis and a widened distal region, usually with an increased lateral epicondyle. This humeral structure is characteristic of semifossorial animals and, only in the extremely specialized state, of entirely fossorial taxa, such as the Chrysochloridae or *Notoryctes* (Reed, 1954; Lessa, 1990). The large canines, well-developed zygomatic arches, robust symphysis, massive horizontal ramus, and relatively weakly developed articular and angular processes of the lower jaw of Didymoconidae are atypical of specialized fossorial insectivores but are characteristic of predators (Carnivora, Creodonta, Mesonychia) and some omnivorous Lipotyphla (for example, *Tenrec ecaudatus*). Thus, it seems plausible that the Didymoconidae were carnivorous–insectivorous semifossorial animals digging most of their food out of the upper soil layers with the snout and forelimbs (Gromova, 1960) and producing deep burrows. The Didymoconinae (including *Khaichinula*, judging from the structure of its ulna, see Fig. 41) were probably characterized by a relatively more surface dwelling mode of life, while *Ardynictis* and *Kennatherium* showed a more fossorial mode of life, developed to a greater or lesser extent.

Erlikotherium edentatum deserves special consideration. The completely reduced incisors, massive, blunt canines with a periapical wear facet on the anterior side of the crown, the long postcanine diastema, the reduced cheek teeth row, which is heavily worn in the course of ontogeny, and the posteriorly curved, acute-angled coronoid process of the lower jaw are evidence of the unique adaptations of *Erlikotherium*. It may be assumed that this entire character set suggests a functionally edentate animal. The completely reduced lower incisors are atypical of insectivores and mammals in general, except for edentates and palaeanodonts. However, the Didymoconidae have small incisors showing a tendency to reduction; therefore, it seems plausible that they could have completely disappeared with further development of respective specialization of their dentition. The large periapical wear facet on the anterior side of the lower canine crown (instead of a facet on the posterior side, as is usually observed in mammals) is probably attributable to the fact that, in *Erlikotherium*, the lower canine rubbed against the upper canine posteriorly, as in sloths, rather than anteriorly, as in the majority of mammals, including ernanodontids and epoicotheriids (see Radinsky and Ting, 1984). In this case, the periapical region of the lower canine, as it occluded with the upper canine, could be worn anteriorly, while the posterior side remained intact, as is observed in *Erlikotherium*. The other possible explanation of such a facet is occlusion with the increased posterior upper incisor combined with normal canine occlusion (with the lower canine anterior to the upper canine). However, it is highly improbably that a complete reduction of the lower incisors was combined with the increased upper incisors. In addition, this would have meant that the upper and lower canines did not occlude, which disagrees with the presence of massive canines. Therefore, I am inclined to accept the first explanation.

A similar structure of the anterior region of the lower jaw is observed in *Melaniella timosa* Fox, 1984 from the Upper Paleocene of Canada, which was referred to ?Palaeanodonta incertae sedis (Fox, 1984a) or Pholidota incertae sedis (McKenna and Bell, 1997). The similarity is the absence of incisors, the presence of large canines, long diastema between the canine and anterior premolar, double-rooted premolariform anterior premolar, long symphysis, and a dorsolabially open mental foramen located slightly ahead of the anterior premolar. These animals are also similar in size, but *Erlikotherium* differs from *Melaniella* in the more massive jaw and the presence of the paraconid on the anterior premolar.

The short coronoid process of the lower jaw is characteristic of early edentates and palaeanodonts, while in sloths it is often similar in shape, looking like a narrow triangle curved posteriorly at the apex (Radinsky and Ting, 1984).

It can be assumed that the functional edentate pattern of *Erlikotherium* was associated with an adaptation to feeding on colonial insects (termites, ants) and their larvae, as in Palaeanodonta (see Fox, 1984a, p. 1337). The canines could have been used for breaking open insect shelters. The incisors disappeared to make room between the canines for the tongue, which could have functioned as a prey capturing tool. The cheek teeth were separated from the canine by a large diastema. They were rapidly worn and became a series of flat surfaces suitable for grinding small food objects.

It is possible to conclude that the Khaychin Insectivore Association is characterized ecologically by the prevalence of medium-sized semifossorial taxa supplemented by terrestrial carnivorous–insectivorous and small aquatic–fossorial taxa. An important point is that, among the Lipotyphla, members of the Recent families Erinaceidae and Soricidae prevail quantitatively. Probably, the significant change in the ecological structure of the community of insectivore mammals occurred against the background of a global fall in temperature in the Middle Eocene (which started at the Early–Middle Eocene boundary, 50–48 Ma) and accompanying biotic changes (see Zachos et al., 2001; Morley, 2003).

Thus, it is possible to conclude that, in the Paleocene and the beginning of the Eocene of Asia, the major insectivorous ecological niches were occupied by small insectivore-like placentals and primitive soricomorphs. The situation began to change in the Middle Eocene, when the Recent groups of hedgehogs, moles, and shrews appeared, which occupied the dominant position by the Oligocene epoch.

CHAPTER 5. EVOLUTION OF INSECTIVORA IN THE PALEOGENE OF ASIA

5.1. Soricomorpha

The early primary radiation of soricomorphs is evident from the wide diversity of primitive Paleogene taxa, many of which show highly specialized dentition. In the Early Paleogene of Asia, the families Micropternodontidae, Geolabididae, Nyctitheriidae, Soricidae, Plesiosoricidae, and Apternodontidae are recorded.

5.1.1. Micropternodontidae

Van Valen (1967) was the first to indicate the similarity between *Sarcodon* and *Micropternodus* and based on this placed *Sarcodon* in the family Micropternodontidae. Robinson (1968) came to a similar conclusion and placed (with caution) *Sarcodon* in the Micropternodontinae. Szalay and McKenna (1971) proposed that this similarity is a result of convergent development and assigned *Sarcodon* and *Hyracolestes* to Deltatheridiidae. The cranial study of *Prosarcodon lonanensis* supported the assignment of *Prosarcodon* and *Sarcodon* to Micropternodontidae; however, Butler (1988) and MacPhee and Novacek (1993) were in doubt about placing these genera in Soricomorpha and even in Lipotyphla. McKenna and Bell (1997) referred *Sarcodon, Prosarcodon, Hyracolestes, Micropternodus, Clinopternodus, Sinosinopa*, and *Carnilestes* to the Micropternodontidae.

Meng et al. (1998) were in doubt about the formula of cheek teeth in *Sarcodon* and *Prosarcodon* ($P^4/_4M^2/_2$), which was established by Szalay and McKenna (1971) and accepted by McKenna et al. (1984). They proposed that large P^4 and P_4 of *Sarcodon* and *Prosarcodon* should be regarded as M^1 and M_1, respectively. However, in the description of the upper teeth of *S. minor* and *?S. pygmaeus* Meng et al. named the typical transversely elongated sarcodont molar as M^1, as did Szalay and McKenna. In addition, Meng et al. did not provide evidence for the presence of three molars in *Sarcodon* and *Prosarcodon*, except for a remark that such variant ($P^3/_3M^3/_3$) cannot be rejected (Meng et al., 1998, p. 160).

The lower jaw fragment of *Sarcodon pygmaeus* from Tsagan-Khushu that is described above (specimen PIN, no. 3104/771) has a talonid of P_4, alveoli of M_1, and almost complete M_2. This specimen shows that the actual formula of the cheek teeth of *Sarcodon* (and presumably all sarcodontines) is $P^4/_4M^2/_2$. The same formula was established for *Prosarcodon lonanensis* (McKenna et al., 1984). *Hyracolestes* is morphologically most similar to *Sarcodon* and *Prosarcodon* and should be regarded as their nearest relative. It probably represents a special lineage within the Sarcodontinae (Lopatin and Kondrashov, 2004).

Early Paleocene *Carnilestes* (Wang and Zhai, 1995) should be regarded as the earliest sarcodontine. It is similar to *Prosarcodon* in the presence of the precingulum and weakly developed hypoconal shelf on the upper molars and the precingulid on the lower molars. *Carnilestes s*hows certain primitive eutherian characters, such as weakly widened upper molars with widely spaced paracone and metacone.

Metasarcodon is the latest genus of the Sarcodontinae (end of the Early–Middle Eocene). It comprises the largest and most advanced sarcodontines with clearly pronounced predatory adaptations. Most of the characters (including the well-developed metastylar crest, hypoconal shelf, and paracristid) show that *Metasarcodon* was most similar to *Sarcodon*. However, the presence of the precingulid suggests that *Metasarcodon* should not be regarded as a direct descendant of the *Sarcodon* lineage. The two genera are originate from a common ancestor. The secondarily narrowed upper molars of *Metasarcodon* resemble those of the highly specialized genus *Micropternodus* from the Upper Eocene and Oligocene of North America (Russell, 1960, text-fig. 2).

Thus, Early Paleogene *Carnilestes, Prosarcodon, Sarcodon, Metasarcodon*, and *Hyracolestes* belong to a special group of Asian micropternodontids ranked as subfamily (Sarcodontinae) which clearly differs from Micropternodontinae in the absence of $M^3/_3$ and hypoconal shelf on P^4 and M^2. The subfamily Micropternodontinae comprises *Micropternodus* and *Clinopternodus* from the Paleogene of North America and *Sinosinopa, Bogdia*, and *Hsiangolestes* from the Eocene of Asia. *Carnilestes* had all main characters of sarcodontines in the Early Paleocene; therefore, the two micropternodontid subfamilies probably diverged even earlier.

Carnilestes is distinguished from the other Sarcodontinae by its primitiveness, *Hyracolestes* differs in the special structure of talonids of the lower molars (small talonid basin and reduced entoconid), while *Prosarcodon, Sarcodon*, and *Metasarcodon* probably belong to the same phylogenetic group, within which *Sarcodon* and *Metasarcodon* are related more closely.

The Sarcodontinae demonstrate the earliest case of the loss of the last molars in Lipotyphla.

The Micropternodontidae apparently appeared in Asia in the Early Paleocene and penetrated into North America in the Eocene. In the Paleocene to the early half of the Middle Eocene of Asia, the Sarcodontinae and Micropternodontinae occupied the niche of small and medium-sized carnivorous–insectivorous taxa, while in North America, descendants of a Micropternodontinae lineage became completely subterranean insectivores, which survived to the Oligocene, i.e., existed for a considerably longer time than their Asian relatives.

5.1.2. Geolabididae

The Geolabididae were originally introduced as a subfamily of Erinaceidae that comprised three genera: *Geolabis* (= *Metacodon*), *Myolestes,* and *Hypacodon* (McKenna, 1960). A little later, *Hypacodon* was regarded as a junior synonym of *Centetodon* (McKenna et al., 1962). Subsequently, *Geolabis* was also included in *Centetodon* as a junior synonym (Setoguchi, 1978; Lillegraven et al., 1981), while the name *Myolestes* Matthew, 1909 (a junior homonym of the insect *Myolestes* Bréthes, 1905) was replaced by *Marsholestes* (McKenna and Haase, 1992).

Before the revelation of the synonymy of *Centetodon, Geolabis*, and *Metacodon*, they were placed in different groups of Insectivora. *Centetodon* was usually assigned to Nyctitheriidae (Simpson, 1945); *Metacodon* was placed in Erinaceidae (Patterson and McGrew, 1937; Galbreath, 1953; Clark, 1966) or a distinct family, the Metacodontidae (along with *Plesiosorex* and *Meterix*, see Butler, 1948); and *Geolabis* was referred to as Insectivora incertae sedis (Simpson, 1945; Saban, 1958). Saban (1958) believed that *Geolabis* could have belonged to Soricoidea. As the subfamily Geolabidinae was established, some researchers proposed that it should be placed in Erinaceidae (McKenna, 1960; Russell, 1960; Clark, 1966). Van Valen (1967) assigned the subfamily Geolabidinae to Adapisoricidae (Erinaceoidea), Robinson (1968) included it in Nyctitheriidae, Gureev (1979) indicated that it is similar to Tenrecidae. Butler (1972) was the first to assign with certainty geolabidids to Soricomorpha and ranked them as family, which was subsequently accepted by other researchers (McKenna, 1975a; Novacek, 1976; Sigé, 1976). Butler believes that the Geolabididae belong to a branch of soricomorphs that gave rise to the families Nesophontidae and Solenodontidae (Butler, 1972, 1988; see also Seiffert and Simons, 2000; Whidden and Asher, 2001).

Maastrichtian *Batodon tenuis* Marsh, 1892 is presumably the earliest geolabidid and even the earliest lipotyphlan (McKenna and Bell, 1997; Benton, 1999). It was considered to belong to Palaeoryctidae (Van Valen, 1967; Kielan-Jaworowska et al., 1979; Butler, 1988; Storer, 1991) or Cimolestidae (Didelphodontinae: Lillegraven, 1969; Clemens, 1973; Cimolestidae: Kielan-Jaworowska et al., 2004) or to be related to

Nyctitheriidae (Szalay and Decker, 1974). McKenna was the first to propose that *Batodon* probably belongs to Geolabididae in 1974 (see Novacek, 1976; Bown and Schankler, 1982). However, there is a significant time gap between the Late Cretaceous *Batodon* and the earliest Paleogene North American geolabidids, i.e., *Centetodon patratus* and *C. neashami* from the Early Eocene of Wyoming (Bown and Schankler, 1982; Butler, 1988). Taking into account some differences in dental structure between *Batodon* and Paleogene Geolabididae, this genus is assigned in some recent studies to Placentalia incertae sedis (see Wood and Clemens, 2001; Hunter and Archibald, 2002; Polly et al., 2005).

Gobigeolabis verigranum described above is referred to Geolabididae based on close similarity in the structure of upper and lower cheek teeth to members of the genera *Centetodon* and *Batodonoides*. In the shape of P_4–M_2 and P^4 *Gobigeolabis* is similar to *Centetodon* (see McKenna, 1960; Setoguchi, 1978, text-fig. 10a; Lillegraven and Tabrum, 1983, text-figs. 3–5), but differs in the wider P^3–M^2. The poorly developed postcingulum (which does not form a hypoconal shelf) and undivided lingual root of the upper molars are characters that are primitive for Geolabididae and observed in Wasatchian *Batodonoides vanhouteni* (Bloch et al., 1998). The upper molars of Early Eocene *Centetodon patratus* and *C. neashami* have not been recorded. In the Middle Eocene *C. pulcher* and *C. bembicophagus*, the lingual root is only slightly doubled or not doubled, in contrast to that of later members of this genus (Storer, 1984, 1995; Russell and Dashzeveg, 1986).

Gobigeolabis shows a number of advanced characters compared to *Batodonoides*: the large lingual lobes of its P^3 and P^4, narrow stylar shelf and reduced conules of M^1 and M^2, shallow ectoflexus and small parastylar wing of M^2, long talonid of P_4, and relatively shorter trigonid of M_1 and M_2.

The considerably transversely expanded upper molars of *Gobigeolabis verigranum* with a weak postcingulum are similar in shape and structure to M^1 and M^2 of *Batodon tenuis* (Lillegraven, 1969; Storer, 1991, text-fig. 10K), but differ in the smaller stylar lobes and conules. *Batodon* is more similar in upper molar structure to *Gobigeolabis* than to *Batodonoides* and *Centetodon*. This does not necessarily mean that *Gobigeolabis* is an intermediate taxon connecting *Batodon* with Eocene North American Geolabididae; however, this gives additional evidence for the assignment of *Batodon* to Soricomorpha.

Thus, *Gobigeolabis verigranum* is the earliest Paleogene member of the family. The fact that it was found in the Upper Paleocene of Mongolia suggests that the Geolabididae could have emerged in Asia, if *Batodon* does not belong to this family (see Butler, 1988; Wood and Clemens, 2001). The alternative possibility is that geolabidids dwelt in Asia during the Paleocene, i.e., the time when they are not recorded in North America. If this is the case, Early Eocene North American geolabidids can also be regarded as descendants of immigrants from Asia. Judging from the structure of the upper cheek teeth, *Gobigeolabis* is too specialized to be related to the origin of the genera *Centetodon* and *Batodonoides.* It probably appeared as a result of earlier adaptive radiation of geolabidids in Asia.

5.1.3. Nyctitheriidae

Praolestes nanus was originally described based on a lower jaw fragment from the Upper Paleocene Gashato Formation (Mongolia) and tentatively referred to Leptictidae (Matthew et al., 1929). In a brief discussion, the authors of the original description noted that *Praolestes* was probably a leptictid, although its M_1 in is more similar in structure to P_4 of Leptictidae. Van Valen (1967) placed *Praolestes* in the subfamily Geolabidinae without comment. Szalay and McKenna (1971) redescribed the holotype of *Praolestes nanus*, assigned it to Zalambdalestidae, and proposed that it probably descended from Late Cretaceous *Zalambdalestes*. Russell and Dashzeveg (1986) indicated that and *Bumbanius* are similar in dental morphology, but did not place with certainty *Praolestes* in Nyctitheriidae. Carroll (1988) referred *Praolestes* to Anagalida fam. indet., while McKenna and Bell (1997), as Leptictida incertae sedis. Ting (1998) included *Praolestes* in Zalambdalestidae, whereas Meng et al. (1998) regarded it as "Insectivora."

The holotype of *Praolestes nanus* contains three cheek teeth, which were originally identified as P_3, P_4, and M_1, and two alveoli anterior to P_3 (Matthew et al., 1929). Szalay and McKenna (1971) also determined the teeth preserved as P_3, P_4, and M_1, while two anterior alveoli attributed to double-rooted P_2. Saban (1958) believed that *Praolestes* is very similar to *Diacodon* and *Prodiacodon* in the structure of P_4. He wrote that P_4 of *Praolestes* is most similar to P_3 of Leptictidae in the presence of a weak unicuspid talonid and two small supplementary cuspules of the trigonid (paraconid and metaconid), while M_1 of *Praolestes* is very similar to P_4 (Saban, 1958, pp. 875, 876). Thus, Saban believed that P_4 of the holotype is in fact P_3, while M_1 is P_4. This point of view probably inclined McKenna and Bell (1997) to placed *Praolestes* in Leptictida.

The specimens described above from Tsagan-Khushu suggest the following (see Kondrashov et al., 2004a). In the tooth rows with M_1–M_3 and with M_1 and M_2 (specimens PIN, nos. 3104/360, 361, and 427), the first molar (M_1) is identical to the posterior tooth preserved in the holotype; thus, this is M_1 rather than P_4, as was proposed by Saban. This is supported by the structure of teeth in an almost complete dentary with P_1–M_2 (specimen PIN, no. 3104/427), in which P_3–M_1 are identical to those of the holotype. The positions of the mental foramina in specimen PIN, no. 3104/427 are the same as in the holotype, and the structure of the anterior teeth shows with certainty that four premolars were present. In another dentary (specimen PIN, no. 3104/360), all alveoli located anterior to M_1 are preserved. Their number and structure enables to reconstruct the formula of lower teeth of *Praolestes* as $I_3C_1P_4M_3$. The dental morphology, including the semimolariform structure of the last premolar, shows that *Praolestes* does not belong to Leptictida.

Szalay and McKenna (1971) assigned *Praolestes* to Zalambdalestidae, but Kielan-Jaworowska (1984) indicated that the last premolar of *Praolestes* is too small and the trigonid of M_1 is compressed to a lesser degree than in Zalambdalestidae. Wang (1995) did not include *Praolestes* in Zalambdalestidae and marked that the material is too scarce to perform a trustworthy comparison. In fact, as has been shown by us using more complete material, *Praolestes* considerably differs from Zalambdalestidae, primarily in the structure of incisors (anterior incisor is not procumbent), the large canine, the absence of a diastema, less longitudinally compressed trigonids with a better developed paraconid and nonreduced M_3 with a posteriorly projecting hypoconulid (Kondrashov et al., 2004a). *Praolestes nanus* and *P. maximus* show characters typical for Nyctitheriidae: (1) the trigonids of lower molars are columnar, and the constriction between the trigonid and talonid is well-pronounced; (2) the hypoconid is relatively high; (3) the sagittal plane of the lower tooth row deviates somewhat lingually in relation to the sagittal plane of the horizontal ramus of the lower jaw; (4) the trigonid is at most twice as high as the talonid; (5) the hypoconulid is small but distinct; (6) the structure of the ascending ramus (see McKenna, 1968; Sigé, 1976); and (7) the positions of the mental foramina (see McKenna, 1968; Sigé, 1976; Russell and Dashzeveg, 1986; Nessov, 1987; Averianov, 1995). The structure of the upper molars referred to *P. nanus* confirms the assignment of *Praolestes* to Nyctitheriidae (Kondrashov et al., 2004a).

The genus *Jarveia* was originally placed in "Proteutheria" (Nessov, 1987). Averianov (1995) redescribed it as a nyctitheriid insectivore. McKenna and Bell (1997) assigned this genus along with *Hyracolestes* and *Sarcodon* to Micropternodontidae. However, *Jarveia* lacks synapomorphies in common with micropternodontids or characters typical for this family, such as considerably or completely reduced M_3 and very high trigonids of lower molars. On the contrary, all characters of the upper and lower teeth of *Jarveia* are typical for nyctitheriids (Averianov, 1995; Kondrashov et al., 2004a).

The structure of the upper molars of *Praolestes* and *Jarveia* is relatively primitive and closer to that of *Leptacodon* than of *Saturninia* (see Krishtalka, 1976b; Sigé, 1976). The structure of the labial region of P^4 is not known in *Praolestes*; however, P^4 of *Jarveia erronea* differs from that of all other nyctitheriids (except for *Asionyctia*) in the absence of metacone. The Asian nyctitheriid *Bayanulanius* of the same age is rather similar to *Praolestes* and *Jarveia* in the shape of upper molars. The most important difference between Paleocene Asian nyctitheres (*Praolestes, Asionyctia, Bayanulanius*, and *Jarveia*) and all North American and European taxa as well as later Asian taxa is the shape of upper molars; they are short and wide, with a weak hypoconal shelf. However, most of the characters of upper cheek teeth of Paleocene Asian Nyctitheriidae are plesiomorphic. Thus, the similarity in the upper molars of *Praolestes, Jarveia, Asionyctia*, and *Bayanulanius* may result from the general primitive evolutionary level of Late Paleocene Asian Nyctitheriidae rather than from their phylogenetic affinity. Moreover, it is possible to divide Asian nyctitheres into four groups based on the structure of the lower cheek teeth: Nyctitheriinae (*Yuanqulestes*), Praolestinae subfam. nov. (*Praolestes* and *Bumbanius*), Asionyctiinae (*Asionyctia, Voltaia, Oedolius, Edzenius, Bayanulanius*, and *Jarveia*), and Eosoricodontinae (*Eosoricodon*).

The taxonomic position and composition of Nyctitheriidae were repeatedly revised (for review, see Robinson, 1968; Sigé, 1976). Originally, *Nyctitherium* was assigned to Chiroptera (Marsh, 1872), then, to Talpidae (Matthew, 1909). Subsequently, two points of view concerning the taxonomic position of nyctitheriids coexisted for a long time; some authors believed that they are primitive members of Erinaceoidea (Repenning, 1967; Van Valen, 1967; McKenna, 1968; Robinson, 1968; Cray, 1973; Crochet, 1974), whereas others assigned them to Soricoidea (Simpson, 1945; Saban, 1954, 1958; Butler, 1972; McKenna, 1975a; Novacek, 1976; Sigé, 1976; Gureev, 1979); finally, the second point of view became generally accepted.

Based on the structure of isolated astragali and calcanei from the Upper Eocene of England that were tentatively referred to the Nyctitheriidae, Hooker (2001) proposed that some nyctitheriids were arboreal taxa resembling the tree shrew. As a result, the Nyctitheriidae were excluded from Soricomorpha and placed in Archonta along with Primates, Dermoptera, and Scandentia (see Hooker, 2001; Averianov, 2003). This taxonomic decision seems ill-founded because the limb bones described by Hooker were not associated with taxonomically identified fossils. Although it is possible to suggest that nyctitheriids could have comprised several family-rank groups, there is no doubt that all of them belong to the same branch of Soricomorpha. It is usually supposed that nyctitheriids include the ancestors of Soricidae (Sigé, 1976; Reumer, 1987; Lopatin, 2002c, 2005a, 2005b; see Section 5.1.4).

In the original concept of Simpson (1928), the family Nyctitheriidae included *Nyctitherium* and *Centetodon*, the type genus of Geolabidinae (and several genera that were regarded later as synonyms or transferred to other mammal group); subsequently, *Micropternodus* (= *Kentrogomphios*: White, 1954) was added. Robinson (1968) divided the Nyctitheriidae into three subfamilies: Nyctitheriinae (comprising the genera *Nyc-*

titherium, Leptacodon, and *Saturninia*), Geolabidinae (*Centetodo*n), and Micropternodontinae (*Micropternodus, Clinopternodus*, and, in question, *Sarcodon*). Subsequently, Geolabidinae and Micropternodontinae were ranked as distinct families (see above), while the concept of Nyctitheriinae sensu Robinson, 1968 was transformed into a new concept of Nyctitheriidae, which was developed in the final form by Sigé (1976), who divided the family into two subfamilies, Nyctitheriinae and Amphidozotheriinae. The generic composition of the family rapidly expanded due to the description of new taxa from Europe, North America, and Asia (see McKenna and Bell, 1997). Butler (1988) believed that nyctitheriids are artificial association and restricted the family to six genera characterized by submolariform P_4: *Leptacodon, Plagioctenodon, Nyctitherium, Saturninia, Scraeva*, and *Amphidozotherium*. In their review, McKenna and Bell (1997) combined the genera referred to Nyctitheriidae in two subfamilies, the Nyctitheriinae (including *Nyctitherium, Leptacodon, Saturninia, Remiculus, Scraeva, Pontifactor, Oedolius*, and *Bumbanius*) and Amphidozotheriinae (*Amphidozotherium* Filhol, 1876, *Paradoxonycteris* Revilliod, 1922, *Darbonetus* Crochet, 1974, and *Plagioctenoides* Bown, 1979); some genera are included in the family without the indication of the subfamily: *Plagioctenodon* Bown, 1979, *Voltaia* Nessov, 1987, *Ceutholestes* Rose et Gingerich, 1987, *Limaconyssus* Gingerich, 1987, and *Wyonycteris* Gingerich, 1987). The genus *Euronyctia* Sigé, 1997, which was described later, is similar to *Saturninia* (see Sigé, 1997; Smith, 2004) and, hence, belongs to Nyctitheriinae.

In 2005, two new subfamilies of Asian nyctitheriids were introduced, i.e., Eosoricodontinae, with the only genus *Eosoricodon* (Lopatin, 2005a), and Asionyctiinae comprising the genera *Asionyctia, Bayanulanius, Bumbanius, Oedolius*, and *Voltaia* (Missiaen and Smith, 2005). In Chapter 3, the family Nyctitheriidae is divided into five subfamilies: Nyctitheriinae, Amphidozotheriinae, Praolestinae subfam. nov. (*Praolestes* and *Bumbanius*), Asionyctiinae (*Asionyctia, Oedolius, Voltaia, Jarveia, Bayanulanius*, and *Edzenius* gen. nov.), and Eosoricodontinae (*Eosoricodon*).

The lower tooth row of all nyctitheriids shows a complete dental formula, including increased I_1; small I_2 and I_3; a small, premolar-like canine; slightly reduced, single-rooted P_1; relatively small P_2 and P_3 simple in structure; relatively large P_4; and molars with a moderately high trigonid, elevated paraconid, protoconid and metaconid approximately equal in size, and wide talonid having three well-developed cusps (hypoconid, entoconid, and hypoconulid). The most primitive nyctitheriids have double-rooted P_2 and P_3; submolariform (or completely molarized) P_4 with a large paraconid, well-developed metaconid, and clearly differentiated talonid (with three cusps and basin); M_1 and M_2 of approximately equal length, with a median hypoconulid; and M_3 with an elongated talonid. This set of primitive characters is completely retained in the basic and most diverse nyctitheriid subfamily, the Nyctitheriinae, including its Late Eocene and Oligocene members. Within Asian nyctitheriids, only Eocene *Yuanqulestes* shows the structure of P_4 and lower molars typical for Nyctitheriinae (Tong, 1997).

The major evolutionary trend in the transformation of the dentition of other nyctitheriid lineages is probably the shortening of the anterior and most posterior regions of the tooth row. These changes include a decrease in the size and number of roots of P_2 and P_3, simplification of P_4 (secondary premolarization, repremolarization, or demolarization after Sigé, 1976, p. 100; see Fig. 55), and reduction of the talonid and general deminution of M_3 in size. Within the subfamily Amphidozotheriinae, this trend is particularly well-pronounced in Late Eocene *Amphidozotherium* and Early Oligocene *Darbonetus*; all premolars (except for P_4) have become single-rooted and very small (especially P_3); in submolariform P_4, the metaconid is reduced, the talonid is short, its cusps are fused and substantially reduced (Fig. 55c); and M_3 considerably decreases and has a reduced talonid (see Crochet, 1974; Sigé, 1976).

In the Asian genera *Praolestes* and *Bumbanius* assigned to a new subfamily, the Praolestinae, P_2 and P_3 remain primitive in structure, while P_4 has become semimolariform, i.e., the talonid is short, the talonid cusps are fused, and the paraconid is reduced, which show that the tooth is semimolarized (Figs. 55d, 55e). M_3 is large, with a trend towards an increase in size of the hypoconulid, forming a considerably projecting posterior lobe. The lower molars are modified because they have acquired high crowns; the trigonid is high, columnar; the paraconid is fused with the metaconid.

Late Paleocene *Limaconyssus habrus* Gingerich, 1987 from North America is similar to *Praolestes* and *Bumbanius* in the high-crowned lower molars with columnar trigonids and semimolariform P_4 with a reduced talonid and moderately developed metaconid (Gingerich, 1987, text-fig. 20). However, before additional support is obtained, it is premature to assign *Limaconyssus* to Praolestinae because the differences in the structure of P_4 (in particular, narrowed, instead of short, talonid with three cuspules) and reduced M_3 are evidence of essential other evolutionary tendencies of this genus compared to *Praolestes* and *Bumbanius*, while the high crowns could have developed in these groups independently. Therefore, at present, *Limaconyssus* should be regarded as Nyctitheriidae incertae sedis.

In *Asionyctia, Voltaia*, and *Oedolius* (Asionyctiinae), primitive characters in the lower premolars and molars (which are the same as in Nyctitheriinae) show a very important difference, i.e., premolariform P_4 (Figs. 55g, 55h). In Early Eocene *Oedolius,* this tooth is premolarized to a greater extent than in Late Paleocene *Voltaia*, demonstrating not only the loss of the metaconid but also complete disappearance of the talonid basin (the variation range of P_4 of *Oedolius* includes

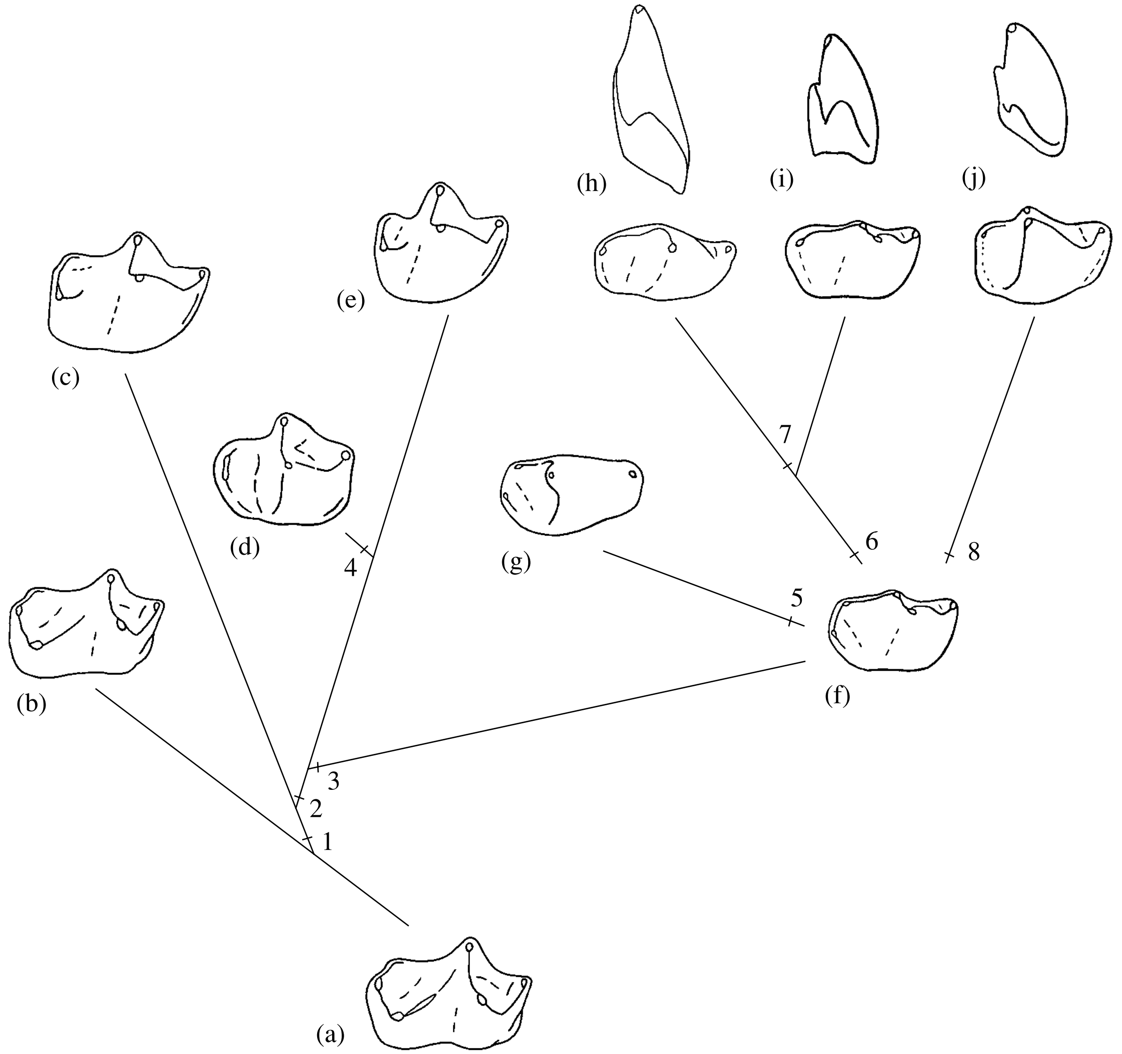


Fig. 55. The scheme of transformation of the P_4 structure in the Nyctitheriidae: (a) hypothetical ancestral submolariform structural type; (b) submolariform structural type of the Nyctitheriinae; (c) submolariform structural type of the Amphidozotheriinae; (d, e) semimolarized, semimolariform structural type of the Praolestinae: (d) *Praolestes* and (e) *Bumbanius*; (f) hypothetical partially molarized, semimolariform structural type, ancestral to the Asionyctiinae and Eosoricodontinae; (g) premolariform structural type of *Voltaia* (Asionyctiinae); (h) premolariform structural type of *Oedolius* (Asionyctiinae); (i) partially molarized structural type of *Edzenius* (Asionyctiinae); (j) partially molarized structural type of *Eosoricodon* (Eosoricodontinae); figures show P_4 in (a–j) occlusal and (h–j) posterior views, out of scale. Characters of premolarization: (*1*) shortened talonid, constriction of the trigonid, decrease in size of the talonid and trigonid basins, and reduction of the hypoconulid; (*2)* fusion of the talonid cusps, decrease in size of the paraconid; (*3*) decrease in size of the talonid cusps; disappearance of the cristid oblique; reduction of the talonid basin, metaconid, and paraconid; (*4*) disappearance of the cristid oblique and reduction of the paraconid (in parallel with *3*); (*5*) disappearance of the metaconid; (*6*) formation of the unicuspid talonid; (*7*) disappearance of the metaconid (in parallel with *5*), and (*8*) reduction of the talonid to the cingulid-like state.

specimens with a cristid oblique and a small talonid basin, which are regarded as rudimentary characters). In Late Paleocene *Asionyctia*, P_4 lacks a metaconid and has a highly elevated paraconid. The last character corresponds to a lesser degree of premolarization than in *Oedolius*. P_4 of Early Eocene *Edzenius* retains a rudimentary metaconid, whereas in the structure of the talonid, protoconid, and paraconid, it is obviously similar to P_4 of *Oedolius* (Figs. 55h, 55i). *Edzenius* is similar to *Eosoricodon* (Eosoricodontinae) in the presence of a rudimentary metaconid on P_4 and but substantially differs in the structure of the talonid of P_4 (which has a high longitudinal lingual crest and a large terminal cusp), lower molars, and P_2, which completely correspond to those of Asionyctiinae; therefore, it is referred to this subfamily. In contrast to *Voltaia* and *Edzenius, Oedolius* has lower molars with a narrow, lingually open talonid and reduced entoconid, which are positioned close to the hypoconulid. The Late Paleocene genus *Jarveia* shows a similar structure of lower molars; hence, it can be tentatively assigned to Asionyctiinae (although there no data on its P_4); this is supported by its similarity to *Asionyctia* in the structure of P^4, M^1, and M^2.

Wyonycterix chalix Gingerich, 1987 from the Upper Paleocene of Wyoming was originally described as the earliest member of Chiroptera (Gingerich, 1987, p. 305). Subsequently, *Wyonycteris* was transferred to insectivores (see Hand et al., 1994) and referred to Nyctitheriidae (McKenna and Bell, 1997) or ?Adapisoriculidae (including *W. richardi* Smith, 1995 from the Paleocene–Eocene transitional beds of Europe; Smith T., 1995, 1997). *Wyonycterix* differs from typical nyctitheriids (Nyctitheriinae) in the single-rooted P_2 and less molarized P_4 (Smith, 1995). In the structure of P_4, *Wyonycterix* resembles Asionyctiinae; thus, the metaconid is reduced and displaced posteriorly relative to the protoconid (although to a much lesser degree than in *Edzenius*), the talonid is considerably shortened and simplified (less than in *Voltaia* and to the same extent as in one specimen *Oedolius*, see Fig. 16l), the protoconid is high and massive, and the paraconid is small, as in most of the Asionyctiinae (except for *Asionyctia*). The low-crowned lower molars of *Wyonycterix* are similar to those of *Voltaia, Asionyctia,* and *Edzenius*. At the same time, *Wyonycterix* is distinguished by the well-developed W-shaped centrocrista of upper molars. At present, it seems plausible to determine its taxonomic position as ?Nyctitheriidae incertae sedis.

A considerable premolarization is observed in P_4 of Early Eocene *Eosoricodon terrigena* (Eosoricodontinae); in particular, its paraconid is reduced, metaconid is rudimentary, and talonid is cingulid-like (Fig. 55j). The combination of these characters suggests that P_4 of *Eosoricodon* is simultaneously partially molarized (due to the presence of metaconid), premolarized (due to the domination of the protoconid), and showing a tendency towards antemolarization (because of the cingulid-like talonid). In addition, *Eosoricodon* differs from Asionyctiinae in that the talonid of its P_4 is more premolarized than the trigonid. P_3 is relatively large, double-rooted, while P_2 is small and its roots are fused. The molars of *Eosoricodon* are also modified; in particular, the metaconid decreases, the hypoconulid is displaced lingually and approaches the entoconid, and the talonid of M_3 is reduced. These features suggest that Eosoricodontinae connect the Nyctitheriidae with the Soricidae, namely, with the Soricolestinae (Lopatin, 2005a, 2005b; see also Section 5.1.4).

Thus, reexamination of the holotype of *Voltaia minuta*, the study of new material of *Praolestes, Bumbanius, Jarveia*, and *Oedolius*, and discovery of *Edzenius* and *Eosoricodon* resulted in the establishment of their relationships within of the family Nyctitheriidae, the development of the concept of secondary premolarization of P_4 in the evolution of nyctitheriids, and the reconstruction of directions and stages of this process (Fig. 55). The nyctitheriid classification proposed above at the level of subfamilies is based mostly on phylogenetic interpretation of transformations in the structure of P_4 (Fig. 55) and lower molars as well as on the differences in the structure of upper molars.

5.1.4. Soricidae

Shrews (Soricidae) compose one of the most specialized insectivore groups, which has developed profound adaptations for feeding on small invertebrates. In the Recent fauna, the Soricidae occur almost everywhere (except for Australia, most part of South America, and polar regions), inhabit various landscapes, and lead terrestrial, subterranean, or semiaquatic mode of life. The Soricidae provide the foundation of species diversity of extant insectivores, comprising about 335 species and 23 genera (Wolsan and Hutterer, 1998), that is, approximately 80% of the total number of species of Insectivora. More than 250 (including about 200 extinct) species and more than 70 genera (60 extinct) have been described from the fossil record (Wolsan and Wójcik, 1998).

Recent taxonomic diversity of the major groups of shrews was formed in the Late Miocene and Pliocene (Repenning, 1967; Rzebik-Kowalska, 1997, 1998; Storch et al., 1998). In the Neogene, the Soricidae were represented by six subfamilies, including the extinct Heterosoricinae, Crocidosoricinae, Limnoecinae, and Allosoricinae and extant Soricinae and Crocidurinae. In the Oligocene, only the Heterosoricinae and Crocidosoricinae were recorded. The subfamily Heterosoricinae, which is known from the end of the Middle Eocene to the beginning of the Pliocene, was regarded for a long time as the most primitive shrew group, and some researchers ranked it as family (Reumer, 1987, 1998). The subfamily Heterosoricinae includes *Domnina* Cope, 1873 from the Middle Eocene–Early Miocene of North America (McKenna and Bell, 1997; Harris, 1998), which was considered until recently as the earliest genus of Soricidae. In the Middle Eocene, *Domnina* is known from the Late Uintan and Duchesnean (Stucky, 1992); Late Uintan taxa were determined as *Domnina* cf. *gradata* Cope, 1873 (Krishtalka and Setoguchi, 1977) and *Domnina* sp. (Storer, 1984).

The earliest Soricidae of Europe were found in the Lower Oligocene: *Quercysorex* sp. (Heterosoricinae) from MP21; *Srinitium* cf. *marteli* Hugueney, 1976 (Crocidosoricinae) from MP22 (Ziegler and Heizmann, 1991; Rzebik-Kowalska, 1998). Shrews apparently appeared in Europe as a result of immigration of Asian mammals at the Eocene–Oligocene boundary.

From the Middle Eocene Khaychin Formation of the Khaychin-Ula 2 locality in Mongolia, I described the earliest and most primitive shrew *Soricolestes soricavus* Lopatin, 2002 (Lopatin, 2002c; see Chapter 3). The structure of the lower molars of *Soricolestes* is typical for Soricidae; however, its antemolars are differentiated; P_4 is large, partially molarized; M_3 has a hypoconulid; the lower jaw is elongated and low; the masseteric fossa is deep; and internal temporal fossa is superficial. The structural features of the lower jaw, antemolars, P_4, and M_3 support the assignment of *Soricolestes soricavus* to a distinct subfamily, the Soricolestinae Lopatin, 2002. *Soricolestes* is probably close to the common ancestor of all Soricidae.

Repenning (1967) reviewed the data on Soricidae known at that time and proposed that the hypothetical ancestor of all shrews should have had the following characters (only the characters of lower teeth and lower jaw are considered): (1) the lower teeth formula is 1.4.1.3 (I_1A_1–$A_4P_4M_1$–M_3); (2) the lower incisor is large, procumbent (directed anteriorly); (3) the lower antemolars have one triangular cusp, the first and the last (P_4) are the largest, compacting of the antemolar row is poorly pronounced; (4) P_4 is nonmolarized, unicuspid, double-rooted, with distinct cingulids; (5) M_1 has well-developed trigonid and talonid, the metaconid and paraconid are separated to a greater extent than in M_2, the cristid oblique is connected to the trigonid at the center of the tooth or with the metaconid, the entoconid is clearly separated from the postcristid and is connected to the metaconid by a high and well-developed entocristid, the hypoconulid is absent, the ectocingulid is strong, and the hypoflexid reaches the line of the ectocingulid; (6) M_2 is similar to M_1, but the paraconid is positioned closer to the metaconid; (7) M_3 has a trigonid as in M_2, but its talonid is reduced, the entoconid is connected to the postcristid; (8) the internal temporal fossa is pronounced but lacks a pocket; (9) the mental foramen is under P_4 or P_3; and (10) animal is small-sized. This list includes the characters shared by all known Soricidae (1–8), basically, in their most primitive manifestation (1, 3–5, 7, 8), as well as hypothetical characteristics of primitive conditions of particular characters (9, 10).

Repenning believed that shrews evolved from an unknown pre-Oligocene member of Soricoidea (according to the recent geologic time scale, pre-Late Eocene). Subsequent finds of Middle Eocene Soricidae in North America added nothing to the understanding of the origin of this family: *Domnina* cf. *gradata* from the Late Uintan of Wyoming (Krishtalka and Setoguchi, 1977, p. 91) and *Domnina* sp. from the Late Uintan of Saskatchewan (Storer, 1984, p. 44, text-fig. 4H) differ only slightly from the well-known Late Eocene–Early Oligocene *D. gradata.* Thus, Harris (1998) believed that the animal from Wyoming belongs to *D. gradata.*

Soricolestes shows almost all characters indicated by Repenning for the hypothetical common ancestor of shrews. The lower jaw dental formula (1.5.1.3) differs from what was proposed by Repenning; however, the presence of five single-rooted antemolars between the anterior incisor and P_4 has also been recorded in the Oligocene Crocidosoricinae genus *Srinitium* (Ziegler, 1998). The reduced paraconid and rudimentary metaconid of P_4, the absence of connection between the postcristid and entoconid of M_3, and the absence of well-developed ectocingulid on P_4–M_3 clearly show that *Soricolestes* is much more primitive than other shrews. M_1 and M_2 are so similar to those of later Soricidae that, if *Soricolestes* were only represented by these teeth, it would be difficult to distinguishing it from some Oligocene and Miocene taxa.

Let us consider in detail certain morphological features of the lower teeth and jaw of *Soricolestes*, which have evolutionary significance.

Homology of the anterior lower incisor. The homology of the procumbent lower incisor of Soricidae (the so-called soricid incisor, I_1 or I_2) had not been established with certainty until the description of *Soricolestes* (Repenning, 1967; Butler, 1988), although it was commonly believed that it was I_1 (Gureev, 1979; Dannelid, 1998). The number, proportions, and arrangement of alveoli for anterior teeth of *Soricolestes* clearly demonstrate that, in Soricidae, the initially increased incisor is I_1. This shows a considerable gap between the Soricidae and Plesiosoricidae (in which I_2 is increased, see Viret, 1946, text-figs. 1, 2; Green, 1977, text-fig. 2; etc.), which are sometimes placed close together (Van Valen, 1967; Butler, 1988).

Number, differentiation, and homology of antemolars. The small single-rooted teeth of Soricidae that are positioned between I_1 and P_4 are usually called intermediate teeth (Gureev, 1979) or antemolars (Repenning, 1967; Dannelid, 1998; Ziegler, 1998) and are designated sequentially depending on their number as A_1, A_1–A_2, etc., up to A_1–A_5 (Ziegler, 1998). The position, orientation, and relative sizes of five alveoli of antemolars of *Soricolestes* enable these teeth to be identified as I_2, I_3, C_1, and two premolars, probably, P_2 and P_3. Apparently, the same interpretation is true for A_1–A_5 of *Srinitium caeruleum* Ziegler, 1998 from the Upper Oligocene of Germany (Ziegler, 1998). However, the alveoli of antemolars of *Srinitium* are more closely spaced than in *Soricolestes* and are approximately equal in size and shape (Ziegler, 1998, pl. 6, fig. 77); this reflects a greater compacting of the antemolar row.

As the premolar row of insectivores is reduced, P_1 is the first to disappear; therefore, it is safe to propose that *Soricolestes* has lost this tooth. In *Soricolestes*, the alveoli of I_3 and I_2 are the smallest; therefore, it seems plausible that, in more advanced Soricidae, further reduction of the antemolar row was associated with the loss of the third and second incisors. P_2 of *Soricolestes* is smaller than P_3, thus, it probably disappeared earlier in the evolution of Soricidae. Thus, the antemolars were probably lost in the evolution of shrews according to the following sequence: $P_1 \longrightarrow I_3 \longrightarrow I_2 \longrightarrow P_2 \longrightarrow P_3$. On the other hand, this process could have develop differently in different lineages. In particular, the alveolus of A_1 of *Srinitium caeruleum* is substantially larger than alveoli of four other antemolars (Ziegler, 1998); consequently, I_2 of early Crocidosoricinae did not show a tendency towards reduction.

Structure of P_4. *Soricolestes* considerably differs from other Soricidae in size and structure of the last premolar and resembles in this respect Plesiosoricidae, and some Talpidae and Chiroptera. Repenning (1967) believed that nonmolarized P_4 of shrews is a primitive character and proposed that Soricoidea are closely related to Chiroptera and deviated along with them from insectivores with molariform P_4 in the pre-Cenozoic time. Sigé (1976) has shown that the molariform structure of the last premolar is a primitive character of Lipotyphla (and Chiroptera), while simplified structural types of P_4 developed in parallel and characterize advanced groups. Partially molarized P_4 of *Soricolestes* with a reduced paraconid, a rudimentary metaconid, and unicuspid cingulid-like talonid are evidence that specialized P_4, which is characteristic of later shrew groups, was formed as a result of directional demolarization (secondary premolarization) of the last premolar, which is recorded in the earliest Soricidae.

Structure of the talonid of M_3. In contrast to other shrews, the talonid of M_3 of *Soricolestes* has three cusps (instead of one or two) and its postcristid is separated from the reduced entoconid, as in the talonid of M_1 and M_2. The talonid structure in M_3 of *Soricolestes* suggests that, in later Soricidae, the lingual talonid cusp of M_3 is the completely fused hypoconulid and entoconid rather than the sole entoconid (as is usually thought), while most part of the entoconid is included in the entocristid. The element of M_1 and M_2 of shrews that is named the entostylid is homologous to the hypoconulid (Sigé, 1976). The entostylid is formed as a result of displacement of the hypoconulid in the posterolingual corner of the occlusal surface accompanied by its connection with the hypoconid and primary isolation from the entoconid, as in nyctalodont bats (Menu and Sigé, 1971). In the evolution of Soricidae, this element lost the initial conical shape and subsequently (independently in different groups) was considerably reduced or completely disappeared (as the postcristid was connected to the entoconid).

Position of the mental foramen. In the majority of shrews, the mental foramen is located under M_1 or, less often, under P_4; in advanced Heterosoricinae, it is displaced to under M_2 (Repenning, 1967; Engesser, 1975). The position of the mental foramen under P_4 is characteristic of many Oligocene–Miocene genera of Crocidosoricinae (Crochet, 1975; Ziegler, 1989, 1998). An anterior position of the foramen (under P_3) observed in *Soricolestes* is a more primitive condition. It is commonly believed that the posterior displacement of the mental foramen in the evolution of shrews correlated with increasing size of the incisor (Engesser, 1979); consequently, the anterior lower incisor of *Soricolestes* was not increased considerably.

Structure of the ascending ramus of the lower jaw. Available material does not provide data whether or not *Soricolestes* had the basic autapomorphic character of the Soricidae (Repenning, 1967; MacPhee and Novacek, 1993), i.e., the double articulation of the lower jaw with the skull, which is evidenced by the presence of a double condyle with separate upper and lower articular facets. However, the formation of the double jaw articulation correlated in shrews with significant functional changes in jaw muscles, including the loss of most of the masseter and displacement of a portion of the temporal muscle onto the medial side of the coronoid process (MacPhee and Novacek, 1993). As a result, in the majority of shrews, the masseteric fossa disappears, while the external and internal temporal fossae are formed. Therefore, the presence of a large and deep masseteric fossa on the coronoid process of the lower jaw of *Soricolestes* and the absence of distinct internal temporal fossa is indirect evidence for the absence or very weak development of the double condyle.

Asher (2005, p. 61) indicated that it is impossible to corroborate the absence of double articulation between the lower jaw and skull in *Soricolestes* based on the absence of a pocketlike internal depression and the presence of masseteric fossa, because the heterosoricine genus *Trimylus*, which resembles *Soricolestes* in the structure of the coronoid process, nevertheless, has widely spaced articular facets of the mandibular condyle (Asher, 2005, text-fig. 5.3B), and *Domnina* always has these facets, although they are much less separated.

In fact, the Heterosoricinae have a masseteric fossa, while their internal temporal fossa is small and lacks a pocket. However, the masseteric fossa of *Soricolestes* is substantially larger and deeper than in the Heterosoricinae, and its internal temporal fossa is hardly discernible. Apparently, the condyle of *Soricolestes* was more primitive in structure, even in comparison with that of *Domnina* (Repenning, 1967, p. 8, text-fig. 2; Asher, 2005, text-fig. 5.3A). Additional indirect evidence of the absence of a detached lower articular facet in *Soricolestes* is the absence of a posterior medial crest, which in other shrews overhangs the mandibular foramen and extends to the condyle.

It should be emphasized that the characters listed suggest that *Soricolestes* lacked a well-developed double temporomandibular joint; however, it is not improbable that the mandibular condyle showed the initial stage of division into the upper and lower articular facets (see also Lopatin, 2002c).

The high vertical coronoid process with an acute apex, which is observed in *Soricolestes* is typical in shape for the Soricidae. In the Nyctitheriidae, the coronoid process is usually longer, low, gently slopes, and has a more rounded apex (Figs. 14, 17; McKenna, 1968, text-figs. 3, 4; Sigé, 1976, text-figs. 2, 95); however, *Praolestes maximus* described above has a coronoid process of the soricid type (see Fig. 13).

The long (compared to the other Soricidae) ascending ramus of the lower jaw at the level of the lower sigmoid incisure and the shallow incisure between the angular process and the lower edge of the dentary should be regarded as primitive characters of *Soricolestes*.

Soricolestes extends the known history of shrews for at least 5 m.y. The above morphological features of the lower jaw and teeth of *Soricolestes* provide new data for checking the hypotheses concerning the origin of Soricidae.

It is usually believed that the closest soricomorph relatives of soricids are the Paleogene Holarctic Nyctitheriidae. Simpson (1945) regarded nyctitheriids as a group of primitive shrew-like soricoids lacking the most significant adaptations of the Soricidae. Saban (1958), Gureev (1971, 1979), and Sigé (1976) tentatively associated the origin of Soricidae with Eocene nyctitheriids. Simpson, Saban, and Gureev placed the Late Eocene–Early Oligocene European nyctitheriid genus *Saturninia* in the family Soricidae; in addition, Gureev assigned it to a separate subfamily, the Saturniniinae Gureev, 1971, and opposed to all other shrews, which he assigned to the subfamily Soricinae. Repenning (1967) took *Saturninia* away from the Soricidae and did not accept the Nyctitheriidae as an ancestral group for shrews mostly because they have molariform P_4.

Van Valen (1967) proposed that the Soricidae could have evolved from Plesiosoricidae or Adapisoricidae (including nyctitheriids in latter family). Butler (1988) believed that the Soricidae and Nyctitheriidae are only remote relatives within Soricomorpha and that shrews have common ancestor with Plesiosoricidae.

Reumer (1987) believes that Heterosoricidae and Soricidae evolved independently from Eocene Nyctitheriidae, and the more primitive Heterosoricidae deviated much earlier.

Morphological differences between nyctitheriids and typical shrews are great. Typical nyctitheriids differ from the Soricidae in the long lower jaw, deep masseteric fossa, complete dental formula; usually, molarized P_4; the molars with large, median hypoconulid; and elongated M_3. The major evolutionary changes of nyctitheriids include a shortening of the infraorbital canal, reduction of canines, development of denticulate incisors, widening of the hypoconal shelf, expansion of the mandibular condyle, the loss of the anterior mental foramen, and a more vertical position of the coronoid process in European genera (Butler, 1988). Tendencies towards reduction of premolars, directional demolarization of P_4, and reduction of the talonid of M_3, which were manifested in some nyctitheriid groups, for example, in the Late Eocene European Amphidozotheriinae (Sigé, 1976), developed too late to be related to the origin of Soricidae and, hence, resulted from parallel development.

Soricolestes demonstrates the lower molar structure characteristic of shrews and is intermediate between Nyctitheriidae and typical Soricidae in the following important morphological characters: the slightly reduced antemolar row which is differentiated into incisors, canine, and premolars; large, unspecialized P_4 with the paraconid, rudimentary metaconid, and short talonid; well-developed hypoconulid of M_3; and the primitive structure of the ascending ramus of the lower jaw. In my sight, this provides additional evidence for the hypothesis of the origin of shrews from Early Paleogene Asian nyctitheriids (Sigé, 1976; Lopatin, 2002c).

The structure of the lower jaw and teeth of *Soricolestes* suggests that it could have been a common ancestor of all later shrews, which implies common origin of Heterosoricinae and the subfamily Crocidosoricinae, which is ancestral to others Soricidae. Thus, there is no need to rank Heterosoricinae as a distinct family, as was proposed by Reumer (1987). It is noteworthy that the nearest common ancestor of Heterosoricinae and Crocidosoricinae would have been more advanced than *Soricolestes* with reference to some dental characters, in particular, it probably had a shorter antemolar row and more reduced P_4 and M_3. Apparently, the Heterosoricinae deviated rather early from the Soricolestinae and as early as the end of the Middle Eocene formed a special specialized shrew group retained a primitive structure of the ascending ramus of the lower jaw. The Crocidosoricinae were probably established in Asia in the Middle–Late Eocene.

The discovery of *Eosoricodon terrigena* Lopatin, 2005, a specialized nyctitheriid from the basal Eocene of Mongolia, which is described above, provided additional support to the hypothesis of the origin of the Soricidae from Nyctitheriidae (Lopatin, 2005b).

Eosoricodon is rather similar to *Soricolestes* in the structure of P_4, differing in the presence of P_1, less reduced P_2 and P_3, and the presence of distinct hypoconulid, which is not transformed into the entostylid, on M_1–M_3 (Fig. 56). The structure of M^1, M^2, M_1, and M_2 of *Eosoricodon* is generally similar to that of Nyctitheriidae of the evolutionary level of *Saturninia*. Accordingly, *Eosoricodon* is not included in the Soricidae and regarded as a member of Nyctitheriidae with a particular specialization type (placed in the distinct subfamily Eosoricodontinae).

The lower molars of *Eosoricodon terrigena* have a high entocristid and a small hypoconulid positioned close to the entoconid, but separated from it by a distinct fold. It is possible to propose that such a sublingual hypoconulid could have been modified in the entostylid characteristic of shrews (including *Soricolestes*). The talonid of M_3 of *Eosoricodon* is more reduced than in the other nyctitheriids (excluding Amphidozotheriinae) and shows the same structure as M_3 of *Soricolestes*, but has relatively larger hypoconulid and entoconid.

Eosoricodon fills (or, at least, considerably decreases) the morphological gap between *Soricolestes* and typical nyctitheriids and demonstrates a morphological state that could have given rise to dental characters typical for shrews.

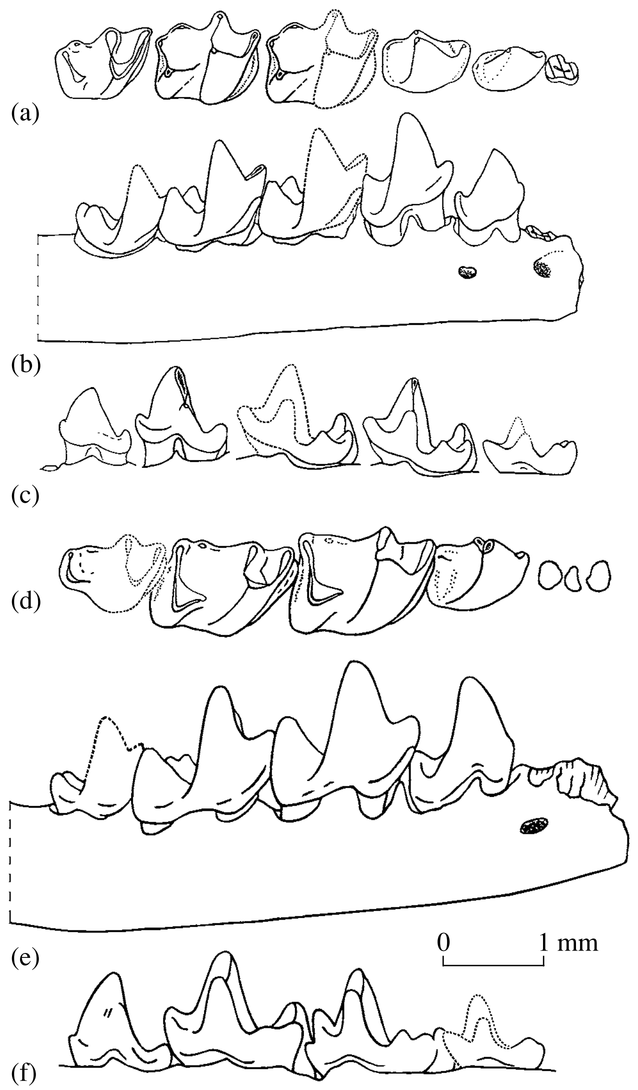


Fig. 56. Lower tooth rows of *Eosoricodon* and *Soricolestes*: (a–c) *Eosoricodon terrigena* Lopatin, 2005 (Nyctitheriidae, Eosoricodontinae); a composite tooth row of right P$_2$–M$_3$ in the lower jaw fragment reconstructed based on the holotype PIN, no. 3104/900 and specimens PIN, nos. 3104/890 (left dentary fragment with P$_3$ and the base of P$_2$), 3104/891 (right dentary fragment with P$_4$), 3104/893 and 894 (specimens with M$_2$ and talonid of M$_1$), and 3104/481 (right dentary fragment with M$_2$ and M$_3$): (a) occlusal, (b) labial, and (c) lingual views; Tsagan-Khushu locality, Mongolia; Bumban Member, Naran-Bulak Formation, Lower Eocene; (d–f) *Soricolestes soricavus* Lopatin, 2002 (Soricidae, Soricolestinae), holotype PIN, no. 3107/405, right dentary fragment with P$_4$–M$_3$ and alveoli of C$_1$–P$_3$: (d) alveoli and teeth, occlusal view, (e) general appearance, labial view, and (f) P$_4$–M$_3$, lingual view; Khaychin-Ula 2 locality, Mongolia; Khaychin Formation, Middle Eocene. Reconstructed regions of teeth are outlined by dash lines.

It should be noted that *Soricolestes* and *Eosoricodon* represented the group of the smallest insectivores in their associations. Apparently, the Soricidae as an ecological group composed from the very beginning the smallest size category of insectivores.

Zaitsev (2005) was the first to show that living Soricidae are distinguished by a special masticatory pattern that he named “horizontal shearing” (rasping or grating), while other insectivorous and carnivorous mammals are characterized by “vertical shearing” (or cutting). This unique mechanism includes (1) the capture of prey by the pair of anterior (upper and lower) incisors; (2) fixation by piercing prey by the apices of the anterior upper incisors and pressing it against the upper molars using strong temporal muscle combined with the retention of mobility of the lower jaw; and (3) dissection of prey by small-amplitude and weak movements of the lower jaw during a long phase of slow opening of the mouth (SO phase) by the masseter, medial and lateral pterygoid muscles, and digastric muscle. Food objects are cut by small, mostly anteroposterior movements of the lower jaw in the horizontal plane, with only slightly opening mouth; according to the metaphorical expression of Zaitsev (2005, p. 142), this resembles “rasping vegetables with the use of a grater turned upside down.” This mechanism enables shrews to hunt large (in relation to their own body size), mobile prey and, hence, to consume a large amount of high-caloric food, providing a high level of metabolism combined with the preservation of relative small body sizes, and, in the long run, provided the evolutionary success of Soricidae.

It is possible to assume that the formation of this adaptation resulted in the emergence of the group that gave rise to the Soricidae within the Nyctitheriidae. The prerequisite to such adaptation was the presence of a relatively large temporal muscle, which was probably typical for some nyctithere groups.

This scenario agrees with the hypothesis proposed by Nikolskii (1983, 1990) that structural features of the masticatory apparatus of shrews are connected with the skull flattening resulted from the adaptation for getting food in the holes of leaf litter, which are shaped as horizontal cracks with a low roof because of gradual compression of the litter during its formation.

5.1.5. Plesiosoricidae

Ordolestes ordinatus gen. et sp. nov. is the earliest representative of the subfamily Butseliinae and the family Plesiosoricidae in general. Plesiosoricids occur in the Eocene–Miocene of Asia, Oligocene–Miocene of Europe, and Miocene of North America (McKenna and Bell, 1997; Tucker and Voorhies, 2005). Previously, Middle Eocene *Pakilestes lathrius* from Pakistan (Russell and Gingerich, 1981; Gingerich, 2003) and *Ernosorex jilinensis* from China (Wang and Li, 1990) were the earliest known members of the family. *Ernosorex* is similar in dental structure to *Plesiosorex* and *Meterix*, typical plesiosoricids with erinaceoid molars. *Ordolestes* and *Pakilestes* are similar to *Butselia* from the Lower Oligocene of Europe (Butler, 1972, 1988). These three genera are placed in the subfamily Butseliinae (see above), which is characterized by relatively broad upper molars with a moderately developed hypocone and a strong precingulum, high and clearly differentiated metaconid of P_4, and reduced ridgelike entoconid of M_1–M_3.

The insectivore *Butselia biveri* Quinet et Misonne, 1965 was described from the Lower Oligocene of Belgium based on isolated upper molars (Quinet and Misonne, 1965); somewhat later, this material was supplemented by upper and lower molars and a lower jaw fragment from England (Butler, 1972). In the original description, the upper molars of *Butselia* were considered to represent a separate primitive stage of zalambdodonty; therefore, this genus was placed in a separate family named Butselidae (Quinet and Misonne, 1965, p. 6). Butler (1972) proposed that *Butselia* belongs to the Plesiosoricidae and, later, the name Butseliidae was regarded as a junior synonym of Plesiosoricidae (McKenna and Bell, 1997, p. 286). Based on the similar lower molar structure in the Eocene genera *Ordolestes, Pakilestes*, and *Butselia* and clear differences from the later genera *Plesiosorex* and *Meterix*, it is proposed here to restore the group name Butseliinae as a subfamily of Plesiosoricidae.

Within the Butseliinae, the genus *Ordolestes* is distinguished by certain lower molar characters indicating its predatory specialization (despite the earlier age in comparison with other genera), i.e., the reduced metaconid, narrow talonid, and rudimentary entoconid. *Ordolestes* probably appeared as a result of early radiation of Butseliinae at the Paleocene–Eocene boundary, while plesiosoricids differentiated into two subfamilies even earlier.

5.1.6. Apternodontidae

The zalambdodont soricomorph insectivores from the Paleogene of the Northern Hemisphere are usually assigned to the only family Apternodontidae (Matthew, 1903; Hough, 1956; Bown and Schankler, 1982; Stucky, 1992; McKenna and Bell, 1997); recently, Asher et al. (2002) divided it into three families: Parapternodontidae, Oligoryctidae, and Apternodontidae sensu stricto.

With the addition of Asiapternodontinae subfam. nov., it seems plausible to recognize four apternodontid groups, which are ranked above as subfamilies. The Parapternodontinae include two genera, *Parapternodus* Bown et Schankler, 1982 and the poorly known *Koniaryctes* Robinson et Kron, 1998 (Robinson and Kron, 1998; Asher et al., 2002), the other subfamilies are represented by the type genera, *Oligoryctes* Hough, 1956, *Apternodus* Matthew, 1903, and *Asiapternodus* Lopatin, 2003. In addition, the so-called "unnamed taxon from Tabernacle Butte," which was earlier designated "*Eoryctes* nomen nudum" (Romer, 1966; Asher et al., 2002) from the Middle Eocene of the United States, and, in question, "*?Apternodus* sp." (Tong, 1997) from terminal Middle Eocene of China are referred to the Oligoryctinae.

Asher et al. (2002) referred the Parapternodontidae, Oligoryctidae, and Apternodontidae to as Eutheria ordo indet. At the same time, phylogenetic analysis they performed has shown close relationships of these groups with shrews, which strongly suggest that they belong to Soricomorpha and Soricoidea sensu lato (McKenna and Bell, 1997). Formal cladistic analysis has shown that *Parapternodus* and *Oligoryctes* are closer to Soricidae than to *Apternodus;* therefore, Asher et al. concluded that Apternodontidae sensu lato is a polyphyletic taxon. In my opinion, this statement requires additional support. First, as follows from the discovery of Soricolestinae (Lopatin, 2002c) and Eosoricodontinae (Lopatin, 2005b), the origin of Soricidae is not connected with zalambdodont groups of Soricomorpha (see Section 5.1.4). Second, the characters uniting parapternodontines and soricids are restricted to nonmolariform P_4 and reduced M_3, while the Oligoryctinae are similar to shrews only in the presence of a deep medial depression on the coronoid process of the lower jaw (Asher et al., 2002, p. 106). These characters were undoubtedly acquired by these groups independently, the more so as nonmolariform P_4 of the Soricidae is in fact a result of secondary premolarization and particular specialization (Lopatin, 2002c). Certainly, *Apternodus* clearly differs in cranial structure from *Oligoryctes*. However, distinctions between them suggest various specialization patterns and probably long independent evolution of these lineages rather than phylogenetic remoteness. Until new confirmatory results are obtained, I propose to take the Parapternodontinae, Oligoryctinae, Asiapternodontinae, and Apternodontinae as subfamilies of the family Apternodontidae.

The zalambdomorph teeth of apternodontids have much in common with the teeth of tenrecs and solenodontids; therefore, this group was some time before regarded as a subfamily of Tenrecidae (Matthew, 1910; Van Valen, 1967) or Solenodontidae (Schlaikjer, 1933, 1934; Winge, 1941; Simpson, 1945; Macdonald, 1951; Galbreath, 1953; Saban, 1958; Paula Couto, 1979) or as a special family of Tenrecoidea (Osborn, 1910; Simpson, 1931; Scott and Jepsen, 1936; Clark, 1937; Hough, 1956; McKenna, 1975a; Galbreath, 1979; etc.). Subsequently, the Apternodontidae along with Solenodontidae were placed in Soricoidea (Romer, 1966; McKenna and Bell, 1997) or Solenodontoidea (Paula Couto, 1979) and, hence, stood apart from Tenrecoidea.

Molecular genetic studies suggest polyphyly of extant insectivores, which are composed of Lipotyphla and Afrosoricida (Stanhope et al., 1998; Waddell et al., 1999; Madsen et al., 2001; Murphy et al., 2001), and isolation of Solenodontidae from the group Soricomorpha + Erinaceomorpha (Roca et al., 2004). This complicates the development of systematics of extinct zalambdodont insectivores, which are regarded as members of the grade of insectivores (Asher et al., 2002; Roca et al., 2004).

However, close affinity of Apternodontidae with Solenodontidae is supported by the structure of both teeth and skull (Matthew, 1910; Schlaikjer, 1933, 1934; Scott and Jepsen, 1936; McKenna, 1975a). McKenna (1975a, p. 38) indicated that the cranial structure strongly supports the assignment of apternodontids to soricomorphs and noted that *Apternodus* had pigmented teeth, like *Solenodon* and Soricidae.

Phylogenetic relationships of the genera of Apternodontidae remain uncertain. In the lower molar structure, *Asiapternodus* shows plesiomorphic similarity to *Parapternodus*; however, it is impossible to prove or reject with confidence their close relationship because of the absence of data on the upper teeth of *Parapternodus*. The highly specialized *Oligoryctes* and *Apternodus* certainly belong to distinct lineages, which deviated from the ancestral stem not later than the terminal Early Eocene or the basal Middle Eocene. The lower molars of Asian "cf. *Apternodus* sp." from the upper part of the Middle Eocene of China (Tong, 1997, text-fig. 11, pl. I, figs. 14, 15) are more specialized than in *Asiapternodus*.

The zygomatic process of the maxilla of *Asiapternodus* is reduced to a substantially lesser extent concedes than that of *Apternodus* and *Oligoryctes* (Matthew, 1910; Schlaikjer, 1934; Hough, 1956). Within extant zalambdodont insectivores, *Tenrec, Oryzoryctes*, and *Microgale* show similar shape of the zygomatic process, whereas the zygomatic processes of *Potamogale* and *Solenodon* are longer and more widely spaced (Hough, 1956; Morgan and Ottenwalder, 1993). The incompletely reduced zygomatic arch of *Asiapternodus* is evidence that it is more primitive than the Apternodontidae of approximately the same and later ages.

The specialized characters of *Asiapternodus* include the considerably shortened infraorbital canal, which is located in line with P^4–M^1 (in *Apternodus* and *Oligoryctes*, it is above P^3–M^1).

The primitive characters of the upper teeth of *Asiapternodus* include the slightly molarized P^4, large protocone of M^1–M^3, and nonreduced M^3. A comparison of the upper molars of different apternodontids and living zalambdodont insectivores shows that *Apternodus* is most similar to *Solenodon*, while *Oligoryctes* is similar to the tenrecs *Oryzoryctes* and *Microgale*. The strongly transversely extended protocone of the upper molars of *Asiapternodus* resembles that of the living otter shrew *Potamogale* and Paleocene *Palaeoryctes* (Matthew, 1913; Butler, 1939, 1941). The upper molars of *Potamogale* and *Palaeoryctes* provide an example of an intermediate condition between zalambdodonty and dilambdodonty (Butler, 1939, 1941; Hershkovitz, 1971). Thus, the upper teeth structure of *Asiapternodus* agrees with the hypothesis that the zalambdomorph molars are derivable from the primitive dilambdomorph type through the reduction of the metacone and directional decrease in size of the protocone (Butler, 1941, text-fig. 8; 1996, text-fig. 1).

The terms Zalambdodonta and Dilambdodonta were introduced by Gill (1885, p. 136) as taxonomic names for sections of extant insectivores that he established earlier (Gill, 1875, 1885; Gregory, 1910). The section Zalambdodonta included Centetoidea (including tenrecs, solenodontids, and otter shrews) and Chrysochloroidea, while Dilambdodonta was composed of the Erinaceoidea, Soricoidea, and Tupaioidea. Subsequently, these terms retained only morphological meaning for the designation of respective dental types.

Zalambdodonty is characteristic of apternodontids, tenrecids, chrysochlorids, and solenodontids. The zalambdomorphy as a special type of dental structure means that the trigon of the upper molars is formed by a large lingually positioned paracone, V-shaped (in occlusal view) paracrista and styles, while the metacone and protocone are considerably reduced or absent, and the conules are absent (Butler, 1939, 1941; Hershkovitz, 1971). This is accompanied by the lower molars with excessively developed trigonids, with the formation of the oblique paracristid, very high and wide transverse protocristid, and reduced talonids. The zalambdomorph pattern is a derivative of the dilambdomorph pattern (Butler, 1996). However, in my opinion, the major zalambdomorph variants (tenrecoid and solenodontoid) develop from different dilambdomorph structural types rather than are connected with one another by a series of intermediate variants. The tenrecoid zalambdomorph type evolved from the primitive dilambdomorph type (protodilambdomorphy) characterized by the presence of the paracone, metacone, protocone, and rudimentary hypocone on the upper molars and the well-developed, differentiated talonid on the lower molars. In the lineage leading to tenrecs, this type was initially transformed into the primitive zalambdomorph variant (protozalambdomorphy), where the metacone is considerably reduced (its rudiment is preserved), the paracone is displaced to the center, the protocone and talonid are reduced, and a rudimentary hypocone has disappeared. Such dental structure is characteristic of *Potamogale* and *Protenrec* as well as of Early Paleogene *Palaeoryctes, Eoryctes*, and *Nuryctes*, insectivore-like placentals of the family Palaeoryctidae (Matthew, 1913; Butler, 1941; Thewissen and Gingerich, 1989; Lopatin and Averianov, 2004b). In the advanced condition (euzalambdomorphy), the tenrecoid zalambdomorph teeth lose completely the metacone and protocone, while the paracone is displaced lingually in place of the protocone; additional cingular elements are formed, and the talonid becomes similar to the postcingulid, as in *Tenrec* and *Setifer.* The solenodontoid zalambdomorph type (parazalambdomorphy), which is characteristic of Paleogene apternodontids and extant solenodontids, probably developed from the advanced dilambdomorph type (eudilambdomorphy), which is characterized by the presence of a well-developed hypocone. Apparently, it was also formed through a reduction of the metacone of upper molars and the talonid of lower molars, but in combination with the preservation in the lingual lobe of the upper tooth of the protocone and (at least, initially) hypocone.

Thus, apternodontids and solenodontids possibly belong to the same primitive lineage of soricomorphs, which acquired zalambdodonty in parallel with, and, apparently, much earlier (probably in the Paleocene) than tenrecomorphs and started from a different dilambdomorph variant.

5.1.7. Phylogenetic Relationships of Soricomorpha

Some molecular genetic studies suggest that the group ancestral to Talpidae had deviated from the ancestral stem earlier than the Erinaceidae and Soricidae lineages diverged (Douady et al., 2002; Jow et al., 2002; Malia et al., 2002; Amrine-Madsen et al., 2003; Douady and Douzery, 2003; Springer et al., 2003; Waddell and Shelley, 2003). Taking into account the even earlier origin of Solenodontidae (Waddell and Shelley, 2003; Roca et al., 2004) and the isolated position of tenrecoids, this hypothesis contradicts the concept of Soricomorpha in both the understanding of Gregory (1910: Soricidae + Talpidae) and a wider understanding of Butler (1972) or McKenna (McKenna, 1975a). Other molecular genetic studies show that the Talpidae are closer to Soricidae than to Erinaceidae (Mouchaty et al., 2000; Nikaido et al., 2001, 2003).

Morphological data on extant and extinct taxa are evidence of monophyly of Soricomorpha (excluding the Chrysochloridae) and divide this suborder into two infraorders, the Tenrecomorpha (Tenrecidae) and Soricota (all other families grouped in five superfamilies: Micropternodontoidea, Nesophontoidea, Soricoidea, Talpoidea, and Solenodontoidea). These modifications of the Soricomorpha system are proposed in the present study (see Chapter 3). The family Chrysochloridae is coextensive with the suborder Chrysochloridea (see MacPhee and Novacek, 1993), while the Erinaceidae and related extinct families compose the suborder Erinaceomorpha.

The evolutionary scheme proposed for the major types of dental structure of soricomorph insectivores (Fig. 57) supplemented by other morphological data allow the reconstruction of phylogenetic relationships within this group. The protodilambdomorph type (Figs. 57a, 57b) is regarded as the initial state. This structural type is characterized by the presence of the paracone and metacone (which are only slightly transversely expanded and, hence, their crests do not form a distinct W-shaped pattern), large conules, protocone, rudimentary hypocone (initially, as the hypoconal shelf), and well-developed, differentiated talonid. The excessive development of the paracone and trigonid and reduction of the metacone, conules, rudimentary hypocone, and talonid of this structural type gives rise to the protozalambdomorph type (Figs. 57c–57e); subsequently, as the protocone was reduced and the stylar shelf expanded, the euzalambdomorph type could have developed (Figs. 57f, 57g).

However, it is yet to be explained as to how the protozalambdomorph structural type characteristic of primitive tenrecs and otter shrews could have been derived from the protodilambdomorph type. The earliest member of the Tenrecidae, *Protenrec*, is known from the Lower Miocene of Kenya (Butler and Hopwood, 1957). It already has protozalambdomorph teeth, which are difficult to compare with the protodilambdomorph type (Butler, 1972; Fig. 57e). However, Seiffert and Simons (2000) recently described the insectivore *Widanelfarasia* from the Upper Eocene of Egypt, which is similar to tenrecs in the structure of lower incisors and the lower molars of which show characters of initial zalambdomorphy. The authors of the description with caution classified *Widanelfarasia* as Placentalia incertae sedis. But the basic morphological characters of this animal suggest this is a primitive tenrecomorph insectivore, which is intermediate in dental structure between primitive soricomorphs and previously known tenrecids (Fig. 57c). The Paleocene and Lower Eocene deposits of Africa have yielded fragmentary remains tentatively assigned to Lipotyphla (Gheerbrant et al., 1998; Gheerbrant and Hartenberger, 1999). The deposits of this age could have contained ancestors of tenrecomorphs. It is possible to assume that soricomorphs and tenrecomorphs diverged at the stage of Late Cretaceous insectivores of the *Batodon* evolutionary level (see Fig. 57a). Thus, the primary radiation of soricomorph insectivores probably goes back to Cretaceous Geolabididae or a group of close taxonomic position and geological age.

Most of the Early Paleogene soricomorphs developed the eudilambdomorph type provided by a well-developed hypocone and the formation of a W-shaped pattern of the paracone and the metacone crests (combined with the essentially almost constant structure of the lower molars; see Figs. 57h–57l). Subsequently, this general type underwent different changes manifested to a varying degree in different groups. Advanced Micropternodontidae, Geolabididae, and Nyctitheriidae have retained the most primitive variants of the eudilambdomorph type; the centrocrista is in the middle part, without labial displacement or division into two at the mesostyle; the conules are preserved; and the hypocone is still in the shape of a shelf (Figs. 57h, 57i). It is possible to name this variant the primitive eudilambdomorphy, or entodilambdomorphy. The plesiosoricid variant of entodilambdomorphy developed through the acquisition of a conical hypocone (Fig. 57j), while the soricid–talpoid eudilambdomorphy (ectodilambdomorphy: Figs. 57k, 57l) implies the formation of true W-shaped pattern of the paracone and metacone crests, the strengthening of the hypoconid crests, and transformation of the hypoconulid into the entostylid (with a trend towards reduction of

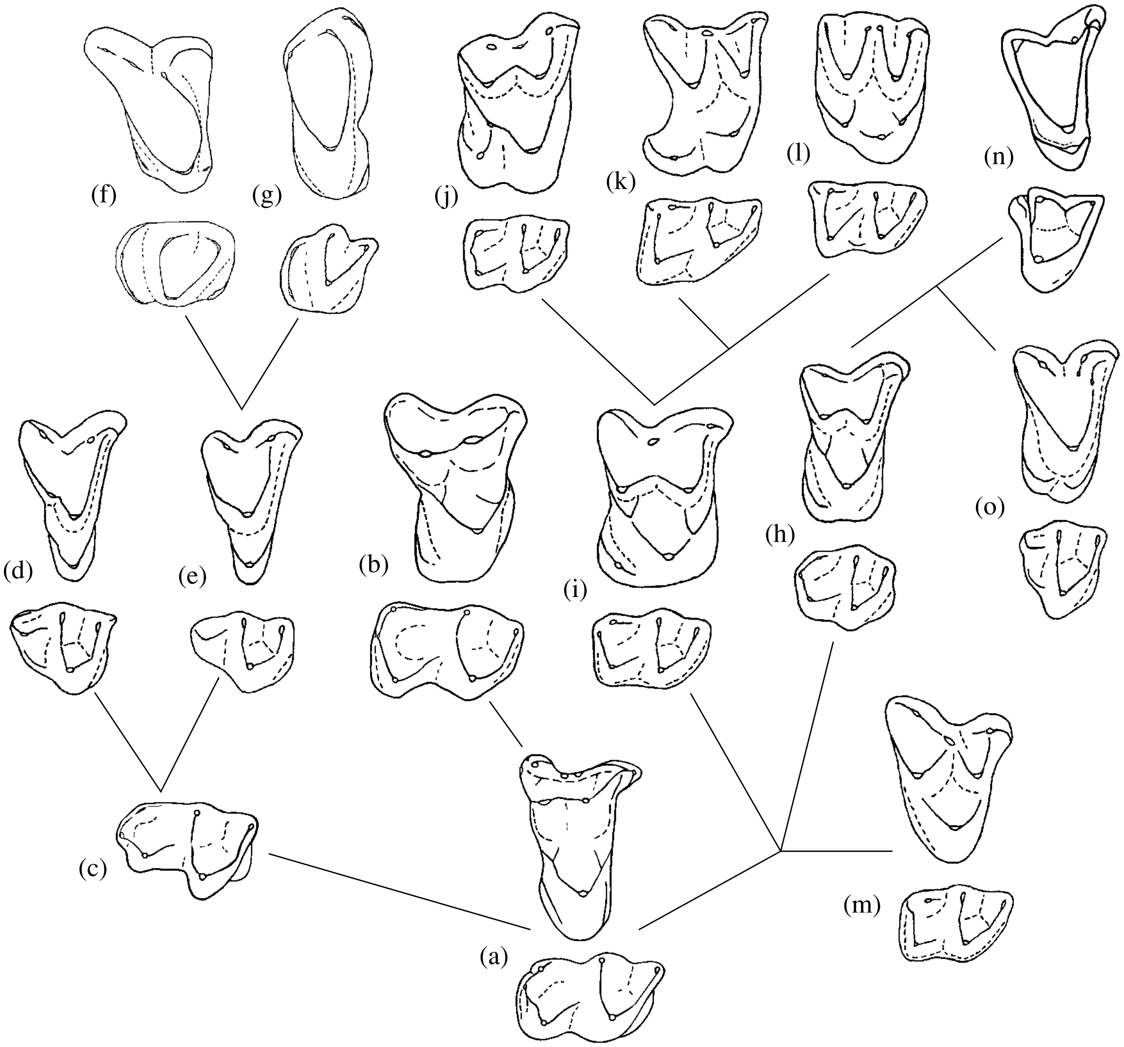


Fig. 57. Succession of molar structural types of Soricomorpha: (a, b) protodilambdomorph type: (a) *Batodon*, Geolabididae, Late Cretaceous, Maastrichtian, North America; (b) *Carnilestes*, Micropternodontidae, Early Paleocene, Asia; (c–e) protozalambdomorph type: (c) *Widanelfarasia*, Tenrecomorpha indet., Late Eocene, Africa; (d) *Potamogale*, Tenrecidae, Recent, Africa; (e) *Protenrec*, Tenrecidae, Early Miocene, Africa; (f, g) euzalambdomorph type: (f) *Tenrec*, Tenrecidae, Recent, Madagascar; (g) *Setifer*, Tenrecidae, Recent, Madagascar; (h–l) eudilambdomorph type: (h–j) entodilambdomorph subtype: (h) *Centetodon*, Geolabididae, Early Eocene–Early Miocene, North America; (i) *Nyctitherium*, Nyctitheriidae, Early–Middle Eocene, North America; (j) *Plesiosorex*, Plesiosoricidae, Late Oligocene–Late Miocene of Europe, Early–Middle Miocene of North America; (k, l) ectodilambdomorph subtype: (k) *Myosorex*, Soricidae, Late Pliocene–Recent, Africa; (l) *Desmana*, Talpidae, Early Pliocene–Recent, Eurasia; (m) metadilambdomorph type, *Nesophontes*, Nesophontidae, Pleistocene–Holocene, Antilles; (n, o) parazalambdomorph type: (n) *Apternodus*, Apternodontidae, Middle Eocene–Early Oligocene, North America; and (o) *Solenodon*, Solenodontidae, Pleistocene–Recent, Antilles. The teeth, right M^2 and M_2, are drawn out of scale, after Schlaikjer (1934, text-fig. 1), Butler (1937, text-figs. 2, 5, 15, 25; 1972, text-figs. 2, 3), Clemens (1973, text-fig. 25b), Storer (1991, text-fig. 10K), Wang and Zhai (1995, text-fig. 2), and Seiffert and Simons (2000, text-fig. 1H), modified; some genera are represented by original drawings based on photographs. Distribution of genera is given after McKenna and Bell (1997).

the hypocone in the Talpoidea and a trend towards disappearance of conules in the Soricidae). The ectodilambdomorphy is functionally an advanced adaptation for the efficient cutting of fibrous food (Butler, 1996).

The Micropternodontidae and Nyctitheriidae apparently appeared during the earliest radiation of Soricomorpha, which also gave rise to the Geolabididae. The Plesiosoricidae possibly also deviated at that time. The origin of the Soricidae from Nyctitheriidae was considered above (see Section 5.1.4). The taxonomic position of the Talpidae is not so clear. Isolated teeth of the earliest Talpidae were found in the Upper Eocene and assigned to *Eotalpa, Myxomygale*, and *Geotrypus* from Europe (Sigé et al., 1977; McKenna and Bell, 1997; Whidden, 2000) and an undetermined genus and species of Talpinae from eastern Kazakhstan (Gabunia, 1987). Talpidae indet. were recorded in the Middle Eocene of Europe (McKenna and Bell, 1997). Gureev

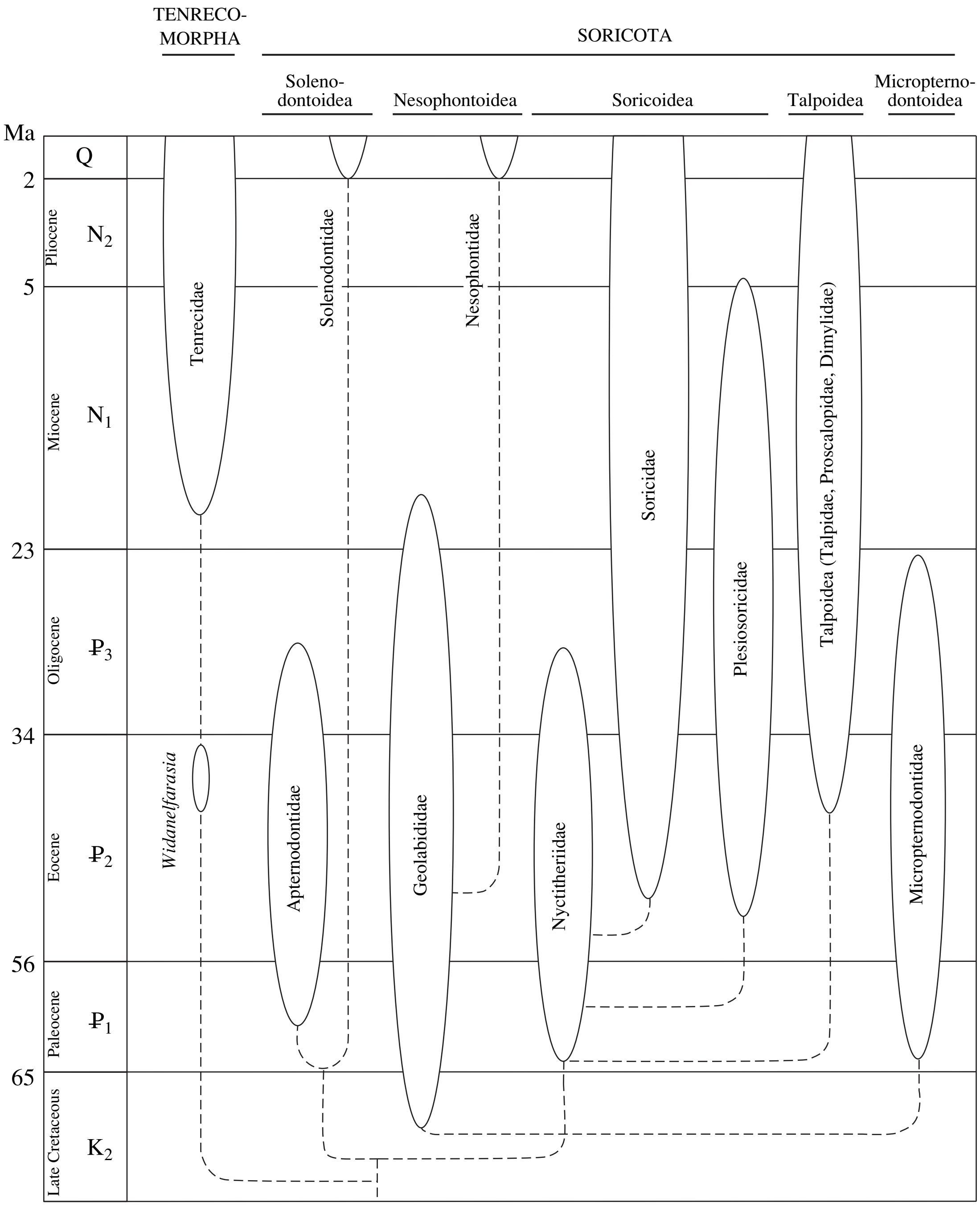


Fig. 58. Scheme of phylogenetic relationships in Soricomorpha.

(1979) believed that moles are closely related to tenrecomorphs, which was supported by the trituberculate structure of the upper molars (the absence of the hypocone), a primitive character in his opinion. However, Butler (1988) indicated that, in fact, primitive Talpidae, such as *Uropsilus*, have a well-developed hypocone, while the absence on this cusp in other Talpidae developed secondarily.

The origin and early differentiation of the Talpidae are poorly understood. It is usually believed that moles are closely related to shrews and belong to Soricomorpha (Gregory, 1910; Saban, 1958; McKenna, 1975a; Novacek, 1986). The features of talpids that McDowell (1958) regarded as erinaceomorph characters, such as the presence of the zygomatic arches and ectopterygoid process, are undoubtedly plesiomorphic; therefore, the assignment of Talpidae to Erinaceomorpha (McDowell, 1958; McKenna and Bell, 1997) is groundless (see Butler, 1988).

Within extinct groups, the family Proscalopidae (Late Eocene–Middle Miocene of North America, Early Oligocene of Asia) is most similar to Talpidae and placed along with them in the superfamily Talpoidea (Barnosky, 1981; Geisler, 2004). The family Dimylidae is also related to the Talpidae and placed in Talpoidea (see Schmidt-Kittler, 1973; McKenna and Bell, 1997). The origin of Talpoidea is probably connected with Early Eocene Asian soricomorphs that are possibly related to nyctitheriids; however, this ancestral group remains unknown (see also Sigé et al., 1977; Butler, 1988).

In the Nesophontidae (Fig. 57m), the upper molars are secondarily simplified due to almost complete reduction of the hypocone and conules and reduction of the paracone (metadilambdomorph type). This structural type could have developed independently from a primitive variant of the eudilambdomorph type.

The eudilambdomorph type could have given rise to the parazalambdomorph type, which is characteristic of Paleogene apternodontids and living solenodontids (see Section 5.1.6). Regarding the degree of development of the paracone and reduction of the metacone and talonid, it exceeds the protozalambdomorph type but is inferior to the euzalambdomorph type. It is qualitatively distinguished by the primary presence of the hypocone on the lingual lobe; however, advanced variants of this type lose the hypocone but retain the protocone and, thus, only slightly differ from the most advanced variants of the protozalambdomorph type (Figs. 57n, 57o).

The analysis of evolutionary changes in the dentition has discovered the following sequences of types of molar structure in soricomorphs:

(1) protodilambdomorphy ⟶ protozalambdomorphy ⟶ euzalambdomorphy;

(2) protodilambdomorphy ⟶ eudilambdomorphy (including ectodilambdomorphy);

(3) eudilambdomorphy ⟶ metadilambdomorphy;

(4) eudilambdomorphy ⟶ parazalambdomorphy.

These sequences admit the following taxonomic interpretation:

(1) primitive protodilambdodont soricomorphs ⟶ protozalambdodont tenrecids ⟶ euzalambdodont tenrecids;

(2) primitive protodilambdodont soricomorphs ⟶ primitive eudilambdodont soricomorphs (including advanced nyctitheriids) ⟶ ectodilambdodont soricomorphs (talpoids and soricids);

(3) primitive eudilambdodont soricomorphs ⟶ nesophontids;

(4) primitive eudilambdodont soricomorphs ⟶ parazalambdodont soricomorph (apternodontids and solenodontids).

In cases 1, 3, and 4, "primitive soricomorphs" imply the Geolabididae or related insectivores, while in case 2, the Nyctitheriidae or related groups. These sequences, in view of their agreement with other morphological data, probably correspond to large evolutionary branches of soricomorph insectivores (Fig. 58), which correspond taxonomically to the infraorders Tenrecomorpha (1) and Soricota (2–4) and the superfamilies Nesophontoidea (3) and Solenodontoidea (4) within Soricota.

The families composing Soricota are grouped in the superfamilies Micropternodontoidea (only Micropternodontidae), Nesophontoidea (Geolabididae and Nesophontidae), Soricoidea (Nyctitheriidae, Soricidae, and Plesiosoricidae), Talpoidea (Talpidae, Proscalopidae, and Dimylidae), and Solenodontoidea (Apternodontidae, Solenodontidae).

5.2. *Erinaceomorpha*

In the Early Paleogene, erinaceomorphs were rather abundant and diverse in North America and Europe (see Krishtalka, 1976a; Gingerich, 1983; Novacek et al., 1985; McKenna and Bell, 1997). In Asia, they played a less significant role up to the Late Eocene and Oligocene. The family Erinaceidae, known in North America from the Paleocene, appeared in Asia in the Early Eocene and widely diversified in the Middle and Late Eocene, while members of other families of Erinaceomorpha have not been recorded in Asia with certainty.

Only a few allegedly nonerinaceid erinaceomorphs were recorded in the Paleogene of Asia (Sulimski, 1970; Russell and Gingerich, 1981; Rich et al., 1983; Gabunia and Gabunia, 1987; Gabounia and Chkhikvadze, 1997). The first reference cited reflects the concept developed in the 1960s and 1970s that the Eocene–Oligocene Asian genera *Tupaiodon* and *Ictopidium* belong to the family Adapisoricidae (McKenna, 1960; Russell, 1964; Romer, 1966; Van Valen, 1967; Sulimski, 1970; etc.); at present, these genera are usually assigned to the subfamily Tupaiodontinae of the family Erinaceidae (Butler, 1988; Storch, Dashzeveg, 1997; McKenna and Bell, 1997; see below, Section 5.2.2). Some researchers placed these genera in the family Dormaaliidae (= Amphilemuridae) (Rich, 1981; Rich et al., 1983). Thus, in my opinion, fragmentary teeth of Erinaceomorpha from the Upper Eocene Caijiachong Formation (China, Yunnan) that were described as "Dormaaliidae genus and species indet." (Rich et al., 1983, p. 61, text-fig. 3) in fact belong to Tupaiodontinae indet. (this concerns at least P_4 and fragmentary M_3 with a distinct hypoconulid; see also Butler, 1988). The specimens described in the same paper as "Dormaaliidae or Erinaceidae" (Rich et al., 1983, p. 69, text-fig. 6) most likely belong to Galericinae (see Lopatin, 2004c). Therefore, it is possible to disregard the data cited in some reviews on presumable presence of Amphilemuridae in the Upper Eocene of China (see McKenna and Bell, 1997, p. 275).

The taxonomic position of *Seia shahi* Russell et Gingerich, 1981 from the basal Middle Eocene of Pakistan (age is given after Gingerich, 2003) was initially indicated as "Suborder ?Erinaceomorpha, family undetermined, probably new" (Russell and Gingerich, 1981, p. 278) and, subsequently, as Erinaceomorpha indet. (McKenna and Bell, 1997, p. 274). In fact, in outlines and general structural pattern of M^1 and M^2, this species resembles primitive erinaceomorphs, such as Paleocene–Early Eocene *Scenopagus* McKenna et Simpson, 1959 (Sespedectidae), but differs in the absence of a well-developed hypocone, which is atypical of erinaceomorphs. In M^1 and M^2 of *Seia*, the position of the hypocone is occupied by a moderately developed hypoconal shelf, with a rudimentary ridgelike cuspule in M^1. At present, *Seia* is assigned to the family Toliapinidae Hooker, Russell et Phélizon, 1999 of the superfamily Microsyopoidea of the order Plesiadapiformes (Hooker et al., 1999).

Another mentioning is "Erinaceoidea cf. Dormaaliidae" from the Upper Eocene Middle Aksyir Subformation of the Zaisan Depression (Gabunia and Gabunia, 1987, text-fig. 1.8). The material is a lower molar, which was identified as M_2 and tentatively assigned to the Dormaaliidae based on the presence of a large hypoconulid. In my opinion, the shape and structure of this tooth suggest this is M_3 of a representative of Tupaiodontinae (see Rich et al., 1983, text-fig. 3E; Storch and Dashzeveg, 1997, text-fig. 1.7). The other similar identification of insectivores from the Paleogene of the Zaisan Depression is "Insectivora cf. Dormaaliidae from the Middle Eocene Obaila Formation (Gabounia and Chkhikvadze, 1997, p. 195); this note is not accompanied by figures or additional comments.

Thus, to date, there are no reliable data on the presence of primitive erinaceomorphs in Asia.

The Erinaceidae appeared in Asia for the first time in the Early Eocene. They probably diverged much earlier, which is evident from the finds of Erinaceidae in the Lower Eocene Wutu Formation of China. "Erinaceidae gen. et sp. nov. cf. *Litolestes*" found there resembles the Galericinae (Tong and Wang, 1998); *Changlelestes dissetiformis* represents a special endemic subfamily Changlelestinae (Tong and Wang, 1993, 1998; Tong, 1997), while "Changlelestidae gen. et sp. nov." is regarded as the earliest representative of the Tupaiodontinae (Lopatin, 2004a). Apparently, the earliest radiation of hedgehogs in Asia occurred during the Holarctic faunal exchange at the Paleocene–Eocene boundary. In the Middle Eocene, the Asian Erinaceidae were represented by the Tupaiodontinae and Galericinae; in the Late Eocene, they were supplemented by the Erinaceinae (*Amphechinus* sp. from the Ergilin-Dzo locality, see Lopatin, 2005a) and, probably, by the Brachyericinae. At the onset of the Oligocene, hedgehogs became the most diverse insectivore group of Asia. In the Oligocene Shand-Gol Fauna of Central Asia, erinaceids are represented by at least 15 species (Lopatin, 1999, 2002a, 2003d, 2003f; Lopatin and Zazhigin, 2003), including both very small and relatively large taxa and taxa adapted to phytophagy or predation. As a matter of fact, in the Oligocene of Asia, hedgehogs occupied almost all niches of terrestrial entomophages.

5.2.1. Changlelestinae

This group was initially established within Soricomorpha as a particular family, the Changlelestidae (Tong and Wang, 1993, 1998; Tong, 1997). In addition to Early Eocene *Changlelestes*, it included Eocene–Oligocene *Tupaiodon* and *Ictopidium* (which along with *Zaraalestes* are usually placed in the Erinaceidae as the subfamily Tupaiodontinae, see Butler, 1988; McKenna and Bell, 1997) as well as *Ernosorex*. The group combining *Tupaiodon* and *Ictopidium* retained subfamily rank and the name Tupaiodontinae (see Tong, 1997); however, contrary to ICZN, the family continued to be called Changlelestidae. McKenna and Bell (1997) assigned *Changlelestes* to the subfamily Tupaiodontinae (which was placed in the Erinaceidae), while *Ernosorex* was assigned to the Plesiosoricidae.

Changlelestes was originally assigned to Soricomorpha based on superficial similarity to primitive Nyctitheriidae, such as *Leptacodon.* It was emphasized that it has distinct denticles on the lower incisors (Tong and Wang, 1993). This character was thought to distinguish Changlelestinae from Tupaiodontinae (Tong, 1997); however, this is not the case, since I have found similar denticles on the lower incisor of *Zaraalestes minutus* (Matthew et Granger, 1924) from the Oligocene of Mongolia (Lopatin, 2003d). The presence of these must not be regarded as a diagnostic character because, on the one hand, it is only observed in some rather than all soricomorphs, such as Soricidae, on the other hand, early erinaceids, for example, Late Paleocene *Litolestes* and Middle Eocene *Eochenu*s, had similar denticles on the lower incisors (Schwartz and Krishtalka, 1976; Wang and Li, 1990, text-fig. 4). *Changlelestes* differs from primitive nyctitheriids in the following erinaceomorph characters: (1) directional decrease in molar size from $M^1/_1$ to $M^3/_3$; (2) strong crests of the postcrista on P^3 and P^4 and of the metacrista on M^1 and M^2; (3) the absence of metacone on P^4; (4) the absence of precingulum on the upper molars; (5) short talonid of P_4; and (6) in the more profound differentiation of the hypoconulid from the entoconid in M_1 and M_2. The cristid oblique highly ascending on the posterior wall of the trigonid, which seems at first sight a distinctive soricomorph character, is in fact characteristic of some primitive Erinaceomorpha, for example, Paleocene *Litolestes* and *Litocherus* (Novacek et al., 1985; Butler, 1988); consequently, it could have been inherited by *Changlelestes* from primitive Erinaceidae.

In my opinion, the Changlelestinae is a separate subfamily of the Erinaceidae. The absence of a distinct hypocone on P^3 and P^4, the presence of three increased lower incisors, nonreduced P_2, reduced paraconid and metaconid of P_4, small talonid basin of P_4, and, particularly, the presence of a large hypoconulid on M_1 and M_2 clearly distinguish the Changlelestinae from the

Tupaiodontinae and other erinaceids. Apparently, the Changlelestinae are an early specialized Asian erinaceid group closely related to the primitive Paleocene North American Erinaceidae incertae sedis. The genus *Entomolestes* Matthew, 1909 from the Middle Eocene of North America, which is usually referred to as Erinaceidae indet. (Novacek et al., 1985), or, sometimes, placed in Tupaiodontinae (Butler, 1988; McKenna and Bell, 1997) is probably related to the subfamily Changlelestinae.

5.2.2. Tupaiodontinae

The Tupaiodontinae are known exclusively from the Eocene and Oligocene of Asia. Like the Changlelestinae, the Tupaiodontinae have serrated incisors resembling those of nyctitheriids. They are small animals, with the dental formula $I^3/_3C^1/_1P^4/_{4-3}M^3/_3$, the cheek teeth of which resemble those of galericines. *Zaraalestes russelli* Storch et Dashzeveg, 1997 comes from the Middle Eocene of Mongolia; *Ictopidium lechei* Zdansky, 1930 is from the Upper Eocene of China; and *Zaraalestes minutus* (Matthew et Granger, 1924) (= *?Tupaiodon minutus*; = *Ictopidium tatalgolensis* Sulimski, 1970) and *Tupaiodon morrisi* Matthew et Granger, 1924 are from the Lower Oligocene of Mongolia (Matthew and Granger, 1924; Zdansky, 1930; Sulimski, 1970; Storch and Dashzeveg, 1997; Tong, 1997). The Lower Oligocene Buran Formation of eastern Kazakhstan yielded *Tupaiodon* sp., *"Ictopidium* cf. *tatalgolensis"* and *Ictopidium* sp. (Gabunia and Gabunia, 1987; Shevyreva, 1995). L.K. Gabunia recorded *Tupaiodon* sp. in the Middle Eocene Sargamys Formation and *Ictopidium* sp. in the Upper Eocene Lower Aksyir Subformation in the Zaisan Depression (Gabounia and Chkhikvadze, 1997).

All species of Tupaiodontinae are represented by jaw fragments. They have three pairs of relatively small incisors in the upper and lower jaws, specialized antemolars (small canines, reduced $P^1/_1$–$P^3/_3$), semimolarized $P^4/_4$, and broad molars. The small hypocone on P^4–M^2, the reduced hypoconulid and wide postcingulid on M_1 and M_2, and the posteriorly projecting hypoconulid on M_3 are characteristic of this subfamily (Storch and Dashzeveg, 1997). The identification of genera and species of Tupaiodontinae is complicated by the incompleteness of specimens used in the original descriptions based of a number of taxa. *Tupaiodon morrisi* is represented by a maxilla with C^1–M^3 and a lower jaw fragment with M_2 and M_3 (Matthew and Granger, 1924); *Zaraalestes minutus* and *Ictopidium lechei* were described based on lower jaw fragments with incomplete tooth rows (Matthew and Granger, 1924; Zdansky, 1930; Sulimski, 1970; Tong, 1997). The material of *Zaraalestes russelli* includes P^4–M^2, C_1, P_4–M_3 (Storch and Dashzeveg, 1997). The formula of the lower teeth is completely known for *I. lechei* ($I_3C_1P_4M_3$), and *Z. russelli* ($I_3C_1P_3M_3$); however, the data on the number of antemolars are based mostly on the interpretation of the number and proportions of alveoli anterior to P_3/P_4.

Sulimski (1970) described a small representative of Tupaiodontinae from the Shand-Gol Formation of the Tatal-Gol and Khatan-Khayrkhan localities and assigned it to a new species, *Ictopidium tatalgolensis.* His material includes lower jaws fragments with incomplete tooth rows, which characterize P_2–M_3 and alveoli of four anterior teeth (I_1–C_1). Sulimski has assigned this species to *Ictopidium* rather than to *Tupaiodon* based on the single-rooted canine and reduced dental formula (although he compared the lower teeth of *I. tatalgolensis* with the upper tooth row of *T. morrisi* and interpreted alveoli of the lower antemolars of *I. lechei* as $I_{1-3}C_1P_{1-3}$, including double-rooted P_2). The researcher indicated that, in the structure of P_3 and P_4 and the presence of the labial cingulid on M_1, *?T. minutus* is similar to *Ictopidium* and possibly belongs to this genus. According to Sulimski, the differences between *I. tatalgolensis* and *?T. minutus* are restricted to their sizes.

Russell and Zhai (1987) synonymized *I. tatalgolensis* with *?T. minutus.* Wang and Li (1990) believed that *Ictopidium* and *Tupaiodon* are closely related genera (if not the same genus) and showed that, between C_1 and P_3, *I. lechei* had two single-rooted premolars (P_1 and P_2) rather than one double-rooted P_2. This inclined them to propose that *I. tatalgolensis*, which lacks P_1 should not be assigned to the genus *Ictopidium.* They disagreed with the idea that *I. tatalgolensis* is a synonym of *?T. minutus* because *I. tatalgolensis* has a better developed metalophid (= protocristid) of P_4–M_3, elongated M_1, and reduced M_3 without a hypoconulid.

Storch and Dashzeveg (1997) indicated that the taxa considered did not differ in the degree of the development of the protocristid or relative sizes of molars. They also showed that *I. tatalgolensis* and *?T. minutus* are identical in the sizes of jaws and teeth and proposed that M_3 of the holotype of *I. tatalgolensis* lacked the hypoconulid because it was broken off. Thus, Storch and Dashzeveg regarded *I. tatalgolensis* as a junior synonym of *?T. minutus* and assigned this species to the genus *Zaraalestes* (based on the same dental formula as in *Z. russelli* and similar structure of P_4–M_3).

The taxonomic position and composition of the Tupaiodontinae were repeatedly revised. In the original descriptions, *Tupaiodon* was tentatively referred to Tupaiidae (Matthew and Granger, 1924), while *Ictopidium* was assigned to Leptictidae (Zdansky, 1930; see also Li and Ting, 1983; Carroll, 1988). Subsequently, they were placed in Erinaceomorpha and both or one of them were included in the Amphilemuridae (Van Valen, 1967; Sulimski, 1970; Rich, 1981; Rich et al., 1983) or Erinaceidae (McKenna and Simpson, 1959; Mellett, 1968; Novacek, 1985; Russell and Zhai, 1987; Butler, 1988; Wang and Li, 1990; Gould, 1995; McKenna and Bell, 1997; Storch and Dashzeveg, 1997). Novacek et al. (1985) referred *Ictopidium* to as Insectivora incertae sedis, possibly related to Palaeoryctoidea or Soricomorpha. Butler (1988) combined *Tupaiodon* and *Ictopidium* in a distinct subfamily (Tupaiodontinae) of Erinaceidae and proposed that it also includes erinaceoids from the Upper Eocene of China (Rich et al., 1983) and *Entomolestes* from the Middle Eocene of North America. Tong and Wang (1993) placed *Tupaiodon* and *Ictopidium* along with *Ernosorex* Wang et Li, 1990 and *Changlelestes* Tong et Wang, 1993 in a special soricomorph family, which they named Changlelestidae regardless of the principle of priority (see above). McKenna and Bell (1997) included *Tupaiodon, Ictopidium, Entomolestes*, and *Changlelestes* in Tupaiodontinae. Storch and Dashzeveg (1997) believed that the subfamily Tupaiodontinae comprised the genera *Tupaiodon*, *Ictopidium*, and *Zaraalestes* established by them, but exclude *Entomolestes* and *Changlelestes* from this subfamily. I share this point of view, and place *Changlelestes* in a distinct subfamily (see above).

It should be noted that *"Tupaiodon" huadianensis* recorded in the Middle Eocene Huadian Fauna (Wang and Li, 1990) does not belong to the genus *Tupaiodon* (Storch and Dashzeveg, 1997) and probably belongs to Galericinae rather than to Tupaiodontinae (Tong, 1997; Lopatin, 2004c). It differs from all Tupaiodontinae in its very large P_4 (relative to M_1), the absence of a paracristid blade of P_4, the lower trigonid of M_1 and M_3, and the deviating more anteriorly (i.e., less transverse) paracristid of M_1.

5.2.3. Galericinae

Hedgehogs of the subfamily Galericinae (gymnures or hairy hedgehogs), the geographical distribution of which is presently restricted to southeastern Asia, were a widespread and rather diverse Holarctic group in the Paleogene and Neogene. In the Late Eocene–Early Pliocene, the Galericinae inhabited Europe; in the Oligocene and Miocene, they dwelt in North America; and in the Miocene, they occurred in the north of Africa (McKenna and Bell, 1997). In Asia, they were recorded beginning from the Middle Eocene (Wang and Li, 1990; McKenna and Bell, 1997); at present, they are also known in the uppermost Lower Eocene (*Protogalericius*; see Chapter 3).

To date, about ten taxa of gymnures have been recorded in the Paleogene of Asia, including Early Eocene *Protogalericius averianovi* gen. et sp. nov. from Kyrgyzstan; Middle Eocene *Eochenus sinensis* Wang et Li, 1990 from northeastern China and two taxa described above, *Eogalericius butleri* Lopatin, 2004 and *Microgalericulus esuriens* gen. et sp. nov. from Mongolia; Late Eocene *Oligochenus grandis* Lopatin, 2005 from Mongolia; Late Eocene or Early Oligocene *Pseudoneurogymnurus shevyrevae* Gureev, 1979 and *P. zhchikvadzei* Gureev, 1979 from eastern Kazakhstan; and Early Oligocene *Neurogymnurus indricotherii* Lopatin, 1999 from western Kazakhstan (Gureev, 1979; Wang and Li, 1990; Lopatin, 1999, 2004c, 2005a). *"Tupaiodon" huadianensis* Wang et Li, 1990 from the Middle Eocene of China may also belong to Galericinae (Lopatin, 2004c). In addition, Galericinae indet. were recorded in several stratigraphical levels of different age from the Upper Eocene–Lower Oligocene deposits of the Zaisan Depression of eastern Kazakhstan (Gureev, 1979; Gabunia and Gabunia, 1987; Gabounia and Chkhikvadze, 1997).

Erinaceids from the Early Eocene Wutu Fauna (China, Shandong) that were determined as "Erinaceidae gen. et sp. nov. cf. *Litolestes*" (Tong and Wang, 1998, text-fig. 3C) and some erinaceoids from the Upper Eocene Caijiachong Formation (China, Yunnan) that were described as Erinaceidae gen. et sp. indet. and "Dormaaliidae or Erinaceidae" (Rich et al., 1983, text-figs. 4A, 4B, 4G, 4H, 6) probably belong to the Galericinae.

Eogalericius butleri, one of the earliest representatives of Galericinae, shows at first sight certain similarity to Tupaiodontinae; it is particularly similar to *Zaraalestes russelli* of approximately the same age from the Middle Eocene of Mongolia (Storch and Dashzeveg, 1997). This similarity is observed in the shape of P^4–M^2 (widened transversely, with a well-pronounced longitudinal constriction in the middle part, large stylar lobes, and small hypocone); in the structure of M_1–M_3; and in the presence of the hypoconulid on M_3. However, the occlusal surface of P^4–M^2 of *Eogalericius* is less widened and the hypocone is much better developed than in *Zaraalestes*. *Eogalericius* is distinguished from all Tupaiodontinae by the presence of the postparaconule crest, well-developed paraconule, and the conical rather than ridgelike metaconule of M^1 and M^2; its I_1 is not increased, C_1 is only slightly reduced, P_2 is double-rooted, the protoconid of P_3 is low and laterally compressed; P_4 is relatively larger, lacks a paracristid blade and has a reduced metaconid and a more median talonid cusp; the trigonids of the lower molars are lower, the cusps and crests are less sharp, the paracristid of M_1 is shorter, and the hypoconulid of M_3 is partially fused with the entoconid.

The dental formula and the structure of upper and lower teeth strongly suggest that *Eogalericius* belongs to Galericinae. The presence of two mental foramina is a primitive character typical for the Amphilemuridae and primitive Erinaceidae, such as *Litolestes, Leipsanolestes*, and *Litocherus* (Novacek et al., 1985). The double mental foramen is occasionally observed in the variation range of later Galericinae, for example, in *Eochenus* (Wang and Li, 1990, p. 193), *Neurogymnurus* (Viret, 1947, text-fig. 4), *Galerix* (Butler, 1948, pp. 465, 468) and *Lanthanotherium* (Baudelot, 1972, text-fig. 69).

The slightly anteriorly deviating (subtransverse) paracristid and short trigonid of M_1 are functionally correlated plesiomorphic characters typical for *Eogalericius, Eochenus*, and primitive Late Paleocene–Early Eocene North American Erinaceidae (Novacek et al., 1985). In *Eogalericius* and *Eochenus*, the paracristid deviates anteriorly to a greater extant than in primitive Erinaceidae.

Within the Galericinae, only *Eogalericius* and *Eochenus* have a hypoconulid on M_3; however, it is also present in Tupaiodontinae (Butler, 1988; Storch and Dashzeveg, 1997). Primitive Erinaceidae have a hypoconulid on each lower molar (Novacek et al., 1985). Thus, this character is also plesiomorphic. At the same time, *Eogalericius* demonstrates partial or even complete fusion between the hypoconulid and entoconid. In the last case (Pl. 7, fig. 7b; Fig. 30k), the lingual region of the talonid forms a relatively large posterior projection resembling that of M_3 of Galericini sensu stricto (see Engesser, 1972, text-fig. 2; 1980, text-figs. 3, 14; Novacek et al., 1985, text-fig. 4A; Mein and Martín-Suarez, 1993, text-fig. 3, pl. I, fig. 6) and *Neurogymnurus* (Viret, 1947, text-fig. 3).

Phylogenetic relationships of gymnures are poorly understood. Most of the genera of Galericinae are usually assigned to the tribe Galericini (Gould, 1995; McKenna and Bell, 1997), exceptions are only provided by the genera *Neurogymnurus* and *Proterix*, each placed in a monotypic tribe. Hoek Ostende (2001a) includes only four genera in Galericini, i.e., *Galerix* (= *Tetracus*; = *Pseudogalerix*), *Parasorex, Schizogalerix*, and *Deinogalerix*. The concept of Galericini sensu stricto returns us to the system proposed by Butler (1948), with the separate tribes Galericini and Echinosoricini (the latter includes *Lantanotherium, Echinosorex, Hylomys*, and *Podogymnura*). The diagnostic characters of Galericini sensu stricto are as follows (Hoek Ostende, 2001a): the width of M^1 and M^2 is much greater than the length; the metaconule of M^1 and M^2 has a posterior arm (postmetaconule crest); P^3 has a well-developed lingual projection, which has at least a well-developed protocone; and M^3 is simplified, usual lacking a metastylar crest (metacrista). The structure of unknown P^3 being excluded, *Eogalericius* corresponds well to the diagnosis of Galericini sensu stricto. However, as indicated above, it considerably differs from the majority of Galericinae in the shape and structure of P^4–M^2 and P_4–M_3. Until a more detailed system of Galericinae is developed, *Eogalericius* should be assigned to Galericini sensu lato.

Within the Galericinae, *Eogalericius* is most similar to *Eochenus* from the Middle Eocene of China (Huadian Fauna). However, all characters shared by these genera (broad and short P^4–M^3, M_1, and M_2, relatively short trigonid and subtransverse paracristid of M_1, and the presence of the hypoconulid on M_3) should be regarded as plesiomorphic; therefore, there is no reason to combine them in a special supergeneric taxon.

Eogalericius is more primitive than *Eochenus* in the following characters: its P_2 and P_3 are reduced to a much lesser extent, P_4 is smaller, the paraconid and metaconid of P_4 are better developed, and the mental canal opens in two foramina. This agrees with the earlier age of the Khaychin Fauna than the Huadian Fauna (Wang and Li, 1990).

Thus, it is plausible that *Eogalericius* is morphologically and phylogenetically close to the ancestor of all Galericinae.

Microgalericulus gen. nov. is similar to *Eogalericius* of the same age in the weakly reduced P_3 and relatively small P_4 with a well-developed paraconid and differs in its laterally compressed P_3, narrow P_4 with a longer talonid and less developed metaconid, relatively narrower and higher M_1 and M_2, elongated and more longitudinal positioned paracristid of M_1, and certain other dental characters (see Chapter 3), which apparently correlate with a more carnivorous feeding adaptation of the new genus.

Early Eocene *Protogalericius* gen. nov. is only poorly characterized by available remains. It is important that *P. averianovi* sp. nov. from Kyrgyzstan has retained P^3 with a large lingual projection and protocone (which coincides with the diagnosis of Galericini, see above). Massive P^4 suggests that *Protogalericius* belongs to an unspecialized lineage of the early Galericinae (compare with broad P^4–M^2 of *Eogalericius*). The relatively narrow trigonid and short subtransverse paracristid of M_1 of *Protogalericius* demonstrate that it is more primitive than Middle Eocene *Eogalericius, Microgalericulus*, and *Eochenus*, which agrees with the earlier age of taxon from Kyrgyzstan.

Late Eocene *Oligochenus* is similar in the structure of P_4–M_1 to Middle Eocene *Eochenus, Eogalericius*, and *Microgalericulus*; however, it has lost P_1 and its P_2 is considerably reduced. Seven alveoli anterior to P_4 of *Oligochenus grandis* are interpreted as alveoli of single-rooted I_1, I_2, I_3, C_1, and P_2 and double-rooted P_3 (Lopatin, 2005a). Within the Galericinae, the presence of large double-rooted P_3 and small single-rooted P_2 combined with the completely reduced P_1 is only characteristic of the genus *Podogymnura* (Butler, 1948; Gould, 1995, 2001). However, *Oligochenus* differs in the absence of diastemata between P_3/P_2 and P_2/C_1. Certainly, the same degree of reduction not necessarily results from close relationships between Paleogene *Oligochenus* and extant *Podogymnura*. In the structure of P_4 and M_1, *Oligochenus* is most similar to *Eochenus*, which also has relatively massive P_4 with a reduced metaconid and small paraconid (Wang and Li, 1990). In my opinion, *Oligochenus* may be a descendant of this taxon, the anterior teeth of which are more specialized.

Oligochenus grandis is large compared to Paleogene Galericinae (see Table 46); its teeth are approximately twice as large as those of *Eogalericius butleri* and *Microgalericulus esuriens*, considerably larger than in *Eochenus sinensis, Neurogymnurus indricotherii* (Lopatin, 1999, 2005a), and most of the species of *Galerix*, although they are substantially smaller than in European species of *Neurogymnurus* (Viret, 1947; Butler, 1948).

5.2.4. Brachyericinae

Short-faced hedgehogs (Brachyericinae) are known in the Oligocene and Miocene of Asia, Early Miocene of Europe, and Miocene of North America. They are characterized by a short facial region of the skull, a number of distinctive structural features in the ear region, and a reduced formula of cheek teeth ($I^3/_2C^1/_1P^2/_{1-2}M^2/_2$). To date, five genera of Brachyericinae have been described: *Brachyerix* Matthew, 1933 and *Metechinus* Matthew, 1929 from North America and *Exallerix* McKenna et Holton, 1967 (= *Metexallerix* Qiu et Gu, 1988), *Synexallerix* Lopatin et Zazhigin, 2003, and *Postexallerix* Lopatin et Zazhigin, 2003 from Asia (Matthew, 1929; Matthew and Mook, 1933; McKenna and Holton, 1967; Rich and Rich, 1971; Rich, 1981; Qiu and Gu, 1988; Gould, 1995; Lopatin, 1996, 2004f; Bi, 1999; Lopatin and Zazhigin, 2003). The isolated teeth described by Ziegler from the Early Miocene Petersbuch 2 locality (MN4a) in Germany under the names "*?Plesiosorex* n. sp." (Ziegler, 1990, p. 31, pl. 5, figs. 3, 5) and "*?Amphechinus* sp. 1 und sp. 2" (Ziegler, 1990, p. 25, pl. 3, figs. 9, 11) in fact belong to Brachyericinae and can be determined as *Synexallerix* sp. Thus, the Early Miocene geographical range of the genus *Synexallerix* included not only Asia but also Europe.

Asian Brachyericinae are known in Mongolia, China, and Kazakhstan. Early Oligocene *Exallerix hsandagolensis* McKenna et Holton, 1967 from Mongolia has two lower premolars, P_3 and P_4 (McKenna and Holton, 1967); this distinguishes it from all other Brachyericinae, which have only one lower premolar, P_4. Apparently, the evolution of the genus *Exallerix* was not unidirectional. In Early Miocene *E. efialtes* Lopatin, 1996 from western Kazakhstan, which presumably retained P_3, P_4 is reduced to at least the same extent as in Late Oligocene *E. gaolanshanensis* (Qiu et Gu, 1988) from China, while M_1 is even more specialized (the paracristid is long and the metaconid is reduced) than in this species. This lineage probably evolved independently of the *E. gaolanshanensis* lineage. In Early Oligocene *E. manahan* Lopatin et Zazhigin, 2003 from Mongolia, P_3 is rudimentary, the talonid of M_1 is shortened, M_2 is considerably reduced, and enamel tubercles on the labial surface of M_1 and M_2 are flat, only slightly differentiated, and form a very weak cingulid. Based on this list of characters (and dimensions), this species is regarded as an early representative of the *E. gaolanshanensis* lineage. Thus, two phylogenetic lineages are recognized within the genus *Exallerix*, i.e., *E. hsandagolensis–E. efialtes* and *E. manahan–E. gaolanshanensis* (Lopatin and Zazhigin, 2003).

The Miocene genus *Postexallerix* shows the most advanced specialization of the trigonid of M_1, developing the trend characteristic of *Exallerix*; in addition, its M_2 and enamel ornamentation of the lower molars are considerably reduced. *Postexallerix* is probably a direct descendant of a lineage that evolved from the genus *Exallerix*.

None of species of *Exallerix* could have given rise to *Synexallerix*, since in *E. gaolanshanensis*, the protocone of P^3, the parastyle of P^4 and M^1, the metastyle of M^2, and the paraconid of P_4 are reduced, while the enamel ornamentation is absent; in *E. hsandagolensis* and *E. efialtes*, the metastylid of M_1 is absent and the metaconid is reduced; in the three species, M_2 is considerably reduced. Thus, we have to hypothesize that, in the Oligocene, there was a special brachyericine lineage that gave rise to Early Miocene *Synexallerix*.

Synexallerix is an Asian brachyericine that is most similar to North American *Brachyerix* and *Metechinus* in the structure of the upper and lower teeth, parameters of M_1, and ratios between P_4, M_1, and M_2. This suggests that it could have been the ancestor of North American Brachyericinae. Since P_4 of *S. junggarensis* is relatively considerably reduced, it is probable that *Brachyerix* evolved from a more primitive species of *Synexallerix*. It is possible that *Brachyerix* and *Synexallerix* are connected by more remote relationship, that is, evolved from a common Oligocene ancestor that developed independently of the *Exallerix–Postexallerix* lineage.

The specialized dentition of Asian short-faced hedgehogs has no analogue among extant and extinct Erinaceidae. They are characterized by the considerably increased and elongated anterior lower incisor, the shortened lower jaw, considerably reduced antemolars, elongated M_1 with a bladelike paracristid, reduced M_2, and well-developed masticatory musculature displaced far anteriorly along the jaws. When describing these features of *Exallerix hsandagolensis* for the first time, McKenna and Holton (1967, p. 9) proposed that they provided the bite with strong compression, although it was slowed down, corresponding to the so-called nutcracker pattern, adapted for feeding on prey with a firm cover. The efficiency of shearing interaction between P^4 and M_1 was increased by the lingually open trigonid and elongated paracristid of M_1.

Gureev (1979, p. 76) believed that the teeth of Brachyericinae were mostly adapted for the treatment of coarse food and that they preyed predominantly on slow-acting animals, which were captured using the increased anterior incisors, and also consumed vegetable food (Gureev, 1979, pp. 98, 140). Apparently, the slow-acting animals with a firm cover imply bivalves and gastropods.

In the *Exallerix hsandagolensis–E. efialtes* lineage, M_1 increases in relation to P_4 and M_2; its trigonid increases in length and decreases in width, while the metaconid of M_1 is reduced; in addition, the masseteric crest is strengthened (Lopatin, 1996, 1999). This is interpreted as directional specialization of members of *Exallerix* for predatory mode of life. Similar changes in M_1 occurred in the Early Miocene *Synexallerix junggarensis–S. otus* lineage, and reached a peak in Early Miocene *Postexallerix securis* and Middle Miocene

P. mustelidens. The lower teeth of Miocene Asian brachyericines acquired clear features of convergent similarity to the teeth of small carnivores of the family Mustelidae: the anterior incisor is excessively developed in connection with functioning as a canine of a predatory type; the teeth anterior and posterior to M_1 are reduced; in M_1, the paracristid is very long and high, the metaconid is reduced, and the talonid is short (thus, M_1 has become a carnassial tooth of a sort). The shortened lower jaw and facial region of the skull, the high and massive horizontal ramus of the lower jaw, and the relatively low coronoid process are also characteristic of small mustelids (for example, *Mustela*). In the latest representative of Asian Brachyericinae, the Middle Miocene *Postexallerix mustelidens*, the talonid of M_2 decreased in size and was strongly simplified; this kind of reduction is atypical for insectivores but occurs in some carnivores, such as Mustelidae.

The efficiency of shearing interaction between the paracristid of M_1 and the postcrista of P^4 of Asian short-faced hedgehogs was provided by the high and sharp cutting edge of these crests. Using these sharp carnassial-like teeth and well-developed masseteric musculature, brachyericines were probably adapted not only for dissecting muscles and tendons of a prey, but also for cracking and splitting bones; this adaptive feature is characteristic of true predators and scavengers, distinguishing them from carnivorous–insectivorous mammals. The presence of massive masseteric musculature and large caniniform anterior incisors enabled them to kill relatively large animals, comparable in size with these predators. The basic prey of short-faced hedgehogs was probably small terrestrial vertebrates (rodents, lagomorphs, insectivores, lizards, frogs, etc.).

A similar predatory specialization in the structure of M_1 and P^4 is observed in members of *Deinogalerix* Freudenthal, 1972, an endemic galericine genus from the Late Miocene insular Gargano Fauna in Italy (Freudenthal, 1972; Butler, 1980; Hoek Ostende, 2001a). M_1 and P^4, which are enlarged compared to other cheek teeth of these gymnures, have high and long blades of the paracristid and postcrista, respectively; in addition, M_1 is very similar in proportions and structure to M_1 Brachyericinae. Consequently, *Deinogalerix*, like brachyericines, could cut muscular tissues and crash bones. *Deinogalerix* has a considerably elongated rostral region of the skull, a long and low lower jaw, increased I^1 and C_1, and other skeletal characters interpreted as adaptations for predation, with specialization of preying on relatively small-sized mobile animals, such as fish, amphibians, and crustaceans (Butler, 1980). According to Butler (1980, p. 54), large P^4 and P_4 and strong trigonid of M_1 of *Deinogalerix* provided effective crushing of bones and crustacean shells. Thus, despite different directions of predatory specialization of *Deinogalerix* and Brachyericinae, the formation of a strong cutting-crashing tool resulted in similar modifications of P^4 and M_1.

Some cranial and lower jaw features of *Exallerix* are correlated with the modification of the masticatory apparatus. The well-developed postorbital processes and frontal crests, the relatively high anterior region of the sagittal crest (Qiu and Gu, 1988, text-fig. 2), and distinct medial crest at the base of the coronoid process suggest a large anterior portion of the temporal muscle, which provide strong pressing effect of the postcrista of P^4 and the paracristid of M_1. The unique (for insectivores) structure of the lower masseteric crest correlates with the excessive development of the anterior portion of the medial masseteric muscle, which functioned as a very strong adductor. The large finlike angular process, with a deep depression, is evidence of well-developed internal pterygoid muscle, which participated in transverse masticatory movements. The large digastric muscle reconstructed based on the presence of a special area on the horizontal ramus of the lower jaw is probably attributable to the significant effort turning the lower jaw down, which provided a rapid and broad opening of the mouth for grasping prey.

The relatively large sizes (for Erinaceidae) of Asian brachyericines are probably also connected with the predatory mode of life. It should be noted that each species of Asian Brachyericinae coexisted with true hedgehogs of the subfamily Erinaceinae of approximately the same sizes and clear insectivorous–omnivorous feeding adaptation. In particular, the Shand-Gol Fauna contains, in addition to *Exallerix hsandagolensis* and *E. manahan*, four species of *Amphechinus*, including large *A. rectus* (Matthew et Granger, 1924) and *A. gigas* Lopatin, 2002 (Matthew and Granger, 1924; Trofimov, 1960; Sulimski, 1970; Huang, 1984; Lopatin, 2002a). The Erinaceidae of the Early Miocene Aral Fauna are represented by both *Exallerix efialtes* and three species of *Amphechinus*, including the relatively large *A. akespensis* Lopatin, 1999 (Lopatin, 1999, 2004f). Early Miocene *Synexallerix junggarensis* coexisted with at least two species of *Amphechinus* (Bi, 2000); and Early Miocene *Postexallerix securis* and Middle Miocene *P. mustelidens* coexisted with *Mioechinus* spp. (Lopatin and Zazhigin, 2003). This suggests the absence of pronounced competition for food between Brachyericinae and Erinaceinae.

5.2.5. Erinaceinae

The earliest remains of true hedgehogs (subfamily Erinaceinae) were recently described from the Upper Eocene Sevkhul Member of the Ergilin-Dzo Formation of the Ergilin-Dzo locality, Mongolia (Lopatin, 2005a). This is a left dentary fragment, with an excessively developed anterior incisor (I_2), roots of three single-rooted antemolars (I_3, C_1, and P_2) in alveoli, and a small double-rooted tooth interpreted as DP_4. The dental formula and increased I_2 suggest the assignment of this specimen to Erinaceinae, namely, to the genus *Amphechinus* Aymard, 1850 of the tribe Amphechinini Gureev, 1979. This find extends the lower limit of the stratigraphic range of Erinaceinae from the basal Oligocene to the uppermost Eocene. However, taking into account morphological and taxonomic diversity of Early Oligocene Erinaceinae, it is evident that in fact this subfamily appeared much earlier.

At present, six species of the Erinaceinae are known in the Early Oligocene Shand-Gol Fauna of Central Asia (Matthew and Granger, 1924; Trofimov, 1960; Mellett, 1968; Sulimski, 1970; Huang, 1984; Lopatin, 2002a, 2003e). They include five representatives of the tribe Amphechinini, i.e., *Palaeoscaptor acridens* Matthew et Granger, 1924, *Amphechinus rectus* (Matthew et Granger, 1924), *Amphechinus* cf. *minimus* Bohlin, 1942, *Amphechinus* aff. *kansuensis* Bohlin, 1942, and *A. gigas* Lopatin, 2002, and one species of the tribe Scymnericini Lopatin, 2003, *Scymnerix tartareus* Lopatin, 2003. *S. tartareus* was described based on an almost complete skull with the lower jaw from the Ulan-Khureh locality situated in the Nemegt Depression in southern Mongolia (Lopatin, 2003e).

The cranial structure of *Scymnerix tartareus* shows with confidence that it belongs to the subfamily Erinaceinae. At the same time, the cranial structure and dentition of *Scymnerix* display certain interesting features. The short facial region of the skull, the structure of the zygomatic arches, large I_2, single-rooted I^3, small C^1, reduced M^2, the absence of M^3, and the presence of enamel ornamentation on teeth of *S. tartareus* superficially resemble short-faced hedgehogs of the subfamily Brachyericinae. However, the ear region of *Scymnerix* lacks certain distinctive features characteristic of Brachyericinae (see Rich and Rich, 1971; Rich, 1981; Gould, 1995). In particular, it lacks ventrally closed tympanic bullae and ossified intratympanic arterial canals. On the contrary, the structure of the ear region strongly suggests that *Scymnerix* belongs to Erinaceinae. In addition, *Scymnerix* differs from Brachyericinae in the position of the lacrimal foramen, the presence of palatine fissures and a very large interparietal, the absence of a sagittal crest, less developed paroccipital processes, the presence of P^2, the better developed protocone of P^3, the presence of the metaconule on M^1, the absence of a well-pronounced extended masseteric crest on the lower jaw, in the relatively large P_4 with a distinctly differentiated trigonid, the shape of trigonids of M_1 and M_2, and the preservation of rudimentary M_3. Apparently, the similar structure of the facial skull region and reduced intermediate antemolars and posterior molars of *Scymnerix* and brachyericines result from parallel development and correlate with the shortening of the snout.

The shortening of the facial region of *Scymnerix* is associated with the relative positions of the upper cheek teeth and elements of the orbital region, i.e., the infraorbital foramen is above the central region of P^3, the anterior orbital border is above the anterior region of P^4, and the base of the zygomatic arch is in line with M^1. This structural pattern is also characteristic of Brachyericinae (Matthew and Mook, 1933; Rich and Rich, 1971; Rich, 1981; Qiu and Gu, 1988), while, in the other Erinaceidae, the infraorbital foramen is above P^4 or P^3/P^4, the anterior orbital border is above M^1, and the base of the zygomatic arch is above M^1/M^2. Within the Erinaceinae, the exception is provided by some Miocene Amphechinini, in particular, European *Dimylechinus bernoullii*, which has lost M^3 and M_3 (Hürzeler, 1944), and African *Amphechinus rusingensis* (Butler, 1956b).

The reduction of the tooth row in *Scymnerix* (its dental formula is $I^3/_2C^1/_1P^3/_2M^2/_3$) is manifested in the loss of M^3, a decrease in the number of roots in I^3 and P^2, a decrease in the size of C^1, and reduction of M^2, M_2, and M_3. M^2 is reduced to a greater extent than in *Dimylechinus* (Hürzeler, 1944), since it has lost the hypocone. M_3 is much more reduced than in Amphechinini or Erinaceini. The Erinaceidae that have lost M^3 usually lack M_3 (Brachyericinae and *Dimylechinus*); otherwise, both teeth are retained in a reduced condition (most of the Amphechinini and all Erinaceini). *Scymnerix* is an exception in this respect. Lipotyphla provide some examples of the presence of considerably reduced M_3 combined with the absence of M^3, for example, *Exoedaenodus* (Dimylidae) and *Suleimania* (Talpidae) (Ziegler, 1990; Hoek Ostende, 2001b). The increased anterior incisors are characteristic not only of Brachyericinae but also of Amphechinini.

The presence of the antorbital fossa is characteristic of small Galericinae, Brachyericinae, and Amphechinini; it is probably associated with small size (Butler, 1948). The position of the lacrimal foramen on the antorbital crest (instead of inside the orbit) is an advanced character typical of Erinaceini. The lacrimal duct is seen in lateral view in Protericini, Brachyericinae, and Erinaceinae. In Protericini, Brachyericinae, and Amphechinini, the lacrimal foramen is in the orbit, while in Erinaceini and Scymnericini, it is on the antorbital crest. Within the Erinaceinae, the relatively small palatine fissures and the absence of a nasopharyngeal fossa are only characteristic of Amphechinini. The large interparietal is a primitive character typical for Galericinae and some Amphechinini (Butler, 1948, 1956b). The nonemarginated occipital condyle is observed in Erinaceini, Brachyericinae, and Protericini. The postglenoid foramen separated from the glenoid fossa by the entoglenoid process is a primitive character distinguishing *Scymnerix* and Amphechinini from Erinaceini. The weak paroccipital processes and low position of the mandibular condyle (level with the tooth row) are also characteristic of Amphechinini.

In the size and shape of the ectotympanic bone (tympanic ring), *Scymnerix* resembles Galericinae and *Amphechinus* (Viret, 1938; Butler, 1948). The tympanic ring and auditory ossicles are infrequently preserved in the fossil record. Therefore, despite a significant amount of data on the ear region of extinct Erinaceidae (Viret, 1938; Butler, 1948, 1956b, 1980; Gawn, 1968; Rich and Rich, 1971; Rich, 1981; MacPhee et al., 1988; Gould, 1995; Meng et al., 1999), only little is known about the ectotympanic. *Scymnerix* displays the semiphaneric pattern, i.e., partial fusion between the ectotympanic and other components of the floor of the tympanic bulla. This pattern is typical for Erinaceidae, while the Brachyericinae are characterized by the aphaneric pattern, i.e., the ectotympanic is completely covered by the auditory capsule, which is formed by the sphenoid and petrosal (MacPhee et al., 1988).

Scymnerix lacks predatory adaptations characteristic of Brachyericinae in the structure of teeth and lower jaw; the structure of its teeth suggests adaptation for feeding on by tough plant and animal food.

The tribe Amphechinini comprised primitive Oligocene and Miocene Erinaceinae. It differs from Erinaceini in the position of the lacrimal foramen inside the orbit (instead of on the antorbital crest), the small palatine fissures, the position of the postglenoid foramen, the absence of a nasopharyngeal pocket, the low position of the mandibular condyle, and in the shape of P^4 and considerably increased I_2. The dental formula is $I^3/_2C^1/_1P^3/_{3-2}M^{3-2}/_{3-2}$. The most primitive representative of Oligocene Asian Amphechinini is probably *Palaeoscaptor acridens* (Rich and Rasmussen, 1973, text-fig. 6), M^3 of which is subtriangular in outline, as in Galericinae (rather than oval, as is characteristic of Erinaceinae); its M_3 has a differentiated talonid; in addition, it has a reduced supernumerary lower premolar (P_3), which is absent from all other Erinaceinae.

The genus *Amphechinus*, which is presently known beginning from the terminal Eocene, is one of the earliest genera of Erinaceinae. It was widespread in the Oligocene–Miocene of Eurasia and occurred in the Miocene of North America and Africa (Gureev, 1979; Gould, 1995; Ziegler, 2005). Seven species were described from Asia: *A. rectus* (Matthew et Granger, 1924), *A. kansuensis* (Bohlin, 1942), *A. minimus* (Bohlin, 1942), and *A. gigas* Lopatin, 2002 from the Oligocene of Mongolia and China; *A. akespensis* Lopatin, 1999, and *A. microdus* Lopatin, 1999 from the Early Miocene of Kazakhstan; and *A. bohlini* Bi, 2000 from the Early Miocene of China (Matthew and Granger, 1924; Bohlin, 1942; Trofimov, 1960; Mellett, 1968; Sulimski, 1970; Huang, 1984; Lopatin, 1999, 2002a; Bi, 2000). *A. minimus* and *A. microdus* are small-sized (approximately as large as extant *Sorex araneus* L.); *A. kansuensis* and *A. bohlini* are somewhat larger; *A. rectus* and *A. akespensis* are comparable in size to the lesser gymnures of the genus *Hylomys*; and *A. gigas* is slightly larger than the extant hedgehog *Erinaceus europaeus* L. (Lopatin, 2002a).

The earliest representative of the extant tribe Erinaceini is *Stenoechinus* Rich et Rasmussen, 1973 from the Lower Miocene of North America (McKenna and Bell, 1997). The Erinaceinae penetrated into North America from Asia as late as the beginning of the Miocene; therefore, the roots of this tribe are probably in the Oligocene of Central Asia.

5.2.6. Phylogenetic Relationships of Erinaceidae

The Erinaceidae probably deviated from primitive Erinaceomorpha early in the Paleocene in North America. Novacek et al. (1985) placed in this family (apart from known subfamilies) a large number of Early Paleogene North American genera, including *Litolestes* Jepsen, 1930, *Leipsanolestes* Simpson, 1928, *Entomolestes* Matthew, 1909, *Neomatronella* Russell et al., 1975, *Auroralestes* Holroyd et al., 2004 (= *Eolestes* Bown et Shankler, 1982), *Dartonius* Novacek et al., 1985, and *Cedrochoerus* Gingerich, 1983 as well as European *Adapisorex* Lemoine, 1883. Butler (1988) assigned *Dartonius* to Scenopaginae, while *Litolestes, Adapisorex*, and *Leipsanolestes* were removed from Erinaceidae based on the essentially different structure of the trigonid of M_1; the first was assigned to Dormaaliidae, the second was referred to as Erinaceomorpha incertae sedis, and the third was regarded as a member of a scenopagid–erinaceid lineage that deviated early from the ancestral stem. At present, *Litolestes* and *Cedrocherus* are regarded as Erinaceidae incertae sedis, while *Leipsanolestes, Auroralestes*, and *Dartonius* are Erinaceoidea incertae sedis (McKenna and Bell, 1997, p. 276; Holroyd et al., 2004).

The Eocene Asian finds of Erinaceidae show that the earliest representatives of the Changlelestinae, Tupaiodontinae, and Galericinae have inherited a number of primitive characters of Paleocene Erinaceomorpha, including the complete dental formula, relatively short trigonid and subtransverse paracristid of M_1, the hypoconulid (in Changlelestinae, on all molars; in Tupaiodontinae and Galericinae, only on M_3), and the double mental foramen. Thus, the ancestral groups of the Changlelestinae, Tupaiodontinae, and Galericinae probably emerged in the Late Paleocene of North America and radiated in Asia in first half of the Eocene. The subfamilies Changlelestinae and Tupaiodontinae are probably closer to each other than to Galericinae.

Apparently, all extant gymnures are descendants of Early Paleogene Galericini sensu lato. The origin of Erinaceinae and Brachyericinae is probably also connect with Paleogene Galericinae. However, it is evident that neither Galericini sensu stricto nor Neurogymnurini may not be regarded as immediate ancestors of these groups because the first are too primitive, while the second are too specialized. Once, Butler (1948) proposed that the erinaceid group comprising *Metechinus* and *Brachyerix* might have been connected with *Neurogymnurus* and even placed the tribe Brachyericini in the subfamily Neurogymnurinae. However, all characters shared by Brachyericini and Neurogymnurini are primitive for Erinaceidae and should not be regarded as evidence of their close relationship.

The tribe Protericini is characterized by the intermediate condition of some cranial characters between typical Galericinae, on the one hand, and Brachyericinae + Erinaceinae, on the other. In particular, in Protericini, the lacrimal duct is seen in lateral view and the lacrimal

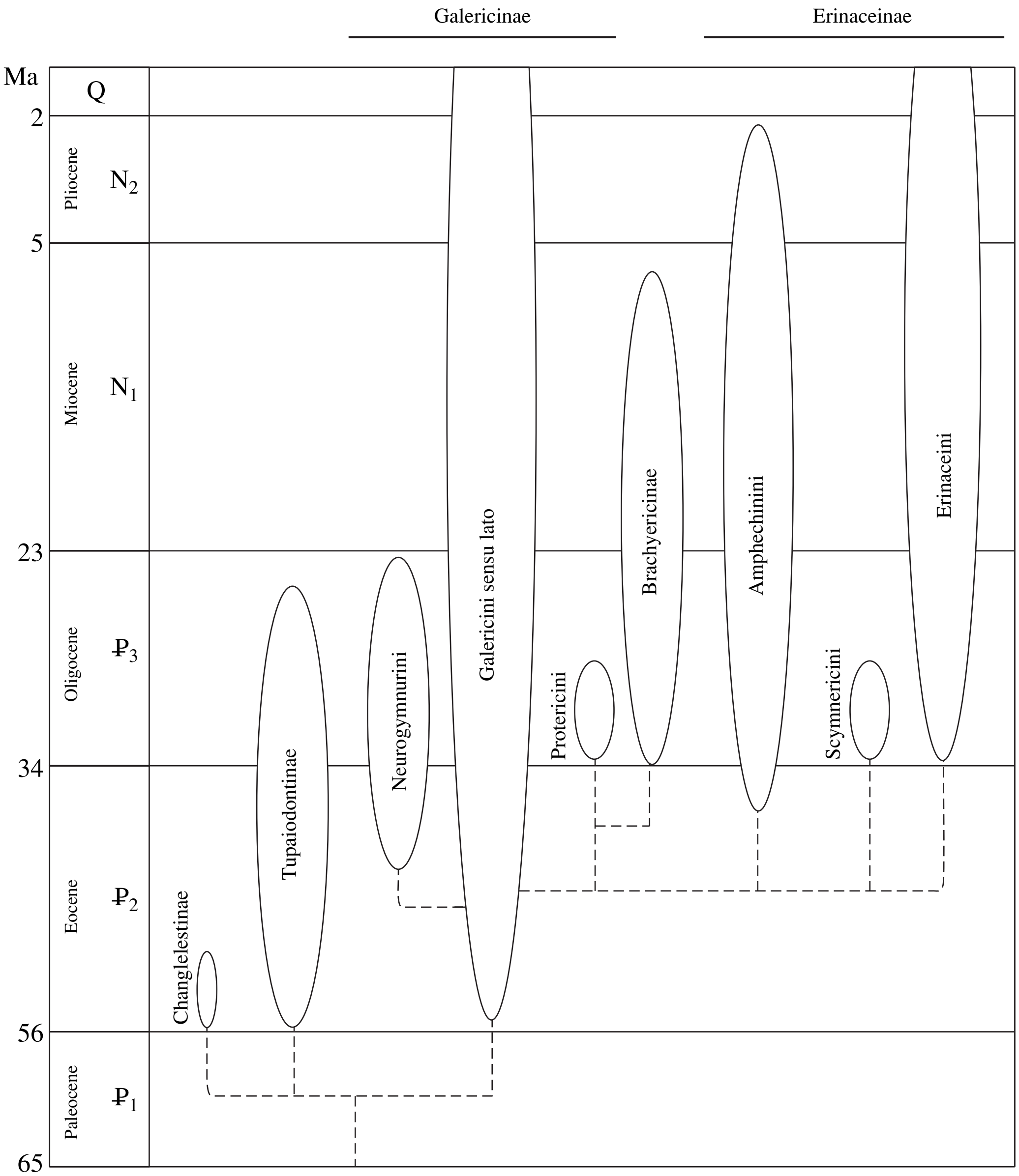


Fig. 59. Scheme of phylogenetic relationships in Erinaceidae.

foramen opens in the orbit, as in Brachyericinae and Amphechinini; the occipital condyle is not emarginated, as is Brachyericinae and Erinaceini. Thus, the taxonomic position of the tribe Protericini is estimated differently, as a primitive tribe of Erinaceinae (Butler, 1948; Gureev, 1979), a specialized tribe of Galericinae (McKenna and Bell, 1997), or a distinct subfamily, the Protericinae (Butler, 1988). Sometimes, *Proterix* is referred to as Erinaceidae incertae sedis (Gawn, 1968). Butler (1988, p. 123) indicated that Protericini is the only hedgehog group that emerged in North America (apparently, in the Late Eocene). Certainly, the Early Oligocene North American *Proterix* by itself is too specialized and lived too late to be related to the origin of Erinaceinae or Brachyericinae. The description of its probable Late Eocene North American ancestor, which was mentioned by Butler (1988, p. 123), has not been published. The Eocene ancestors and close relatives of *Proterix* most likely inhabited Asia. These hypothetical Asian protericines could have appeared as a result of radiation of Galericinae in the Middle Eocene or at the beginning of the Late Eocene. Apparently, they were less specialized than *Proterix*. However, the realization of the same trends towards the shortening of the facial region of the skull and reduction of the dentition could have resulted in the appearance in this group of ancestors of Brachyericinae, which adapted to predation.

It should be noted that I_1 of *Proterix* is increased, while P_3 is substantially larger than P_2 (Gawn, 1968). The increased anterior lower incisor of Brachyericinae is regarded as I_1 (Rich, 1981) or I_2 (Gould, 1995; Bi, 1999), and the lower premolar between the canine and P_4, which is sometimes present in *Exallerix*, is identified as P_3 (McKenna and Holton, 1967; Rich, 1981; Gould, 1995; Lopatin and Zazhigin, 2003) or P_2 (Bi, 1999). The dentition was independently reduced in Brachyericinae and Erinaceinae; therefore, there is no need to reject the hypothesis that the teeth discussed are in fact I_1 and P_3, respectively, which Brachyericinae inherited from Protericini.

The Erinaceinae could have evolved from certain other early group of Galericinae, which was closely related to the group ancestral to Protericini and Brachyericinae and developed in parallel towards the shortening of the snout and reduction of the anterior and posterior regions of the tooth rows. It was distinguished by certain other evolutionary trends, which resulted in the disappearance of I_1, excessive development of I_2, and reduction of P_3 and $M^3/_3$. Perhaps, this unknown ancestral group of relatively short-faced Galericinae deviated from other gymnures relatively early, probably, at the end of the Middle Eocene of at the beginning of the Late Eocene.

The dental structure of *Palaeoscaptor* suggests that the common ancestor of Amphechinini, Scymnericini, and Erinaceini retained P_3 and only slightly reduced $M^3/_3$. Accordingly, further reduction of teeth in each of the three tribes could have developed independently and in parallel. An alternative scenario implies the origin of Scymnericini and Erinaceini from one or two groups of primitive Amphechinini, which had already lost P_3 but had not acquired considerably increased I^1/I_2 (Fig. 59).

5.3. Didymoconida

The first representative of the family Didymoconidae was discovered in 1924, when Matthew and Granger (1924) described the genus *Didymoconus* (including the species *D. colgatei* and *D. berkeyi*) from the Oligocene of Mongolia (Hsanda Gol, or Shand-Gol, locality). The relatively small *D. colgatei* was described based on an incomplete skull, including the lower jaw, and two lower jaw fragments, the larger *D. berkeyi* was based a single lower jaw fragment. In 1925, Matthew and Granger (1925b) described a new genus and species, *Ardynictis furunculus*, represented by upper and lower jaw fragments of two individuals from the uppermost Eocene of Ergilin-Dzo (Ardyn-Obo) in Mongolia. In the same year, they described an upper molar of *?Hapalodectes auctus* from the Middle Eocene Irdin Manha Formation of Inner Mongolia, northern China (Matthew and Granger, 1925c); subsequently, Van Valen (1966) referred it to Didymoconidae. Bohlin (1937) recorded *Didymoconus* sp. in the Upper Oligocene Shargaltein-Tal locality in Gansu Province of China. Later, he described and figured fragmentary remains of Didymoconidae from the Upper Oligocene Taben-Buluk locality in Gansu, including isolated lower molars of *Didymoconus* sp., *?Didymoconus* sp., and an upper jaw fragment with P^3 and P^4, determined as aff. *Didymoconus* sp. (Bohlin, 1946).

Kretzoi (1943) proposed to place the genus *Didymoconus* in a distinct family, the Didymoconidae. Gromova (1960) published a description of the new genus *Tshelkaria*, including two species, *T. rostrata* (from the Oligocene of Kazakhstan, Chelkar-Teniz locality, Kur-Say, "Indricothere Formation") and *T. robusta* (from the Oligocene of Mongolia, Tatal-Gol locality, Shand-Gol Formation). *T. rostrata* is represented by an incomplete skeleton, two lower jaw fragments, and isolated upper teeth; *T. robusta* is represented by fragments of skulls and lower jaws. In addition, Gromova described additional material of *Didymoconus berkeyi*, including four lower jaw fragments from Tatal-Gol. It was the first to combine the genera *Didymoconus, Ardynictis*, and *Tshelkaria* in one family; however, as she was not aware of the paper Kretzoi (1943), she named this family Tshelkariidae.

Following Gromova (1960), I regarded *Tshelkaria* and *Didymoconus* as separate genera in the previous works (Lopatin, 1997, 2001a), although most of the researchers believed that they are synonyms (Gingerich, 1981; Wang et al., 2001; etc.). My opinion was based on the original description and figure of the holotype of *D. colgatei* provided by Matthew and Granger (1924), which showed clear distinctions of *Didymoconus* from *Tshelkaria*, i.e., the absence of a protocone on P^3, a metacone and hypocone of M^2 (Gromova, 1960; Lopatin, 1997), and the absence of rudimentary hypoconulid on P_4–M_1 (Lopatin, 1997). As turned out later, the figure of the holotype was not adequate because of insufficient preparation; the skull and lower jaw were disarticulated and completely prepared by Mellett only in the 1960s (however, the description was not published), while a corrected figure was published for the first time only by Morlo and Nagel (2002, text-fig. 2). At present, it is evident that *Didymoconus* possesses the elements indicated above. The other characters listed in the comparison of the two taxa (Gromova, 1960; Lopatin, 1997) are of little significance and should be regarded as species rather than generic distinctions, some characteristics may be connected with intraspecific (including age and sexual) variation. Thus, *Tshelkaria* is in fact a junior synonym of *Didymoconus*, and *T. robusta* Gromova, 1960 is synonym of *D. colgatei.* In addition, the presence of the protocone on P^3 of *D. colgatei* suggests to reject the hypothesis proposed earlier (Lopatin, 1997) that the largest didymoconine *D. berkeyi* Matthew et Granger, 1924 should be removed from the genus. New specimens found in China (Wang et al., 2001) corroborate the assignment of *D. berkeyi* to the genus *Didymoconus*.

Van Valen (1966) assigned *?Hapalodectes auctus* described by Matthew and Granger (1925c) in a new genus, *Mongoloryctes* of the family Didymoconidae. Mellett and Szalay (1968) described from the Middle

Eocene Ulan Shireh Formation of Inner Mongolia a posterior region of the lower jaw with M_1 and alveoli of M_2 of a small insectivore and referred it to a new genus and species, *Kennatherium shirense,* of Didymoconidae. Tang and Yan (1976) described an upper jaw fragment of the earliest member of Didymoconidae, *Zeuctherium niteles*, from the Lower Paleocene of Anhui Province of China (Wanghudun Formation). Zhai (1978) reported the finds of fragmentary upper and lower jaws with teeth of *Didymoconus berkeyi* in the Upper Oligocene beds of the Turfan Basin (China, Xinjiang Uygyr Autonomous Region, upper part of the Taoshuyuanzi Formation). In 1979, two new Early Paleogene genera and species of Didymoconidae were described from southern China, i.e., Late Paleocene *Archaeoryctes notialis* from Jiangxi Province, Chijiang Formation, Lannikeng Member (Zheng, 1979) and Early Eocene *Hunanictis inexpectatus* from Hunan, Lingcha Formation (Li et al., 1979). Subsequently, Huang (1982) reported finds of *Didymoconus* sp. and *Didymoconus* cf. *berkeyi* in the Early Oligocene Ulantatal locality in Inner Mongolia (China).

Badamgarav and Reshetov (1985) recorded Didymoconidae gen. et sp. indet. in the Tsagan-Khushu locality in Mongolia, i.e., in the Zhigden (Upper Paleocene) and Bumban (Lower Eocene) members of the Naran-Bulak Formation and also in the Middle Eocene Khaychin-Ula 2 locality (Khaychin Formation). Meng (1990) described *Archaeoryctes borealis* based on a lower jaw fragment with P_4–M_2 from the upper Lower Eocene Arshanto Formation of Inner Mongolia.

Meng et al. (1994a) examined the cranial structure of the didymoconid *?Hunanictis* sp. The specimen (incomplete skull with a well-preserved basicranium, but damaged teeth and anterior region) was found in Hubei Province of China, in the Yuhuangding Formation dated the end of the Early Eocene or the beginning of the Middle Eocene.

In 1997, I described four new didymoconid taxa (Lopatin, 1997), including the new species *Didymoconus gromovae* from the Lower Oligocene of the Chelkar-Nura Formation of Kazakhstan and three new genera and species from Mongolia, including *Ergilictis reshetovi* (Ergilin-Dzo locality; Ergilin-Dzo Formation, uppermost Eocene), *Archaeomangus ulanhureensis* (Ulan-Khureh 2 locality, Nemegt Depression; Shand-Gol Formation, Lower Oligocene), and *Tshotgoria shineusensis* (Shine-Us locality, Beger-Nur Basin; Beger Formation, Upper Oligocene). *Ergilictis* and *Archaeomangus* are described based on isolated lower jaw fragments with teeth, *D. gromovae* and *Tshotgoria* are represented by six and three lower jaw fragments, respectively (Lopatin, 1997).

Tong (1997) described of new Middle Eocene Didymoconidae from the Hetaoyuan Formation of the Shipigou locality, China, *Jiajianictis muricatus* and *Ardynictis zhaii.* Gabunia and Chkhikvadze (1997) recorded Didymoconidae in the Eocene and Oligocene of the Zaisan Depression, eastern Kazakhstan: *Ardynictis* sp. in the Upper Aksyir Subformation of the Aksyir Formation and "*Tshelkaria gromovae*" (nomen nudum) in the Buran Formation.

Wang et al. (1998) recorded a skull of *Archaeoryctes* cf. *notialis* in the upper part of the upper member of the Wanghudun Formation (Upper Paleocene) in Anhui Province of China. In addition, Wang et al. (2001) indicated the presence of a new, presently undescribed taxon in the Upper Eocene Ulan Gochu locality in Inner Mongolia, China.

Wang et al. (2001) described remains of *Didymoconus berkeyi* from the Upper Oligocene of the Lanzhou Basin (Gansu, China), including an incomplete skull, lower jaw, atlas, epistropheus, and limb bones.

Recently, I described an almost complete skull of *Archaeoryctes euryalis* from the Upper Paleocene Zhigden Member of the Naran-Bulak Formation of the Tsagan-Khushu locality in Mongolia (Lopatin, 2001a). This was the specimen labeled by Badamgarav and Reshetov (1985) as Didymoconidae gen. et sp. indet. from the Zhigden Member of Tsagan-Khushu. Another work of mine was devoted to the description of a new species, *Ardynictis captor*, from the Middle Eocene of the Khaychin-Ula 2 locality (Lopatin, 2003a).

Chapter 3 gives detailed descriptions of specimens of Early Paleogene Didymoconidae examined by me, provided with the diagnoses of some genera and all subfamilies, including Kennatheriinae subfam. nov. The taxonomic position, classification, and evolutionary history of this family are discussed below.

The Didymoconidae are characterized by a reduced dental formula (usually $I^3/_2C^1/_1P^3/_3M^2/_2$; in *Erlikotherium*, $I_0C_1P_2M_2$), the presence of a preincisor bony rostrum, large canines, cheek teeth of a particular structure, specialized structure of the ear region of the skull (Meng et al., 1994a), and a number of features of the postcranial skeleton indicative of a fossorial mode of life (Gromova, 1960; Wang et al., 2001). The primitive general type of dental structure combined with the typical twinned main cusps and the reduced formula of cheek teeth was treated earlier as evidence of relationships between the Didymoconidae and various groups of mammals, including Oxyaenidae, Leptictidae (Matthew and Granger, 1925b), Miacidae (Kretzoi, 1943), Arctocyonidae (Gromova, 1960), Anagalidae (McKenna, 1963), Palaeoryctidae (Van Valen, 1966; Mellett and Szalay, 1968), Deltatherididae (Romer, 1966; McKenna et al., 1971), Zalambdalestidae (Szalay and McKenna, 1971), and Mesonychidae (Wang, 1976; Gingerich, 1981). According to the ideas concerning the taxonomic position of these families, the Didymoconidae were placed in the orders of carnivores (Carnivora or Ferae), creodonts (Creodonta or Deltatheridia), "carnivorous condylarths" (Condylarthra, Eparctocyonia, Arctocyonia, Mesonychia, or Acreodi), "proteutherians," insectivores, anagalids, or were regarded as Mammalia incertae sedis.

The Didymoconidae were compared with the Leptictidae and Anagalidae only with reference to analogy in the structure of teeth and skeleton. The combination of a deep masseteric fossa, medially deflected angular process, and distinct medial postalveolar projection of the dentary observed in some Didymoconidae (see Mellett and Szalay, 1968) and the Late Cretaceous leptictid *Gypsonictops* was also interpreted as functional similarity (Clemens, 1973). The assumption of close relationship with Zalambdalestidae was based on the presence of molariform $P^4/_4$, longitudinally compressed talonids, and a trend towards lingual hypsodonty of the upper cheek teeth in late Didymoconidae.

The idea of close position of didymoconids with oxyaenids, miacids, arctocyonids, and mesonychids was based on the presence of primitive and simultaneously aberrantly specialized cheek teeth against a background of general predatory type of dentition, which was regarded as a result of early deviation of the group from the ancestral stem of "Carnivora" (in the past broad sense, including true carnivores, creodonts, arctocyonids, and mesonychids) and long subsequent isolated development. The hypothesis of the origin of the Didymoconidae from the Deltatheridiidae (McKenna et al., 1971), which are presently assigned to Metatheria (Marshall and Kielan-Jaworowska, 1992; Rougier et al., 1998; Kielan-Jaworowska et al., 2004), was based on an incorrect interpretation of the dental formula of *Deltatheridium*, i.e., ($I^{?4}/_2C^1/_1P^4/_4M^2/_{3-2}$ instead of the presently established $I^4/_3C^1/_1P^3/_3M^4/_4$).

Wang (1976) and Gingerich (1981) proposed that Didymoconidae are related to Mesonychidae. Gingerich believed that the characters shared by these groups include molariform $P^4/_4$, reduction or absence of $M^3/_3$, almost symmetrical upper molars without metacrista, and the presence of a longitudinal cristid oblique of the lingually open talonid of lower molars, which occluded with the centrocrista of the upper molars. Gingerich proposed that the Didymoconidae evolved from primitive Paleocene mesonychids resembling *Yantanglestes*. Criticizing this hypothesis, Meng et al. (1994a) noted that, in primitive Didymoconidae (such as *Archaeoryctes* and *Ardynictis*), P_4 is nonmolariform, while the cristid oblique is only slightly pronounced in Didymoconidae; in addition, the absence, or, the more so, reduction of $M^3/_3$ is observed in various Mammalia, while simple high trigonids and lingually open (with a reduced entoconid) talonids are characteristic of many Cretaceous and Paleogene mammals. Thus, didymoconids and mesonychids lack shared derived characters in the dental structure (Meng et al., 1994a); they also lack synapomorphies in cranial structure. However, the Didymoconidae share some cranial characters with Hapalodectidae, another family of mesonychians (Ting and Li, 1987), including extensive contact between the maxilla and frontal in the facial region, contact of the maxilla and frontal within the orbit, the absence of a facial process of the lacrimal, the absence of contact between the lacrimal and jugal, the shape and position of the nasals and palatines, and the presence of the supraorbital foramen. On the other hand, they substantially differ in the structure of the rostral and occipital regions, zygomatic arch, and ear region (Ting and Li, 1987) and cannot be close relatives.

In recent studies, based on the cranial structure, the Didymoconidae are considered to be close to Lipotyphla (Meng et al., 1994a) or Leptictida (McKenna and Bell, 1997) or are assigned to a special order, Didymoconida (Lopatin, 2001a), of the superorder Insectivora (sensu Novacek, 1986).

The study of the skull of *?Hunanictis* sp. from the Eocene of China (Meng et al., 1994a) has shown that, in cranial morphology, Didymoconidae are most similar to the superorder Insectivora sensu Novacek (1986). However, they were referred to neither Leptictida nor Lipotyphla. There was no consensus of opinion among the authors of the study cited regarding the taxonomic position of this family; the assignment of the Didymoconidae to Insectivora sensu lato was only proposed by Meng (see Meng et al., 1994a). In the skull of *?Hunanictis* sp. IVPP-V5788 (Institute of Vertebrate Paleontology and Paleoanthropology), the teeth, rostral region, and zygomatic arches are not preserved (Meng et al., 1994a); this complicates the estimation of taxonomic significance of cranial characters. However, the cranial structure of *Archaeoryctes euryalis* described above, which undoubtedly belongs to Didymoconidae, is very similar to that of *?Hunanictis* sp.

The cranial structure of Didymoconidae shows the following characters supporting assignment to Insectivora: (1) reduction of the jugal to the state of an insignificant element of the zygomatic arch between the processes of the maxilla and squamosal; (2) extensive contact between the maxilla and frontal in the facial region and (3) their contacts within the orbit; (4) relatively short infraorbital canal; (5) large common depression for the sphenopalatine and dorsal palatine foramina; and (6) the lacrimal lacking the facial process. The more specialized structure of the middle ear compared to other insectivores (Meng et al., 1994a) is an autapomorphy of the Didymoconidae. Of other diagnostic characters of Insectivora, Didymoconidae lack only one, i.e., the sharp sigmoid outline of the anterior margin of the ventral surface the occipital condyle.

In addition to the structure of the middle ear, the major autapomorphies of the Didymoconidae include the following characters (see Chapter 3, and Meng et al., 1994a): (1) the bony rostrum formed by the nasals and premaxillae; (2) walls of the external auditory meatus are formed by the squamosal and mastoid; (3) tympanic bullae completely ossified, formed by fused ectotympanic and entotympanic bones; (4) molars have twinned cusps in the pairs paracone–metacone and protoconid–metaconid; the paraconid is reduced, low. In addition, the Didymoconidae differ from Lipotyphla in the presence of massive zygomatic arches and from Leptictida in the more reduced jugal (lacking contact with the lacrimal, a character shared by Didymoconidae and Lipotyphla), extensive contact of the maxilla and frontal, the absence of contact between the palatine and lacrimal inside the orbit; in the parietals, which do not participate in the formation of the occipital region; and in the absence of a large suprameatal foramen of the squamosal.

Taken together, the characters listed clearly distinguish didymoconids from Lipotyphla and Leptictida and suggest that they should not be included in these orders. Based on this, I proposed earlier to rank the Didymoconidae as a special order named Didymoconida (Lopatin, 2001a).

Probably, the Didymoconida lineage deviated early from the common ancestral stem of insectivores, i.e., not later than in the Late Cretaceous time, when Leptictida and Lipotyphla were already formed. In the Paleogene, they were represented by a considerable number of taxa varying in size and dental morphology; this is evidence of significant adaptive radiation of Didymoconidae and reflects their high taxonomic diversity. As far as is known, their geographical range was restricted to Central Asia and Kazakhstan.

The Ardynictinae are clearly distinguished from the other Didymoconidae by the characters listed in the diagnosis of the subfamily (see Chapter 3). Judging from the distinctions in the cheek teeth, Ardynictinae and Didymoconinae diverged from each other at least as early as the Paleocene. In the Late Paleocene ardynictine *Archaeoryctes notialis* and *A. euryalis,* P^4 is slightly molarized, M^1 and M^2 have a very broad stylar shelf and a cingular projection in place of the hypocone, P_4 is slightly molarized and has a bladelike protoconid, M_1 and M_2 have a small paraconid and a large hypoconulid without an entoconid (Zheng, 1979; Lopatin, 2001a). The lower teeth characters listed are retained in Eocene *A. borealis.*

Ardynictis captor and *A. furunculus* lack a hypocone on P^4–M^2, retain the entoconid on M_1, and have lost the hypoconulid on M_2. In young *A. furunculus* (Matthew and Granger, 1925a, p. 4, text-figs. 6, 7, AMNH, no. 20366), DP_4 is molarized to a much greater extent than P_4 of adults (AMNH, no. 20365; PIN, no. 3109/246), has a clearly differentiated trigonid with the metaconid and bicuspid talonid and differs from molars only in the larger paraconid. DP^3 of specimen AMNH no. 20366 differs from P^3 of adult *Ardynictis* in the presence of the metacone. Thus, the deciduous teeth of Ardynictinae are similar to the permanent teeth of Didymoconinae in the presence of the metacone on the middle upper premolar and the degree of molarization of the posterior lower premolar. The deciduous premolars of Didymoconinae are also molarized (Gromova, 1960; Morlo and Nagel, 2002). Apparently, the molarization of $(D)P_{3-4}/(D)P_4$, which is in general characteristic of Didymoconidae, was realized in the Ardynictinae only in the deciduous generation, while, in the Didymoconinae, in both deciduous and permanent generations. In the Didymoconinae, the degree of molarization of P_4 gradually increased in the *Khaichinula–Ergilictis–Didymoconus* lineage (see also Lopatin, 1997).

The Didymoconinae reached their acme in the Early Oligocene, when the Ardynictinae had already become extinct (the last ardynictine *Ardynictis furunculus* coexisted in the Ergilian Age with *Ergilictis reshetovi,* which probably occupied a position at the base of the Early Oligocene radiation of didymoconines: Lopatin, 1997). Typical representatives of Didymoconinae are the Oligocene Shand-Gol genera *Didymoconus, Archaeomangus*, and *Tshotgoria*. Morphologically, the predecessor of these late Didymoconidae was *Ergilictis reshetovi* (Lopatin, 1997). Its less molarized P_4 and well-developed hypoconulids of P_4–M_2 correspond to the initial stage in this morphological series. In turn, Middle Eocene *Khaichinula lupula* morphologically precedes *Ergilictis reshetovi.* This statement is supported by such primitive characters as relatively less molarized P_4, with a high, large paraconid, and a short talonid with a well-developed hypoconulid. Thus, the discovery of *Khaichinula lupula* gives evidence that the beginning of adaptive radiation of didymoconines occurred at least as early as the beginning of the Middle Eocene.

Kennatherium shirense, which is known as the smallest member of Didymoconidae, was described based on the only specimen with heavily worn M_1 and alveoli of M_2 (Mellett and Szalay, 1968). Because of poor preservation, the assignment of *Kennatherium* to Didymoconidae was sometimes put in question (Gingerich, 1981; Russell and Zhai, 1987). The study of more complete specimens described above of this species from the Khaychin-Ula 2 locality corroborated the assignment of *Kennatherium* to Didymoconidae and showed its special position in this family.

Some dental characters of *Kennatherium shirense* (strongly transversely expanded P^4–M^2, with well-pronounced lingual hypsodonty; densely fused, considerably longitudinally compressed cusps of the trigonid; the lingual paraconid and rudimentary precingulid on M_1 and M_2) resemble Gypsonictopidae. However, the reduced dental formula, massive canines, the absence of trigonid basin, fusion between the protoconid and metaconid, the structure of the talonid of P_4–M_2, infraorbital canal, and lower jaw strongly suggest the assignment of *Kennatherium* to Didymoconidae. The increase in lingual hypsodonty can be regarded as a pronounced manifestation of the general trend characteristic of the family, while the structure of the paraconid of M_1 and M_2 and the presence of a rudimentary precingulid on M_1 are probably primitive eutherian characters retained in the structure of the lower molars.

The deep masseteric fossa, medially deflected angular process, and distinct postalveolar projection of the dentary, which are characteristic of *Kennatherium* and, to a different degree, of other Didymoconidae, are also observed in some Late Cretaceous eutherian mammals, such as *Kennalestes, Asioryctes, Barunlestes, Zalambdalestes*, and, particularly, *Gypsonictops* (Clemens, 1973; Kielan-Jaworowska, 1981). This similarity is interpreted as a consequence of similar functional features rather than close phylogenetic relationships (Clemens, 1973).

Kennatherium occupies a special position among Didymoconidae, because it is impossible to compare its dental structure to the other genera, except for *Zeuctherium*. P^4–M^2 of *Kennatherium* lack hypocones, i.e., resemble Ardynictinae in this respect; at the same time, P^4 and P_4 are quite molariform, as those of Didymoconinae. *K. shirense* is distinguished from the other Didymoconidae by the unique structure of the paraconid region and by the talonid of P_4–M_2. In the structure of the upper teeth, *K. shirense* resembles *Zeuctherium niteles* from the Lower Paleocene of China. They are similar in the shape (very narrow) and structure (reduced styles and the paracone and metacone positioned close to the labial edge) of P^4–M^2. Apparently, *Kennatherium* and *Zeuctherium* represent the most primitive condition of the cheek teeth in Didymoconidae.

Erlikotherium edentatum sp. nov. sharply differs from the other Didymoconidae in the functionally edentate pattern, i.e., the absence of lower incisors, wear traces on the anterior side of the canine, the absence of P_2, large postcanine diastema, and the broad paraconid of the lower molars. In the structure of the ascending ramus of the lower jaw, *Erlikotherium* is distinguished by the acute-angled coronoid process, with a posteriorly curved apex. Nevertheless, it undoubtedly belongs to Didymoconidae because its lower cheek teeth show the structure unique to this family. The characters of the talonid structure of P_4–M_2, including the primarily well-developed cristid oblique, the presence three cusps, and the fusion between the hypoconulid and entoconid support the similarity of *Erlikotherium* to *Kennatherium* and the assignment of this genus to the subfamily Kennatheriinae. The considerably widened paraconid of the special structure on M_1 of *Erlikotherium* could have developed in the evolution by the fusion of the true paraconid with the precingulid, a rudiment of which is present in *Kennatherium.* The number of incisors, the pattern of canine wear, and the structure of the upper part of the coronoid process of *Kennatherium* are not known; however, the considerable reduction of P_2, morphology of P_3–M_2, and the structure of the lower part of the ascending ramus of the lower jaw suggest that it is related phylogenetically to *Erlikotherium.* The ancestor of *Erlikotherium* was probably similar in dental structure to *Kennatherium*, while the essential morphological differences between these genera are connected with the more profound specialization of *Erlikotherium.*

The most primitive Didymoconidae apparently had broad P^4–M^2, with a small hypoconal shelf and weak styles and conules, submolariform P_4, and relatively high-crowned lower molars of a primitive "proteutherian" type, i.e., with a high paraconid, twinned protoconid and metaconid, and a tricuspid talonid. The Kennatheriinae probably retained many primitive characters of the group.

Apparently, Late Cretaceous ancestors of the Didymoconidae were morphologically similar to the Gypsonictopidae (Leptictida). This is supported by the similarity in the structure of their molars and morphological correspondence of DP_3 and DP_4 of Didymoconidae to permanent P_3 and P_4 of *Gypsonictops* (see Clemens, 1973, text-figs. 5, 6). As shows the structure of M_1 of *Kennatherium*, the low, wide paraconid without a basal precingulid, which are characteristic of the lower molars of Didymoconidae, could have been formed based on the structure usually observed in primitive placentals by the fusion of the paraconid and precingulid. Thus, the dental characters of *Kennatherium,* which are described for the first time in the present study, reduce the morphological gap between the structural patterns of cheek teeth of Didymoconidae and primitive eutherians and indicate the group that is presumably most similar to the family considered, namely, the Gypsonictopidae.

5.4. System of Insectivora

Complete reviews of the development of ideas concerning the composition and classification of insectivores from C. Linnaeus to the present time were published by Butler (1972) and Symonds (2005). In this section, I give only brief characteristics of changes in the conceptual base, which provided the foundation for the system of the order and, then, consider the concept of the systematics of Insectivora, modified according to the results of original study.

The first concept of the order Insectivora could be named the *generalist* concept. It is based on a belief that insectivores can integrally be characterized by their morphological primitiveness, i.e., the absence of specialized features observed in other groups and, at least roughly, determining their composition (such as incisors of rodents, hooves of ungulates, teeth of carnivores, wings of chiropterans, brain of primates, etc.). In fact, this is not the initial concept; thus, Illiger (1811), who was the first to combine hedgehogs, moles, and shrews in a special group named it "the family Subterranea," that meant a general fossorial adaptation. The term *insectivores* (Cuvier, 1817), which was latinized by Bowdich (1821), combined not only *Erinaceus, Sorex*, and *Talpa* but also the genera *Desmana, Scapanus, Condylura, Tenrec, Setifer*, and *Chrysochloris*. It also implied certain general insectivorous food specialization and terrestrial, semiaquatic, or subterranean mode of life. The initial concept of the group was extended by Wagner (1855), who included the tree shrews *Tupaia* and *Ptilocercus*, the elephant shrews *Macroscelides, Petrodromus, a*nd *Rhynchocyon*, and the flying lemur *Cynocephalus* (= *Galeopithecus*) in

Insectivora. From this point onwards, insectivores have been treated in accordance with the generalist concept. At that time, the first attempts at morphological substantiation of the composition and classification of this group were made. Peters (1864) indicated that the tree shrews, elephant shrews, and flying lemur have a blind gut (cecum), while insectivores in traditional understanding (hedgehogs, moles, shrews, tenrecs, and golden moles) lack it. Subsequently, Haeckel (1866) divided Insectivora into two suborders: Menotyphla (taxa provided with the blind gut) and Lipotyphla (taxa without blind gut); Gill (1872) removed the flying lemur and placed it in the suborder Dermoptera. Then, following Leche (1855), Dermoptera were regarded as a separate order, while all other Menotyphla continued to be included in Insectivora. Huxley (1880) indicated that Insectivora occupy "the central position" among Eutheria, because members of this group have retained characters that are primitive to other orders of placentals ("stem group" in the modern terminology: see Novacek et al., 1988). The hypothesis of the origin of all Eutheria from Insectivora gained wide recognition. Following this hypothesis and based on the generalist concept of the order, any extinct placental mammals that did not show clear relationships with other orders, was placed in Insectivora. For example, Osborn (1910), developing the system proposed by Matthew (1909) and Gregory (1910), divided the order Insectivora into the suborders Lipotyphla, Menotyphla, Hyopsodonta (Hyopsodontidae), and Proglires (Apatemyidae and Mixodectidae). With the increase in knowledge of Early Paleogene and Mesozoic mammals, the number of taxa assigned to Insectivora sharply increased. As a result, extinct insectivores considerably surpassed extant taxa in morphological and taxonomic diversity, and the order Insectivora became a taxonomic wastebasket for small early placentals.

The progress in the study of insectivores rode on the formation of a new concept of the order, the concept of Lipotyphla, developed primarily by Butler (1972). He turned to the idea of Gregory (1910), who divided Insectivora sensu Heackel, 1866 into two orders, Lipotyphla and Menotyphla, corresponding to the suborders introduced by Heackel, in belief that Lipotyphla are allied to Carnivora, while Menotyphla are related to Primates. The ordinal status and monophyly of Lipotyphla sensu Butler were supported by a large number of shared characters, many of which cannot be regarded as primitive: the absence of blind gut, reduction of the jugal, expansion of the maxilla within the orbit, displacing the palatine, a mobile proboscis controlled by a special muscular complex, which influences the skull shape, reduction of pubic symphysis, and hemochorial placenta (see also Novacek, 1986; MacPhee and Novacek, 1993; Asher, 2005). Butler believed that insectivores in the composition of Lipotyphla are a natural group that evolved from a common ancestor; therefore, it is possible to designate this concept as *monophyletic*. In this composition, the order Lipotyphla corresponds to the order Insectivora sensu Bowdich, 1821; therefore, Insectivora sensu stricto could have been retained as an ordinal name. However, because of the wide use of the term Insectivora sensu lato throughout most of the 20th century, Butler believed this were undesirable.

Butler (1972) divided Lipotyphla into four suborders: Erinaceomorpha (including the families Adapisoricidae, Erinaceidae, and ?Dimylidae), Soricomorpha (Geolabididae, Plesiosoricidae, Solenodontidae, Micropternodontidae, Nyctitheriidae, Talpidae, Soricidae, Nesophontidae, and ?Apternodontidae), Tenrecomorpha (Tenrecidae), and Chrysochlorida (Chrysochloridae). It should be noted that, at the time of publication of Butler's study, the system of insectivores at the subordinal level was developed. Gregory (1910) had introduced the taxa Erinaceomorpha and Soricomorpha, regarded as sections (infraorders) in the suborder Lipotyphla of the order Insectivora. The subordinal rank had been given to Erinaceomorpha and Soricomorpha by Saban (1954).

Kalandadze and Rautian (1992) included in the order Lipotyphla the suborders Deltatheridia (Deltatheridiidae), Soricomorpha (with the infraorders Zalambdodonta [including Tenrecoidea and Chrysochloroidea], Solenodonta, and Soricota), Erinaceomorpha (including Pantolestoidea), and Amblypoda (with the infraorders Pantodonta and Dinocerata). Later, in the coauthorship with Agadjanian, they removed Amblypoda from Lipotyphla (Agadjanian et al., 2000). The Deltatheridiidae are presently included in Metatheria (Marshall and Kielan-Jaworowska, 1992).

In general, after works of Butler (1972, 1988), McKenna and coauthors (McKenna, 1975a; McKenna and Bell, 1997; Shoshani and McKenna, 1998), Novacek (1986), and MacPhee and Novacek (1993), the monophyletic concept of Lipotyphla, with the division into Erinaceomorpha, Soricomorpha, and Chrysochloridea, was established with certainty. However, simultaneously with it the third concept of insectivores, which can be designated as *paraphyletic* or *dichotomic* concept, was developed (see Gabriel and Polly, 2005), according to which the Lipotyphla are a heterogenous group, so that golden moles, tenrecs and, in some systems, solenodontids and (or) tenrecs should be transferred from it in a special order. Gill (1875, 1885) divided extant insectivores into "section" (and, then, suborders) Zalambdodonta and Dilambdodonta. Zalambdodonta comprised Centetoidea (including tenrecs, solenodontids, and otter shrews) and Chrysochloroidea, and Dilambdodonta comprised Erinaceoidea, Soricoidea, and Tupaioidea. Broom (1916) was the first to establish the order Chrysochloridea for the family of the golden moles, based on a number of cranial characters and the structure and Jacobson's organ (see also Roux, 1947; Roberts, 1951; Graaff, 1957). Heim de Balsac and Bourlière (1954) divided Lipotyphla into two suborders, Chrysochloroida (golden moles) and Euinsectivora (all other groups). Van Valen (1967) transferred the suborder Zalambdodonta from Insectivora to the newly established order Deltatheridia, which also included creodonts and palaeoryctoids, while the other insectivore families assigned to the suborder Erinaceota of the order Insectivora (along with the suborders Proteutheria, Macroscelidea, and Dermoptera). Vandebroek (1961) ranked Zalambdodonta as order and included Paleocene–Eocene Palaeoryctidae in this group. Thenius (1969) believed that Zalambdodonta developed independently of other Insectivora, but removed palaeoryctids from this taxon.

Despite these events, the monophyletic concept of Lipotyphla still dominated. The crisis burst out when the paraphyletic concept was supported by molecular genetic studies. Stanhope et al. (1998) performed a molecular analysis that included representatives of all six extant families of insectivores, as well as 37 other taxa representing marsupials, monotremes, and all but two extant orders of placentals. As a result of this analysis, tenrecids and golden moles were grouped in one clade (Afrotheria) with other placentals of African origin, i.e., proboscideans, sirenian, hyraxes, aardvarks, and elephant shrews. Statistical analysis rejected the idea of the monophyletic order Insectivora (Lipotyphla) and the concept of the suborder Soricomorpha (as a group including Soricidae, Talpidae, Solenodontidae, and Tenrecidae). Thus, the traditional monophyletic concept of insectivores was regarded erroneous, and Lipotyphla was thought to be an artificial order. The African families Tenrecidae and Chrysochloridae were combined in a special order, Afrosoricida (or Tenrecoidea). The other insectivore families were assigned based on mitochondrial data to two monophyletic groups, Soricomorpha (including Solenodontidae, Talpidae, and Soricidae) and detached Erinaceomorpha (Erinaceidae). It was proposed to retain the ordinal name Insectivora for these insectivores (later, some researchers attempted to introduce a new name, Eulipotyphla, see Waddell et al., 1999). The absence of cecum, reduction of the pubic symphysis, and significant participation of the maxilla in the formation of the orbital wall were considered by Stanhope et al. and their followers (Waddell et al., 1999; Madsen et al., 2001; Murphy et al., 2001; etc.) as convergent characters; the zalambdodonty of Afrosoricida and Solenodontidae were also considered to appear convergently. In some subsequent molecular genetic works, the *polyphyletic* rather than paraphyletic concept of insectivores was developed, which followed from the detached position of Erinaceidae (Mouchaty et al., 2000; Arnason and Janke, 2002; Arnason et al., 2002), Talpidae (Malia et al., 2002), Solenodontidae (Waddell and Shelley, 2003), or all extant families of "eulipotyphlan" insectivores (Emerson et al., 1999).

Leaving aside the problem of Afrotheria, since it is beyond the scope of the present study, it should be noted that this concept is far from the system commonly accepted by taxonomists–morphologists. Even compromise variants implying the assignment of independent orders "Afrosoricida" and "Eulipotyphla" or Chrysochloridea, Erinaceomorpha, and Soricomorpha to the nearest superordinal taxon (see McKenna and Bell, 1997; Pavlinov, 2003), in fact, proceed from the idea of monophyletic insectivores.

The study of Early Paleogene insectivores support the monophyletic concept of insectivores. In view of all data on extinct taxa, Insectivora is regarded as morphologically clearly outlined superorder within the cohort Epitheria (see diagnosis in Chapter 3). The superorder Insectivora includes three orders: Lipotyphla and extinct Leptictida and Didymoconida. Each is also diagnosed clearly morphologically; the same is true of the suborders Soricomorpha, Erinaceomorpha, and Chrysochloridea traditionally included in Lipotyphla (see Chapter 3; see also Novacek, 1986; MacPhee and Novacek, 1993) as well as the infraorders and superfamilies assigned to the suborder Soricomorpha. The infraorder Soricota is named after Kalandadze and Rautian (1992), although its composition is changed because of the inclusion of the superfamily Solenodontoidea (infraorder Solenodonta sensu Kalandadze and Rautian, 1992, but for Palaeoryctidae). The infraorder composed of the family Tenrecidae (without Chrysochloridae) retains the name Tenrecomorpha (see Butler, 1972). The assignment of Chrysochloridae and Tenrecidae in a particular taxon (Afrosoricida or Tenrecoidea) is not supported.

At present, there is no universally accepted division of Soricomorpha into taxa of infraordinal and superfamily ranks (see MacPhee and Novacek, 1993; Asher, 2005; Symonds, 2005; etc.); earlier, I tentatively proposed the division of the suborder Soricomorpha into the infraorders Tenrecomorpha (coextensive with the family Tenrecidae), Solenodonta (Apternodontidae and Solenodontidae), and Soricota (all other families), while superfamilies were not indicated (Lopatin, 2005c).

Within the superorder Insectivora, the group Lipotyphla + Didymoconida is distinguished from Leptictida by the presence of large orbital process of the maxilla, which is bordered by the frontal (excluding contact between the palatine and lacrimal), and the stronger reduction of the jugal (without contact with the lacrimal). However, apomorphic distinctions in the structure of the tympanic bulla (petrosal and basisphenoid in Lipotyphla, entotympanic in Leptictida, and both tympanic bones in Didymoconida) suggest long independent development and equal taxonomic rank of the groups discussed. In addition, it is not improbable that reduction of the jugal and expansion of the orbital process of the maxilla in Didymoconidae and Lipotyphla developed in parallel. In the pattern of tooth replacement, Didymoconida and Leptictida demonstrate plesiomorphic similarity (see West, 1972; Morlo and Nagel, 2002); in the majority of groups of Lipotyphla the deciduous generation is more or less reduced, reaching

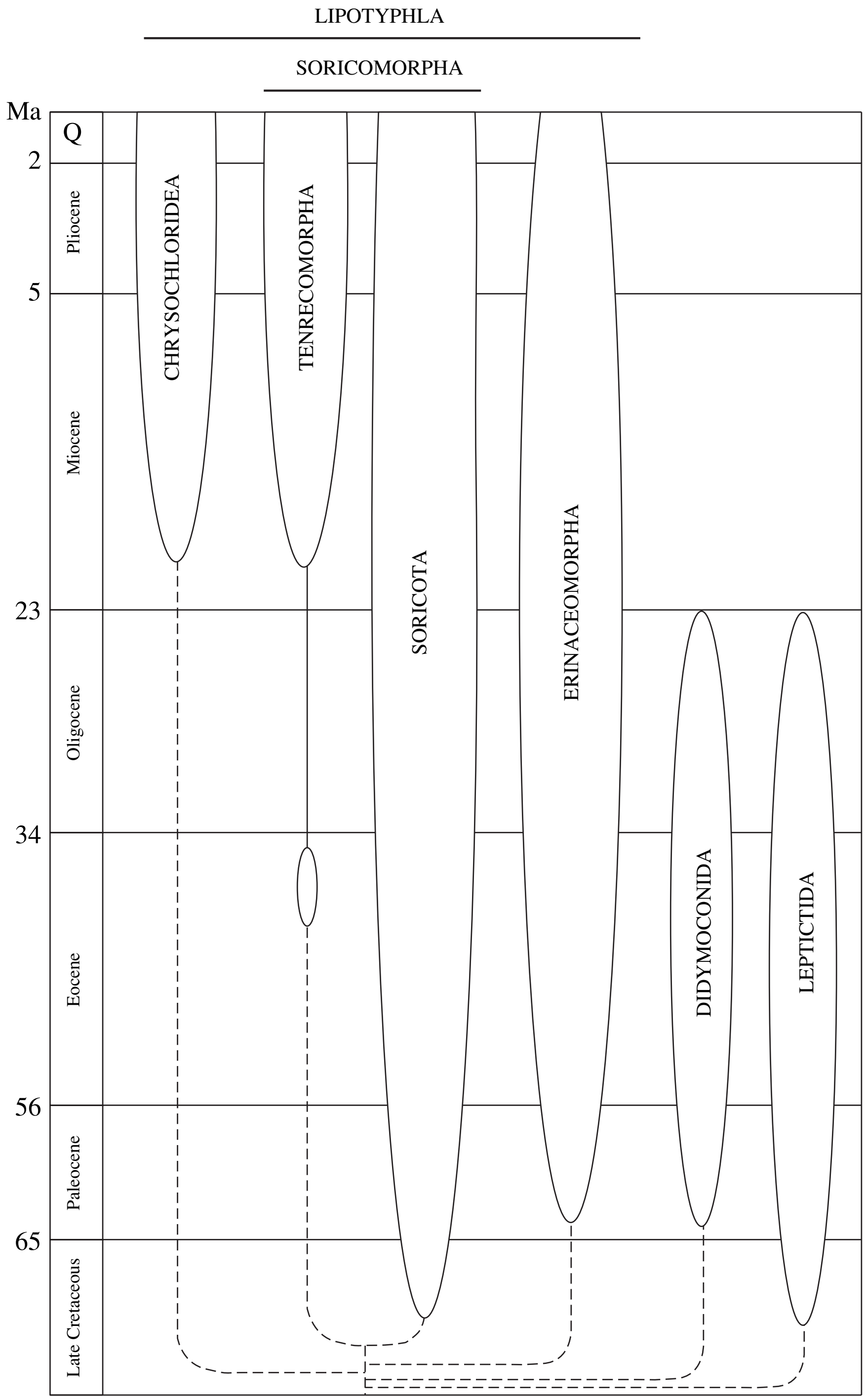


Fig. 60. Scheme of phylogenetic relationships in Insectivora.

the functional monophyodonty in Soricidae and some Talpidae (see Nievelt and Smith, 2005).

The Chrysochloridea differ from the group Erinaceomorpha + Soricomorpha in the preservation of a rudimentary entotympanic bone (most likely, this is a plesiomorphic character) and in the specialized structure of the jaw articulation, which supports formal taxonomic isolation of the two branches (suborders Chrysochloroida and Euinsectivora sensu Heim de Balsac and Bourlière, 1954). However, taking into account the profound morphological differences between Soricomorpha and Erinaceomorpha, it is appropriate to retain identical taxonomic rank of the three groups (see MacPhee and Novacek, 1993; McKenna and Bell, 1997).

Table 50. Presumable time of emergence and divergence of extant insectivore groups (molecular data after Stanhope et al., 1998; Douady et al., 2002a; Douady and Douzery, 2003; Springer et al., 2003; Roca et al., 2004)

Taxon	Molecular data	Paleontological data
Eulipotyphla (Lipotyphla)	73–76 ± 5 Ma	>70 Ma (Late Cretaceous)
Soricomorpha	Not supported	~65–73 Ma (Maastrichtian)
Solenodontidae	76 ± 5 Ma	No adequate data, known from Pleistocene
Talpidae	65 ± 5 Ma	ca. 40 Ma (Middle Eocene)
Uropsilinae	52 ± 5 Ma	ca. 35–37 Ma (Late Eocene)
Talpinae	38–42 ± 5 Ma	ca. 40 Ma (Middle Eocene)
Soricidae	55–65 Ma	ca. 45–47 Ma (Middle Eocene)
Soricinae	38–42 ± 5 Ma	ca. 18 Ma (Early Miocene)
Crocidurinae	38–42 ± 5 Ma	ca. 18 Ma (Early Miocene)
Erinaceidae	55–65 Ma	ca. 61–63 Ma (Early Paleocene)
Galericinae	38–42 ± 5 Ma	ca. 45–47 Ma (Middle Eocene)
Erinaceinae	38–42 ± 5 Ma	ca. 35 Ma (Late Eocene)
Tenrecoidea (Afrosoricida)	69 ± 5 Ma	Not supported
Chrysochloridae	63 ± 5 Ma	No adequate data, known from Early Miocene
Tenrecidae	63 ± 5 Ma	No adequate data, known from Early Miocene, while Tenrecomorpha are known from the Late Eocene
Potamogalinae	51–55 Ma	No adequate data
Tenrecinae/Oryzorictinae/Geogalinae	37–43 ± 5 Ma	No adequate data, Geogalinae are known from Early Miocene

Thus, based on the results obtained in the present study, the classification of insectivore families and higher taxa appears as follows (see also Figs. 58 and 60):

Superorder Insectivora Bowdich, 1821:
- Order Didymoconida Lopatin, 2001 (Didymoconidae),
- Order Leptictida McKenna, 1975 (Gypsonictopidae and Leptictidae),
- Order Lipotyphla Haeckel, 1866:
    - Suborder Chrysochloridea Broom, 1915 (Chrysochloridae),
    - Suborder Erinaceomorpha Gregory, 1910 (Erinaceidae, Amphilemuridae, Sespedectidae, and Creotarsidae),
    - Suborder Soricomorpha Gregory, 1910:
        - Infraorder Tenrecomorpha Butler, 1972 (Tenrecidae),
        - Infraorder Soricota Kalandadze et Rautian, 1992:
            - Superfamily Micropternodontoidea Stirton et Rensberger, 1964 (Micropternodontidae),
            - Superfamily Nesophontoidea Anthony, 1916 (Geolabididae and Nesophontidae),
            - Superfamily Soricoidea Fischer von Waldheim, 1817 (Nyctitheriidae, Soricidae, and Plesiosoricidae),
            - Superfamily Talpoidea Fischer von Waldheim, 1817 (Talpidae, Proscalopidae, and Dimylidae),
            - Superfamily Solenodontoidea Gill, 1872 (Apternodontidae and Solenodontidae);

Lipotyphla indet.: ?Adapisoriculidae, ?Chambilestidae.

5.5. Scenario of Insectivora Evolution

The times of emergence of extant insectivore groups reconstructed based on paleontological and molecular genetic data (Table 50) are mostly in agreement (when adequate fossil data are available). Exceptions are provided by the dates of the origin of Talpidae, Soricidae, Uropsilinae, and extant subfamilies of Soricidae; molecular data suggest earlier dates than the fossil record. The first two cases are probably attributable to the fact that molecular datings concern the divergence of Soricomorpha and Erinaceomorpha rather than differentiation of the families Talpidae and Soricidae. The case of Uropsilinae is probably explained by the incompleteness of the fossil record, since it may well be that the emergence of these primitive talpids occurred in the Early Eocene (see also Shinohara et al., 2003). The early divergence of the Soricinae and Crocidurinae based on molecular data may be accounted for by the fact that their ancestors belonging to the extinct subfamily Crocidosoricinae, which is known from the beginning of the Oligocene, diverged much earlier within this group.

Based on the entire set of potentially compatible data, it is possible to propose the following evolutionary scenario for insectivores. The primitive Cretaceous placentals were dominated by small, unspecialized carnivorous taxa. The competition between groups that developed specializations for predatory and omnivorous feeding forced some groups of small placentals to turn to feeding mostly on invertebrates, including both terrestrial and subterranean and aquatic creatures. They were represented by some Cimolesta (Palaeoryctida, Didelphodonta, and Pantolesta) and ancestral Insectivora (including Leptictida and ancestors of Lipotyphla and Didymoconida). This adaptive differentiation probably developed in North America in the first half of the Late Cretaceous. Similar adaptive zones on other continents were occupied by primitive Metatheria and Eutheria.

Among presently known Mesozoic placentals, only two genera, *Paranyctoides* and *Batodon*, are assignable to Lipotyphla. *Paranyctoides*, represented by teeth and jaws from North America and Asia, is assigned to Nyctitheriidae (Fox, 1979, 1984b; Kielan-Jaworowska et al., 2004) or Soricomorpha indet. (McKenna and Bell, 1997). Judging from the dental structure, *Paranyctoides* is probably related to Adapisoriculidae, a family of primitive insectivores of uncertain taxonomic position (Lipotyphla indet.: McKenna and Bell, 1997) from the Paleocene and Lower Eocene of Europe and North Africa.

Batodon is regarded as the earliest soricomorph of the family Geolabididae (Novacek, 1976; McKenna and Bell, 1997) or referred to Cimolestidae (Lillegraven, 1969; Clemens, 1973; Butler, 1988; Kielan-Jaworowska et al., 2004). In my opinion, the assignment of *Batodon* to Geolabididae is well grounded by its dental characters (see above).

Adaptive radiation of Lipotyphla in the Late Cretaceous provided the dominant position of this group in respective adaptive zone. Other insectivores and insectivore-like groups did not achieve significant diversity and occupied relatively narrow ecological niches, becoming semiaquatic (Pantolesta) or fossorial (Palaeoryctida and Didymoconida). Erinaceomorpha and Soricomorpha, possessing protodilambdomorph teeth, differentiated within Lipotyphla in the Late Cretaceous. The two groups initially occupied the same adaptive zone; however, soricomorphs were inferior to erinaceomorphs in the large-size class, but achieved higher rates in the specialization of the dental apparatus, jaw muscles, and, probably, physiology, which allowed them to reach a much greater taxonomic and adaptive diversity, which is evident from the fossil record. The earliest primitive protodilambdodont soricomorphs probably penetrated into Africa at least as early as the Late Cretaceous and gave rise to a local adaptive radiation of insectivores. The teeth of tenrecomorphs transformed from protodilambdomorph to protozalambdomorph pattern and, then, became euzalambdomorph. Apparently, tenrecomorphs achieved some diversity as early as the Paleocene, since insectivores and insectivore-like placentals of Holarctic origin that entered Africa at that time could not supersede them from the common adaptive zone.

To the Cretaceous–Paleogene boundary, Erinaceomorpha and the majority of Soricomorpha independently acquired the eudilambdomorph teeth, and further morphological evolution of the dentition developed on this basis. At the end of the Cretaceous, primitive protodilambdodont and eudilambdodont soricomorph insectivores probably penetrated into Asia and gave rise to the local Paleocene radiation of Soricomorpha. A group of soricomorph insectivores, in which eudilambdomorph molars were transformed into parazalambdomorph molars, emerged in North America. This apternodontid group became rather diverse in the Paleogene of North America and, in the Middle Eocene, penetrated into Asia. Subsequently, they were replaced by other groups of similar specialization and became extinct; only Solenodontidae isolated within the Antilles survived to the Recent Time. Until recently, the Nesophontidae coexisted with the Solenodontidae (see MacPhee et al., 1999), but their adaptive zones substantially differed.

Erinaceomorphs were very diverse in the Paleocene and Eocene of North America and Europe; however, they penetrated into Asia only during the subglobal faunal exchange at the Paleocene–Eocene boundary. Further major events in the evolution of insectivores developed in this continent. In the Early Eocene, eudilambdodont soricomorphs clearly prevailed over erinaceomorphs. The nyctitheres were particularly abundant, and, in the Middle Eocene, gave way to shrews (their descendants) and erinaceids, in which the Galericinae appeared as early as the Early Eocene. In the Late Eocene, the Erinaceinae and, probably, a predatory erinaceid lineage, the Brachyericinae, appeared. In the Oligocene, the Erinaceidae dominated over soricomorphs (apparently, this was the only time interval of their prevalence in the geological history), at least, in the inner regions of Asia, where erinaceids were rather abundant, very diverse taxonomically, and widely differentiated in size (from a small shrew to the extant common hedgehog) and adaptations, whereas the Soricidae, Talpidae, and Proscalopidae were represented there by isolated finds (see Sulimski, 1970; Lopatin, 2002b, 2003f; Geisler, 2004). However, this disproportion was undoubtedly connected with ecological features of the Central Asian biochore, since the Soricidae and Talpidae were relatively more abundant and diverse in relatively humid regions (for example, in eastern Kazakhstan or Europe).

The Erinaceidae, which disappeared from North America in the Middle Eocene, penetrated again into this continent at the Eocene–Oligocene boundary, but disappeared at the end of the Miocene, in the time of the peak of diversity of Soricidae and Talpidae. At the beginning of the Miocene, erinaceids appeared in North

Africa. Soricidae penetrated from Asia into North America in the Middle Eocene and entered Europe at the beginning of the Oligocene, Africa in the middle of the Miocene, and South America in the Pleistocene. Talpidae, which probably appeared in Asia in the Early–Middle Eocene, had time to enter Europe earlier than it was isolated in the Late Eocene, and penetrated into North America in the Late Oligocene.

Primitive insectivore-like placentals were completely replaced by Lipotyphla in the Oligocene, and primitive groups of Lipotyphla quit the evolutionary stage in the first half of the Miocene, in the epoch of great faunal exchanges.

The scenario proposed for the evolution of insectivores characterizes the major stages of their history:

(1) In the first half of the Late Cretaceous of North America, the ancestral Insectivora adapted primary for feeding on invertebrates (along with insectivore-like groups) emerged among primitive placentals;

(2) In the Late Cretaceous, Insectivora underwent adaptive radiation, and the orders Leptictida, Didymoconida, and Lipotyphla as well as the suborders Erinaceomorpha and Soricomorpha differentiated;

(3) At the Cretaceous–Paleocene boundary, the primary radiation of primitive Soricomorpha, with the differentiation of ancestors of Tenrecomorpha in Africa and Soricota (Geolabididae) in North America;

(4) The Paleocene expansion of Soricota (Geolabididae, Nyctitheriidae, Micropternodontidae, and Apternodontidae) in the Northern Hemisphere; the primary Paleocene radiation of Erinaceomorpha in North America, and the appearance of Erinaceidae (the earliest extant family of Lipotyphla);

(5) At the Paleocene–Eocene boundary, radiation of Soricomorpha (at the level of subfamilies of primitive families) and Erinaceidae;

(6) At the Early–Middle Eocene boundary, the extant groups Soricidae, Talpidae, and Galericinae (the earliest extant subfamily of Lipotyphla) appeared;

(7) In the Middle Eocene–Oligocene, primitive insectivore groups (and all insectivore-like mammals) were replaced everywhere by the rapidly evolving extant families and related groups; the Recent subfamilies of Soricidae, Talpidae, Erinaceidae, and Tenrecidae were formed;

(8) In the Miocene–Pliocene, primitive groups of Recent families (Heterosoricinae and Crocidosoricinae within Soricidae and Brachyericinae and Amphechinini within Erinaceidae) and related groups (Plesiosoricidae, Proscalopidae, and Dimylidae) disappeared and Recent groups occupied the dominant position; the diversity of Erinaceomorpha decreased; and Recent insectivore genera were formed.

CONCLUSIONS

(1) The study performed has shown that Early Paleogene insectivore associations of Asia include true insectivores (superorder Insectivora: order Lipotyphla: suborders Erinaceomorpha and Soricomorpha; orders Didymoconida and Leptictida) and insectivore-like placentals (superorder Ferae: order Cimolesta: suborders Didelphodonta, Palaeoryctida, and Pantolesta). The analysis of the associations investigated has shown that, from the end of the Paleocene to the beginning of the Middle Eocene of the central area of Asia, the taxonomic composition and ecological structure of insectivore communities gradually changed. In the Middle Eocene, insectivore-like placentals (Cimolestidae, Palaeoryctidae, and Pantolestidae) and primitive soricomorph groups (Micropternodontidae, Geolabididae, Nyctitheriidae, Plesiosoricidae, and Apternodontidae) began to be replaced by Recent families of Lipotyphla (Erinaceidae, Soricidae, and Talpidae), which occupied a dominant position in the Oligocene.

(2) In the Late Paleocene association from the Zhigden Member of the Naran-Bulak Formation of the Tsagan-Khushu and Naran-Bulak localities the following soricomorph insectivores are described: the micropternodontids *Sarcodon pygmaeus* Matthew et Granger, 1925 and *Hyracolestes ermineus* Matthew et Granger, 1925 (Sarcodontinae); the geolabidid *Gobigeolabis verigranum* Lopatin, 2004; the nyctitheriids *Praolestes nanus* Matthew, Granger et Simpson, 1929, *P. maximus* Kondrashov, Lopatin et Lucas, 2004 (Praolestinae subfam. nov.), and *Jarveia erronea* Kondrashov, Lopatin et Lucas, 2004 (Asionyctiinae); the didymoconid *Archaeoryctes euryalis* Lopatin, 2001 (Ardynictinae); the palaeoryctid *Pinoryctes collector* gen. et sp. nov.; and the pantolestid *Zhigdenia nemegetica* gen. et sp. nov. (Pantolestinae).

The Early Eocene association from the Bumban Member of the Naran-Bulak Formation of the Tsagan-Khushu locality includes the micropternodontid *Prosarcodon maturus* Lopatin et Kondrashov, 2004 (Sarcodontinae); the nyctitheriids *Bumbanius rarus* Russell et Dashzeveg, 1986 (Praolestinae), *Oedolius perexiguus* Russell et Dashzeveg, 1986, *Edzenius lus* gen. et sp. nov. (Asionyctiinae), and *Eosoricodon terrigena* Lopatin, 2005 (Eosoricodontinae); the plesiosoricid *Ordolestes ordinatus* gen. et sp. nov. (Butseliinae); and the cimolestids *Naranius infrequens* Russell et Dashzeveg, 1986, *Tsaganius ambiguus* Russell et Dashzeveg, 1986, and *Bagalestes trofimovi* gen. et sp. nov. (Cimolestidae).

The Middle Eocene association from the Khaychin Formation of the Khaychin-Ula 2 and Khaychin-Ula 3 localities includes the erinaceomorphs *Eogalericius butleri* Lopatin, 2004 and *Microgalericulus esuriens* gen. et sp. nov. (Erinaceidae, Galericinae); the soricomorphs *Metasarcodon reshetovi* Lopatin et Kondrashov, 2004 (Micropternodontidae, Sarcodontinae), *Soricolestes soricavus* Lopatin, 2002 (Soricidae, Soricolestinae), and *Asiapternodus mackennai* Lopatin, 2003 (Apternodontidae, Asiapternodontinae subfam. nov.); the didymoconids *Ardynictis captor* Lopatin, 2003 (Ardynictinae), *Khaichinula lupula* gen. et sp. nov. (Didymoconinae), *Kennatherium shirense* Mellett et Szalay, 1968, and *Erlikotherium edentatum* gen. et sp. nov. (Kennatheriinae subfam. nov.); and the palaeoryctid *Nuryctes gobiensis* Lopatin et Averianov, 2004 (Palaeoryctidae).

Late Paleocene insectivores from the Dzhilga 1a locality in southern Kazakhstan are represented by the nyctitheriids *Voltaia minuta* Nessov, 1987 and *Jarveia minuscula* Nessov, 1987 (Asionyctiinae).

The faunal assemblage dated terminal Early Eocene from the Andarak 2 locality in Kyrgyzstan includes the micropternodontid *Metasarcodon udovichenkoi* (Averianov, 1994), the hedgehog *Protogalericius averianovi* gen. et sp. nov. (Galericinae), and the palaeoryctids *Nuryctes alayensis* Lopatin et Averianov, 2004 and Palaeoryctidae gen. et sp. indet.

(3) The study of morphology and evolution of Early Paleogene Asian insectivore mammals provided the following results important for a better understanding of phylogeny and classification of Insectivora and some groups of insectivore-like placentals.

(3.1) It is shown that the Early Paleogene genera *Carnilestes, Prosarcodon, Sarcodon, Hyracolestes,* and *Metasarcodon* belong to the endemic Asian subfamily Sarcodontinae Lopatin et Kondrashov, 2004 of the family Micropternodontidae and, thus, represent an early differentiated branch of primitive soricomorphs.

(3.2) Late Paleocene *Gobigeolabis* Lopatin, 2004 is the first find of the family Geolabididae in Asia and the earliest known Paleogene representative of the family, which connects morphologically and chronologically Late Cretaceous *Batodon* with Early Eocene *Centetodon* and *Batodonoides*.

(3.3) It is shown that the basic trend in the evolution of dentition of the Nyctitheriidae consisted of the shortening of the tooth row, including secondary premolarization of P_4. Based on phylogenetic interpretation of these changes, a classification of this family with the division into five subfamilies is proposed: Nyctitheriinae Simpson, 1928, Amphidozotheriinae Sigé, 1976, Eosoricodontinae Lopatin, 2005, Asionyctiinae Missiaen et Smith, 2005, and Praolestinae subfam. nov.

(3.4) The establishment of morphological continuity between Eosoricodontinae (Nyctitheriidae) and Soricolestinae Lopatin, 2002 (Soricidae) supports the origin of Soricidae from eosoricodontine nyctitheriids.

(3.5) Early Eocene *Ordolestes* gen. nov. is the earliest representative of the family Plesiosoricidae. The genera *Ordolestes, Pakilestes*, and *Butseli*a are combined in the subfamily Butseliinae, which is characterized by predatory specialization. The well-pronounced dental specialization of *Ordolestes* suggests that it appeared as a result of early radiation of Butseliinae that occurred at the Paleocene–Eocene boundary, plesiosoricids differentiated into the subfamilies Butseliinae and Plesiosoricinae even earlier.

(3.6) The zalambdodont soricomorph insectivores of the family Apternodontidae are divided into four subfamilies: the North American Parapternodontinae Asher et al., 2002, Oligoryctinae Asher et al., 2002, and Apternodontinae Matthew, 1910 and the Asian Asiapternodontinae subfam. nov. In the lower molar structure *Asiapternodus* shows plesiomorphic similarity to *Parapternodus*; however, at present, it is impossible to support or reject their close relationship because of the absence of data on the upper teeth of *Parapternodus*.

(3.7) The analysis of evolutionary changes in dentition has shown the continuity of structural patterns of molars (in the original typology) in the suborder Soricomorpha, phylogenetic interpretation of which (along with other morphological data) supports the establishment of the infraorders Tenrecomorpha and Soricota.

(3.8) It is shown that the suborder Erinaceomorpha is represented in Asia only by the Recent family Erinaceidae (which is recorded beginning from the Early Eocene), while all data on the presence of primitive Early Paleogene erinaceomorph groups are in error. In addition to the subfamilies Tupaiodontinae, Galericinae, Brachyericinae, and Erinaceinae, it is proposed to recognize the subfamily Changlelestinae in the family Erinaceidae. The discovery of *Protogalericius* gen. nov. suggests that the Recent subfamily Galericinae emerged in the Early Eocene, and the study of Middle Eocene *Eogalericius* Lopatin, 2004 and *Microgalericulus* gen. nov. gives evidence of considerable morphological diversity of Eocene gymnures.

The earliest representatives of Changlelestinae, Tupaiodontinae, and Galericinae inherited a number of primitive characters of Paleocene Erinaceomorpha. Their ancestral groups probably emerged in the Late Paleocene of North America and radiated in Asia at the beginning of the Eocene. The Changlelestinae and Tupaiodontinae are closer to each other than to the Galericinae. The origin of Brachyericinae was probably connected with a special Eocene group of relatively short-faced gymnures, which included Protericini, while the Erinaceinae probably evolved from another early group of Galericinae, which was similar to the ancestral group of Protericini and Brachyericinae and developed in parallel towards shortening the snout and reduction of the anterior and posterior regions of the tooth row. In the common ancestor of Amphechinini, Scymnericini, and Erinaceini, the dentition was still moderately reduced. Further reduction of teeth in each of the three tribes probably occurred in parallel; otherwise, Scymnericini and Erinaceini evolved from one or two groups of primitive Amphechinini, which had already lost P_3, but had not got considerably increased anterior incisors.

(3.9) The endemic Asian family Didymoconidae is considered to belong to the distinct order Didymoconida Lopatin, 2001, which along with the orders

Lipotyphla and Leptictida compose the superorder Insectivora. The family Didymoconidae is divided into three subfamilies: Ardynictinae Lopatin, 1997, Didymoconinae Kretzoi, 1943 and Kennatheriinae subfam. nov. (*Kennatherium, Zeuctherium*, and *Erlikotherium* gen. nov.). The study of Early Paleogene Didymoconidae considerably enlarged the knowledge of morphological, taxonomic, and ecological diversity of the family. The subfamily Didymoconinae is recorded in the Middle Eocene (*Khaichinula* gen. nov.). The differences between *Didymoconus, Ardynictis*, and *Kennatherium* in the extent to which the semifossorial specialization is developed are recognized. The functional "edentate pattern" of *Erlikotherium* gen. nov. is revealed and interpreted as adaptation for feeding on colonial insects.

(3.10) Relatively high taxonomic diversity and abundance of representatives of endemic genera of Cimolestidae (*Naranius, Tsaganius*, and *Bagalestes* gen. nov.) in the basal Eocene of Mongolia are regarded as a unique faunal characteristic of the Bumbanian Asian Land Mammal Age.

(3.11) The Palaeoryctidae, which were previously recorded in Asia only in the Middle Eocene, are also recorded in the Upper Paleocene (*Pinoryctes* gen. nov.) and Lower Eocene (*Nuryctes alayensis,* Palaeoryctidae gen. et sp. indet.). The trends in the morphological evolution of the lower jaw and teeth of the Asian genus *Nuryctes* are established, including the displacement of the posterior mental foramen from the level of P_4 to the level of M_1, directional reduction of P_3, the talonid of P_4, and the paraconid of M_2. Asian palaeoryctids are similar in plesiomorphic characters; this suggests their early deviation from the lineage of *Palaeoryctes* and the fact of Early Paleogene radiation of Palaeoryctidae in Asia.

(3.12) Late Paleocene *Zhigdenia* gen. nov. is the earliest Asian representative of Pantolestidae. The considerably reduced anterior premolars suggest significant specialization and assignment of this genus to a distinct evolutionary lineage, which developed independently of North American and European lineages.

(4) The results of the present study support the monophyletic concept of insectivores, which is substantiated by morphological methods, and disagree with the data of molecular analysis, which suggest a detached position of Tenrecoidea (Tenrecidae and Chrysochloridae). Taking into account fossil data, insectivores are regarded as a distinctly morphologically outlined superorder within Epitheria. In the classification proposed in the present study, the superorder Insectivora Bowdich, 1821 is divided into the orders Leptictida McKenna, 1975 (Gypsonictopidae and Leptictidae), Didymoconida Lopatin, 2001 (Didymoconidae), and Lipotyphla Haeckel, 1866. Lipotyphla is divided into the suborders Chrysochloridea Broom, 1915 (Chrysochloridae), Erinaceomorpha Gregory, 1910 (Erinaceidae, Amphilemuridae, Sespedectidae, and Creotarsidae), and Soricomorpha Gregory, 1910, including the infraorders Tenrecomorpha Butler, 1972 (Tenrecidae) and Soricota Kalandadze et Rautian, 1992. The families of Soricota are grouped in the superfamilies Micropternodontoidea Stirton et Rensberger, 1964 (Micropternodontidae), Nesophontoidea Anthony, 1916 (Geolabididae and Nesophontidae), Soricoidea Fischer von Waldheim, 1817 (Nyctitheriidae, Soricidae, and Plesiosoricidae), Talpoidea Fischer von Waldheim, 1817 (Talpidae, Proscalopidae, and Dimylidae), and Solenodontoidea Gill, 1872 (Apternodontidae and Solenodontidae).

(5) Based on the entire set of potentially compatible data, the following scenario for the evolution of insectivores is proposed, which characterizes the major stages of their history: (1) in the first half of the Late Cretaceous of North America, the ancestral Insectivora differentiated from primitive placentals; (2) in the second half of the Late Cretaceous, Insectivora underwent an adaptive radiation, and the orders Leptictida, Didymoconida, and Lipotyphla as well as the suborders Erinaceomorpha and Soricomorpha differentiated; (3) at the Cretaceous–Paleocene boundary, the primary radiation of Soricomorpha, with the differentiation of ancestors of Tenrecomorpha in Africa and Soricota in North America; (4) in the Paleocene, Soricota expanded in the Northern Hemisphere; Erinaceomorpha underwent primary radiation in North America; and the Erinaceidae appeared; (5) at the Paleocene–Eocene boundary, radiation of Soricota and Erinaceidae; (6) at the Early–Middle Eocene boundary, the extant groups Soricidae, Talpidae, and Galericinae appeared; (7) in the Middle Eocene–Oligocene, primitive groups were replaced everywhere by the rapidly evolving extant families and related groups; the Recent subfamilies of Soricidae, Talpidae, Erinaceidae, and Tenrecidae were formed; (8) in the Miocene–Pliocene, primitive groups of Recent families disappeared; Recent groups occupied the dominant position; the diversity of Erinaceomorpha decreased; the Soricidae diversified at a high rate; and Recent insectivore genera were formed.

Thus, Early Paleogene nyctitheriid insectivores of Asia probably included the direct ancestors of shrews. It seems plausible that future finds in the Eocene of Asia will provide a better understanding of the origin of moles. The study of geolabidids, nyctitheriids, and apternodontids will surely clarify the evolution of primitive soricomorph groups, which are connected with the origin of tenrecs, nesophontids, and solenodontids. The origin and establishment of Recent erinaceid subfamilies also took root in the Early Paleogene. It will be possible to solve most of the problems concerned with the establishment of tenrecs and golden moles after new finds in the Paleogene of Africa. Thus, further studies of Early Paleogene insectivores are very promising for the formation of integral concepts of the evolution, phylogeny, and systematics of these placentals.

ACKNOWLEDGMENTS

First of all I would like to express my most sincere gratitude to the late Valerii Yu. Reshetov, Boris A. Trofimov, and Nina S. Shevyreva (PIN), remarkable Russian scientists, who rendered me all possible support from the very beginning of my research into small mammals from the Paleogene of Asia.

I am greatly indebted to Professor A.K. Agadjanian (PIN) for valuable discussions and editorial remarks. I am grateful to Professor M.A. Akhmetiev (GIN) for consultation concerning the problems of stratigraphy of the Paleogene and Neogene of Asia, to V.S. Zazhigin (GIN) and A.O. Averianov (ZIN) for useful discussions on the morphology of some of the insectivore groups under consideration. I am thankful to P.E. Kondrashov (PIN) and S.G. Lucas (Museum of Natural History of New Mexico, USA) for fruitful collaboration, which resulted in particular in a number of papers devoted to Early Paleogene mammals of Asia, and to A.V. Mazin (PIN) for help in producing photographs.

This study was supported by the Program of the Presidium of the Russian Academy of Sciences "Biosphere Origin and Evolution," the Board of the President of the Russian Federation (project nos. MK-726.2004.4, NSh-1840.2003.4), the Russian Foundation for Basic Research (project nos. 04-05-64805 and 05-04-48493), the Russian Science Support Foundation, and the American Paleontological Society (PalSIRP Sepkoski Grants, 2002–2005).

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