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Microtoid cricetids and the early history of arvicolids (Mammalia, Rodentia)

Oldrich Fejfar, Wolf-Dieter Heinrich, Laszlo Kordos, and Lutz Christian Maul

ABSTRACT

In response to environmental changes in the Northern hemisphere, several lines of brachyodont-bunodont cricetid rodents evolved during the Late Miocene as “microtoid cricetids.” Major evolutionary trends include increase in the height of cheek tooth crowns and development of prismatic molars. Derived from a possible *Megacricetodon* or *Democricetodon* ancestry, highly specialised microtoid cricetids first appeared with *Microtocricetus* in the Early Vallesian (MN 9) of Eurasia. Because of the morphological diversity and degree of parallelism, phylogenetic relationships are difficult to detect. The Trilophomyinae, a more aberrant cricetid side branch, apparently became extinct without descendants. Two branches of microtoid cricetids can be recognized that evolved into “true” arvicolids: (1) *Pannonicola* (= *Ischymomys*) from the Late Vallesian (MN 10) to Middle Turolian (MN 12) of Eurasia most probably gave rise to the ondatrine lineage (*Dolomys* and *Propliomys*) and possibly to *Dicrostonyx*, whereas (2) *Microtodon* known from the Late Turolian (MN 13) and Early Ruscinian (MN 14) of Eurasia and possibly parts of North America evolved through *Promimomys* and *Mimomys* eventually to *Microtus, Arvicola* and other genera. The Ruscinian genus *Tobienia* is presumably the root of Lemmini. Under this hypothesis, in contrast to earlier views, two evolutionary sources of arvicolids would be taken into consideration. The ancestors of *Pannonicola* and *Microtodon* remain unknown, but the forerunner of *Microtodon* must have had a brachyodont-lophodont tooth crown pattern similar to that of *Rotundomys bressanus* from the Late Vallesian (MN 10) of Western Europe. Possibly, *Pannonicola* and *Microtodon* share a common ancestor. The fossil record suggests that an important center of origin for arvicolids was located in northeast Asia. From this region arvicolids could have dispersed to Europe and North America and vice versa during the late Cenozoic at various times.

Oldrich Fejfar, Charles University, Institute of Geology and Paleontology, CZ-128 43 Praha 2, Albertov 6, Czech Republic, fejfar@natur.cuni.cz
Wolf-Dieter Heinrich, Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin, Invalidenstraße 43, D-10115 Berlin, Germany, wolf-dieter.heinrich@mfn-berlin.de
Laszlo Kordos, Hungarian Geological Institute, Stefania u. 14, H-1143 Budapest, Hungary

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kordos@mafi.hu
Lutz Christian Maul, Senckenberg Research Institute , Senckenberg Research Station of Quaternary Palaeontology Weimar, Am Jakobskirchhof 4, D-99423 Weimar, Germany, lmaul@senckenberg.de

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INTRODUCTION

Arvicolids are muroid rodents that first appeared in the Late Miocene of Eurasia and North America and have been widely dispersed in the Northern Hemisphere since that time (Repenning 1987; Repenning et al. 1990; Fejfar et al. 1997). Today, arvicolids include the lemmings, muskrats, meadow mice, red-backed voles, heather voles, sagebrush voles, and the mole voles. They are one of the most successful groups of rodents to inhabit the northern continents during the late Cenozoic.

The fossil record of arvicolids is outstandingly rich. Their high-crowned prismatic molars can be readily distinguished from those of any other rodent group. Arvicolid cheek teeth and other skeletal remains can easily be obtained in great quantities by washing and sieving sediment. Enormous numbers of sites scattered widely in Eurasia and North America have produced diverse assemblages of fossil arvicolids. An increasing body of literature provides much information about their taxonomy, distribution, biostratigraphy, evolution, and phylogeny. However, data about the roots and early history of arvicolids are rather limited (e.g., Hinton 1926; Repenning 1968; Kretzoi 1969; Rabeder 1981; Fejfar and Heinrich 1983; Nesin and Topachevskij 1991; Topachevskij and Nesin 1992; Fejfar et al. 1997; Chaline et al. 1999; Agadjanjan 2009) and a generally accepted model about the origin of voles and lemmings has not yet been established.

Today, there is no doubt that arvicolids evolved from a specialised branch of advanced cricetid rodents designated by the informal name “microtoid cricetids” by Schaub (1934). “Microtoid” means arvicolid-like, since not all of these forms evolved to the group of true arvicolids. The terms arvicolids and microtids (Arvicolidae and Microtidae) are currently used as synonyms, traceable back to Miller (1896) who considered the genus *Arvicola* as a junior synonym of *Microtus* and therefore rejected the name Arvicolidae Gray, 1821 and used Microtidae Cope, 1891 (Kretzoi 1990).

The systematic rank of arvicolids has been debated for many years (e.g., Kretzoi 1969; Musser and Carleton 1993 and references herein). Many authors refer arvicolids to subfamily rank (Arvicolinae), but given high species diversity and the specialised adaptive level, they are considered by some workers to be of family rank (e.g., Niethammer 1982), a view shared by the present authors.

Extant arvicolids and cricetids are morphologically well distinguished, but fossil forms display transitions in many characters. Arvicolids are ecologically and morphologically adapted to digging and eating less nutritious vegetative plant remains, mainly monocots (Gramineae), and do not hibernate, whereas Eurasian cricetids mainly eat seeds and roots and do hibernate (Niethammer 1982).

A crucial feature of arvicolid molars is that they are, or show tendency to become, hypsodont. Parallel and angled lateral walls (in some older forms slightly conical) cause a more or less constant occlusal surface in all grinding levels, which is called a “prismatic” form. The chewing surface is flat with serial prisms alternating on buccal and lingual sides. The enamel band is undifferentiated in primitive taxa and mainly differentiated in derived taxa. Cricetids originally have brachyodont and bunodont molars with cutting edges at the tubercles and not planar occlusal surface. Arvicolids and cricetids differ in several cranial features and in enamel microstructure, adapted to various modes of chewing and biomechanical forces resulting from the positions of muscles (Repenning 1968; von Koenigswald 1980).

However, since it is evident that arvicolid-like characters evolved independently within cricetids at several times, the question remains as to which cricetid rodents gave rise to “true” early arvicolids. In the following, we summarise data from the relevant time interval and discuss possible phylogenetic relationships between the various microtoid cricetids and early arvicolids in order to enlighten the basal phase of arvicolid evolution. Primitive cricetids and arvicolids of Eurasia are the main focus of the present paper.

The biochronological framework used in the present paper is that of Repenning (1987), Tedford et al. (1987, 2004), Fejfar and Heinrich (1990), Fejfar et al. (1997, 1998) and Martin (2003a). The use of MN zones of the European Neogene mammal chronology follows Mein (1990, 1999), usage of the Neogene mammal faunal units (NMU) in China Qiu et al. (1999) and Qiu and Li (2003). A graphical review of the significant taxa of cricetids, microtoid cricetids and early arvicolids is given in Figures 1-6. The palaeogeographical and stratigraphical ranges of the considered taxa are shown in Figure 7. In the following descriptions, lower case denotes lower teeth and upper case denotes upper teeth. For elements of the occlusal surface the terminology of Fahlbusch (1964) and van der Meulen (1973) is used.

CHEEK TOOTH ADAPTATIONS IN CRICETIDS, MICROTOID CRICETIDS AND ARVICOLIDS

During the Late Miocene various lineages of cricetids developed similar dental adaptations toward increasing hypsodonty. The acquisition of hypsodont molars was a remarkable advantage, because high-crowned cheek teeth are more adapted to wear and therefore are more suitable for a diet of abrasive grasses (e.g., Gramineae), which were gaining prominence on a worldwide scale at this time (Fortelius et al. 2003). A second adaptation of certain cricetid rodents, the development of a more complex crown pattern of the cheek teeth, began slightly before hypsodonty was achieved. It also evolved progressively and had the same advantage, increasing the amount of enamel available for chewing and ensuring that a chewing surface with enamel ridges (cutting edges) persisted throughout life.

Complexity of tooth crown pattern was in the form of transverse infolding of the enamel walls of the sides of the teeth in these muroids, and this produced a series of transverse ridges, or lophs. This lophodont condition was ideal for chewing by moving the teeth horizontally across each other. This type of chewing is comparable to sharpening an axe by holding a file parallel to the cutting edge and drawing it parallel to the axe head; all grinding points come into contact with the cutting edge of the axe, but for a very short stroke. In combination with increased hypsodonty, the lophs could be worn flat, producing a series of enamel edges at the site of infolded enamel walls of the lophs. A Morpho-functional model of evolution towards longitudinal masticatory movement from Cricetids to Arvicolids is demonstrated by Lazzari et al. (2008).

Propalinal chewing, moving the teeth forward and backward over each other, greatly increases the number of enamel-to-enamel contacts with one stroke, maximizing return for muscle effort in chewing; it also evolved in many other types of mammals, e.g., elephants.

Evidence indicates that development of hypsodonty in cricetid molars happened simultaneously in several lineages and in different areas of Eurasia and North America in response to a grazing habit (e.g., Fejfar and Heinrich 1983; Repenning 1987; Repenning et al. 1990; Fejfar and Repenning 1992; Fejfar 1999; Kälin 1999; Bell 2000).

Lineages have yet to be traced through the labyrinth of varied combinations of specialization by molar hypsodonty, complexity, and chewing methods. The fossil record of microtoid cricetids suggests that dental complexity followed two patterns: first, initial opposition of the cusps to form complete cross-lophs on the teeth; and second, initial alternation of the cusps to produce alternating hemi-lophs on the molars. The latter apparently led to the particular arvicolid condition characterised by the increasing development of alternating prismatic columnar cusps on high-crowned molars. However, the fossil record reveals that some microtoid cricetids gradually changed well-developed lophodont molars to cheek teeth with alternating triangular hemi-lophs, indicating an independent evolutionary pathway to the arvicolid condition.

In any case, alternating prismatic triangles seem to be the optimum condition in hypsodonty and complexity of molar structure, presumably because they reduce by half the force needed to perform propalinal chewing at any specific moment. Nevertheless, efficient propalinal chewing required some modification of jaw musculature, and this appears to be another typical arvicolid specialization, judging from its general absence in microtoid cricetids (Repenning 1968).

In this paper, selected true early arvicolids and microtoid cricetids are reviewed and possible relationships between microtoid cricetids and their ancestors are discussed briefly. The molars of the considered rodent taxa are arranged morphologically (typologically) in eight tooth groups (A-H), ranging from brachyodont-bunodont to hypsodont-prismatic cheek teeth (Table 1, Figures 1, 7). It is beyond the scope of this paper to provide a taxonomic classification, which can only follow clarification of many uncertainties rendered in the following discussions.

TABLE 1. The morphological (typological) tooth groups (A-H) with included taxa and their ranges

Tooth groups	Taxa	Distribution			Range
Group A					
Brachyodont and mesodont molars with bunodont dental pattern	*Megacricetodon*	Europe	Asia		Late Orleanian (MN 4b) to Early Vallesian (MN 9) Turkey: up from MN 3 China: MN 4 to MN 8
	Democricetodon	Europe	Asia		Late Orleanian (MN 4a) to Late Vallesian (MN 10) Turkey: up from MN 1 China: MN 4 to MN 9
	Kowalskia	Europe	Asia		Early Vallesian (MN 9) to Early Villanyian (MN 16b) China: MN 11 to MN 16
	Collimys transversus	Europe			middle Astaracian (MN 7)
	Collimys longidens	Europe			Early Vallesian (MN 9)
	Collimys primus	Europe			Early Turolian (MN 11)
	Copemys			North America	Late Arikareean to Late Blancan
Group B					
Brachyodont molars with lophodont dental pattern and planar occlusal surface	*Rotundomys bressanus*	Europe			Vallesian (MN 9, MN 10)
	Rotundomys montisrotundi	Europe			Late Vallesian (MN 10)
Group C					
Mesodont molars with tendencies towards prismatic dental pattern	*Microtocricetus molassicus*	Europe			Vallesian (MN 9, MN 10)
Group D					
Mesodont and hypsodont molars with prismatic dental pattern and opposing and slightly alternating triangles	*Microtoscoptes praetermissus*		Asia		Late Turolian (MN 13) or Early Ruscinian (MN 14)
	Microtoscoptes tjuvaensis	East Europe			Late Turolian (MN 13)
	Paramicrotoscoptes hibbardi			North America	Early Hemphillian
	Goniodontomys disjunctus			North America	Early Hemphillian

TABLE 1 (continued).

Tooth groups	Taxa	Distribution		Range
Group E				
Mesodont and hypsodont molars with prismatic dental pattern and opposing triangles; M1, m1, and m2 trilophodont	*Trilophomys pyrenaicus*	Europe		Early Ruscinian (MN 14) to Late Ruscinian (MN 15)
	Trilophomys	Europe		Early Ruscinian (MN 14) to Late
	Trilophomys	Europe		Early Ruscinian (MN 14) to Late
	Trilophomys	Europe		Late Ruscinian (MN 15)
	Trilophomys sp.	Europe		Late Villanyian (MN 17)
Group F				
Mesodont molars with prismatic dental pattern and opposing and alternating triangles	*Pannonicola sp.*	Europe		Late Vallesian (MN 10)
	Pannonicola (=Ischymomys) brevidens	Europe		middle Turolian (MN 11)
	Pannonicola (=Ischymomys) ponticus		Asia	Early Turolian (MN 11)
	Pannonicola (=Ischymomys) quadriradicatus	Europe		middle Turolian (MN 12)
Group G				
Mesodont molars with prismatic dental pattern and alternating triangles	*Anatolomys teilhardi*		Asia	Late Turolian (MN 13) to Early Ruscinian (MN 14)
	Celadensia nicolae	Europe		Late Turolian (MN 13) to Early Ruscinian (MN 14)
	Baranomys loczyi	Europe		Late Ruscinian (MN 15) to Early Villanyian (MN 16)
	Baranomys longidens	Europe		Late Ruscinian (MN 15)
	Baranomys kowalskii	Europe		Early Ruscinian (MN 14a)
	Bjornkurtenia canterranensis	Europe		Early Ruscinian (MN 14) to Late Ruscinian (MN 15)
	Microtodon atavus		Asia	Late Turolian (MN 13) to Early Ruscinian (MN 14)
	Baranarviomys admirabilis	Europe		Late Turolian (MN 13)
	Promimomys cor	Europe		Early Ruscinian (MN 14b)
	Promimomys insuliferus	Europe		Early Ruscinian (MN 14a)
	Promimomys sp.	Europe	Asia	Late Turolian (MN 13)

TABLE 1 (continued).

Tooth groups	Taxa	Distribution			Range
	Prosomys mimus			North America	Late Hemphillian
Group H					
Hypsodont molars with prismatic dental pattern and alternating triangles	*Mimomys vandermeuleni*	Europe			Late Ruscinian (MN 15a)
	Tobienia kretzoii	Europe			Late Ruscinian (MN 15b)
	Lemmini nov. gen., nov. sp.	Europe			Late Ruscinian (MN 15b)
	Mimomys	Europe			Late Ruscinian (MN 15b)
	Mimomys	Europe			Late Ruscinian (MN 15b) to Early
	Aratomys bilikensis		Asia		Early Ruscinian (MN 14)
	Aratomys multifidus		Asia		Early Ruscinian (MN 14)
	Dolomys adroveri	Europe			Late Ruscinian (MN 15a)
	Dolomys milleri	Europe			Late Ruscinian (MN 15b) to Early
	Dolomys nehringi	Europe			Early Ruscinian (MN 14b) to Late
	Propliomys	Europe			Early Ruscinian (MN 14b) to Early
	Cosomys primus			North America	Middle Blancan
	Cosomys taylori			North America	Middle Blancan
	Ogmodontomys poaphagus			North America	Early Blancan II
	Cosomys sawrockensis			North America	Blancan I
	Ophiomys mcknigthi			North America	Blancan I
	Pliophenacomys finneyi			North America	Blancan II
	Pliophenacomys wilsoni			North America	Blancan I
	Protopliophenacomus parkeri			North America	Late Hemphillian

MIOCENE AND PLIOCENE CRICETIDS, MICROTOID CRICETIDS AND ARVICOLIDS

Tooth group A: Brachyodont and mesodont molars with bunodont dental pattern

Megacricetodon Fahlbusch, 1964
Democricetodon Fahlbusch, 1964
Kowalskia Fahlbusch, 1969
Collimys Daxner-Höck, 1972
Copemys Wood, 1936
Figures 1, 7

Among cricetids *Megacricetodon* and *Democricetodon* appeared together with *Eumyarion*, *Anomalomys* and *Neocometes* during the early Miocene of Europe (Late Orleanian, MN 4) as immigrants (e.g., Kälin 1999; Doukas 2003; Mein 2003), but only *Megacricetodon* and *Democricetodon* could belong to the stock that gave rise to microtoid cricetids, arvicolids and extant cricetids owing to their specific molar patterns. *Democricetodon* entered the fossil record slightly before *Megacricetodon* (Kälin 1999; Sesé 2006). *Megacricetodon* has relatively small molars characterised by a double-cusped antercone and anteroconid. Major evolutionary trends of *Mega-cricetodon* include (Kälin 1999): increase in size, differentiation of the anteroconid along with the reduction of the mesoloph(id)s as well as the reduction and thickening of the posterolophid. In addition, the mesosinus became directed more anteriorly in stratigraphically younger species.

In contrast to *Megacricetodon*, the molars of *Democricetodon* are relatively shorter and broader. The anteroconid is short and undivided. The paracone is double-cusped in primitive species or three-cusped in advanced forms. There are well-developed elongated mesolophs and mesolophids as well as external ridges ("Zwischensporne" in the sense of Fahlbusch 1964). Major evolutionary trends are restricted to size increase and the development of additional ridges.

Democricetodon and *Megacricetodon* are most common in the Middle Miocene of Europe. Important lineages have been reported for *Megacricetodon* in Central Europe (Kälin 1999; Abdul Aziz et al. 2007) *M*. aff. *collongensis* - *M*. cf. *bavaricus* - *M. bavaricus* - *M*. aff. *bavaricus* - *M. lappi*) and Western Europe (Kälin 1999: *M. primitivus* – *M*. *ibericus*). *Megacricetodon* ranges in Europe from late Orleanian (late MN 4) to Early Vallesian (late MN 9), *Democricetodon* from late Orleanian (early MN 4) to Late Vallesian (MN 10) (Heissig 1990; Kälin 1999; Sesé 2006; Prieto et al. 2010). A similar age range is known from Asia. Among the last occurrences of *Democriceton* in Europe are the sites of Masia del Barbo (Spain) and Suchomasty (Czech Republic) from early MN 10 (Mein 2003).

Democricetodon, for which the center of development was likely central to eastern Europe (Freudenthal 2006), gave rise to *Kowalskia*, which first appeared as a morphotype in advanced populations of *Democricetodon freisingensis* and *Democricetodon* sp. during the late Early Vallesian (MN 9). However, derivation from another *Democricetodon* species seems also possible (Kälin 1999).

The double-cusped paracone and paraconid, the pronounced elongated mesoloph and mesolophid, and the relatively long and broad tooth crowns of M1 and m1 are typical traits that distinguish *Kowalskia* from other contemporary cricetid genera. In Europe, there is a gradual evolutionary sequence of taxa (lineage) within *Kowalskia* ranging from the late Early Vallesian (MN 9) up to the Early Villanyian (MN 16) (Daxner-Höck 1995). *Kowalskia* was one of the most common cricetids in the European Late Miocene (Daxner-Höck et al. 1996; Kälin 1999). Many species were described from the Late Miocene and Early Pliocene of western, southern and central Europe, among them (Daxner-Höck 1995; Kretzoi and Fejfar 200534): *Kowalskia fahlbuschi* (e.g., Rudabanya, Hungary, MN 9; Kohfidisch, Austria, MN 10), *Kowalskia occidentalis* (Crevillente 2, Spain, MN 11), *Kowalskia schaubi* (Csakvar, Hungary, MN 11), *Kowalskia skofleki*, Tardosbanya, Hungary, MN 12), *Kowalskia nestori* (Baccinello V-3, Italy, MN 13/14), *Kowalskia browni* (Maramena, Greeke, MN 13/14), *Kowalskia polonica* and *Kowalskia magna* (Podlesice, Poland, MN 14), and *Kowalskia intermedia* (Ivanovce, Slowakia, MN 15). In eastern Europe, *Kowalskia progressa* (MN 9?, Topachevskij and Skorik 1992) and *Kowalskia moldavica* (MN 10?, Lungu1981) were reported. One tooth of *Kowalskia polonica* was found in the Polish locality Rebielice Krolewskie (MN 16b) (Pradel 1988), but according to Kowalski (2001) this record needs confirmation. According to Daxner-Höck (1995), at least two lineages are recognised in Central Europe: *Kowalskia fahlbuschi* that developed to *Kowalskia polgardiensis*, and *Kowalskia schaubi* evolving through *Kowalskia skofleki* – *Kowalskia magna* – *Kowalskia polonica* to *Kowalskia intermedia*.

Collimys has been reported from the Middle and Late Miocene of Central Europe. Dental traits are (Kälin 1999): the loss of the anterior protolophule in M2 and a flat chewing surface along with distinctly increased and thickened mesoloph(id)s. The stratigraphically oldest species is *Collimys transversus* from the Middle Astaracian (MN 7) at Steinheim am Aalbuch, Germany (Heissig 1995). *Collimys transversus* possessed brachyodont molars with a primitive crown pattern characterised, for instance, by the absence of the ectomesolophid in lower molars (Heissig 1995). The crowns of *Collimys longidens* from the Early Vallesian (MN 9) of Nebelbergweg, Switzerland, are slightly higher (mesodont) than those of *Collimys transversus* (Kälin and Engesser 2001). Much more derived is *Collimys primus* from the Early Turolian (MN 11) site Eichkogel, Austria, (Daxner-Höck 1972) that displays distinctly hypsodont cheek teeth. Among Cricetini, the Middle Miocene *Collimys* developed first tendencies toward hypsodonty followed by *Cricetulodon* and *Rotundomys* that occurred in the Late Miocene (Kälin 1999). *Collimys* is likely to have evolved from *Democricetodon*.

Democricetodon, *Megacricetodon*, and *Kowalskia* have a more cosmopolitan fossil record than does *Collimys* for which localities are confined to Europe. *Democricetodon* and *Megacricetodon* were widely distributed across Asia during the Middle Miocene. Important records of *Democricetodon* and *Megacricetodon* are known, for instance, from

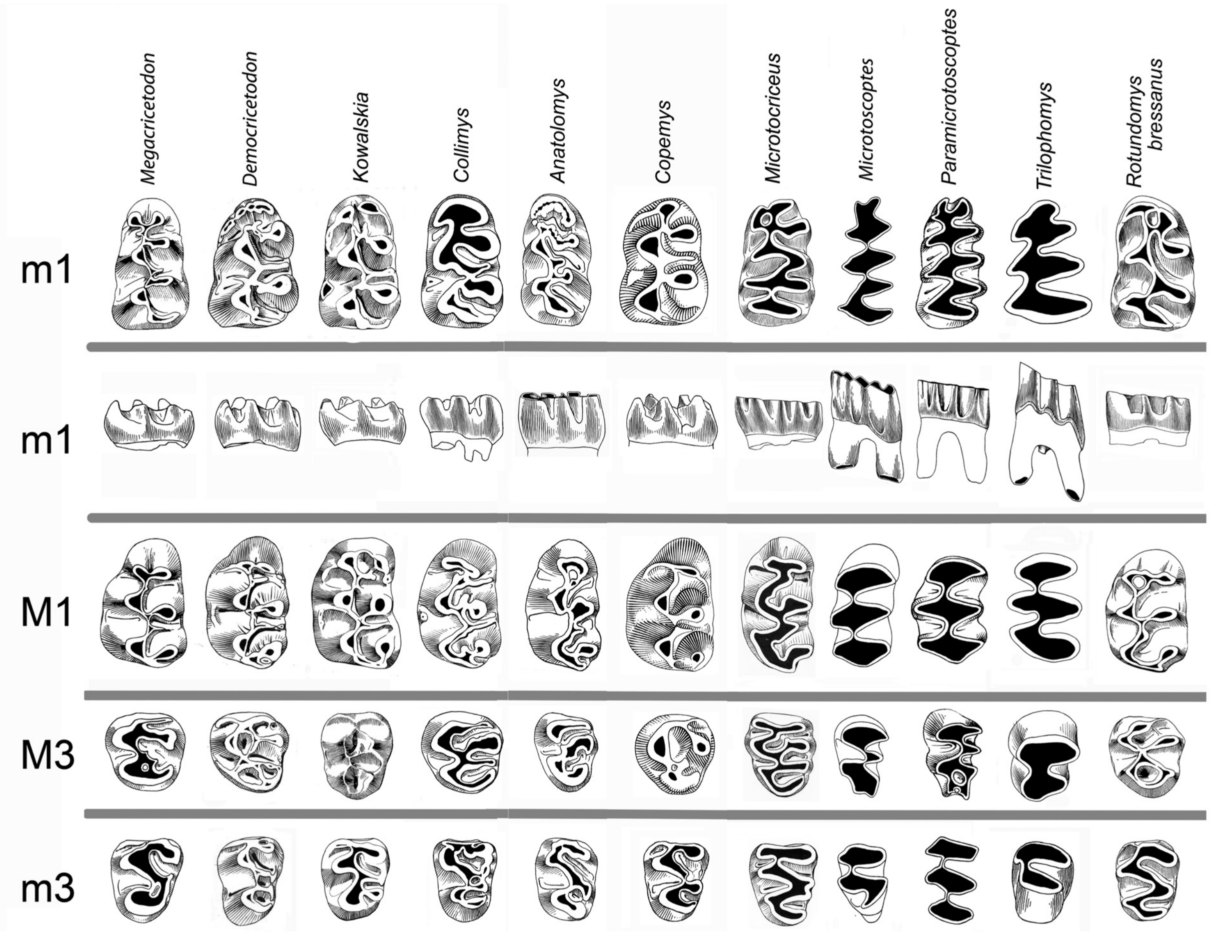

FIGURE 1. (left and right) Overview of Late Miocene and Pliocene genera of cricetids of Eurasia and North America. Typical molars are assemblaged in five rows: m1 occlusal and buccal views; M1, M3, m3 occlusal views. All are figured as left molars; not to scale.

many early to late Middle Miocene sites of China (e.g., Fahlbusch 1969; Qui et al. 1981; Qui 1990; Lindsay 1994; Qiu and Qiu 1995) and Pakistan (e.g., Bruijn and Hussein 1984; Jacobs and Lindsay 1984; Lindsay 1987, 1988, 1994), those of *Kowalskia* from Late Miocene and Early Pliocene localities in China (e.g., Lindsay 1994; Qiu and Qiu 1995; Qiu and Storch 2000).

Both *Democricetodon* and *Megacricetodon* appeared in China for the first time during the late Early Miocene (late Shanwangian, MNU 4), equivalent with the late Orleanian (MN 4, and perhaps parts of MN 3) in Europe (Qiu and Li 2003). Important sites of this temporal interval are, for instance, Sihong (*Democricetodon* sp., *Megacricetodon* sp.) and Gashunyinadege (*Democricetodon* cf. *lindsayi*, *Megacricetodon* cf. *sinensis*) as well as from Wuerte in northern China (*Megacricetodon* sp.) (Qiu et al. 1999; Qiu and Wang 1999; Qiu and Li 2003). *Megacricetodon yei* is known from the first sand bed of the early Middle Miocene Halamagai Formation exposed at Site XJ 98018 of the Tieersihabahe locality in the northern Junggar Basin, China (Bi et al. 2008). According to Qiu and Qiu (1995), the evolutionary level of *Democricetodon* sp., *Megacricetodon* sp. from Sihong corresponds approximately with that of *Megacricetodon collongensis* and *Democricetodon brevis* of the European mammal zone MN 4. As revealed by the Tunggur local fauna (Qiu et al. 1999; Qiu and Li 2003), *Megacricetodon sinensis*, *Megacricetodon pusillus*, *Democricetodon lindsayi* and *Democricetodon tongi* were distributed in the northern parts of China during the late Middle Miocene (late Tunggurian, NMU 7), roughly correlatative with the European late Astaracian (MN 7, MN 8). *Democricetodon* sp. was reported from the early Late Miocene locality Amuwusu, Nei Mongol (early

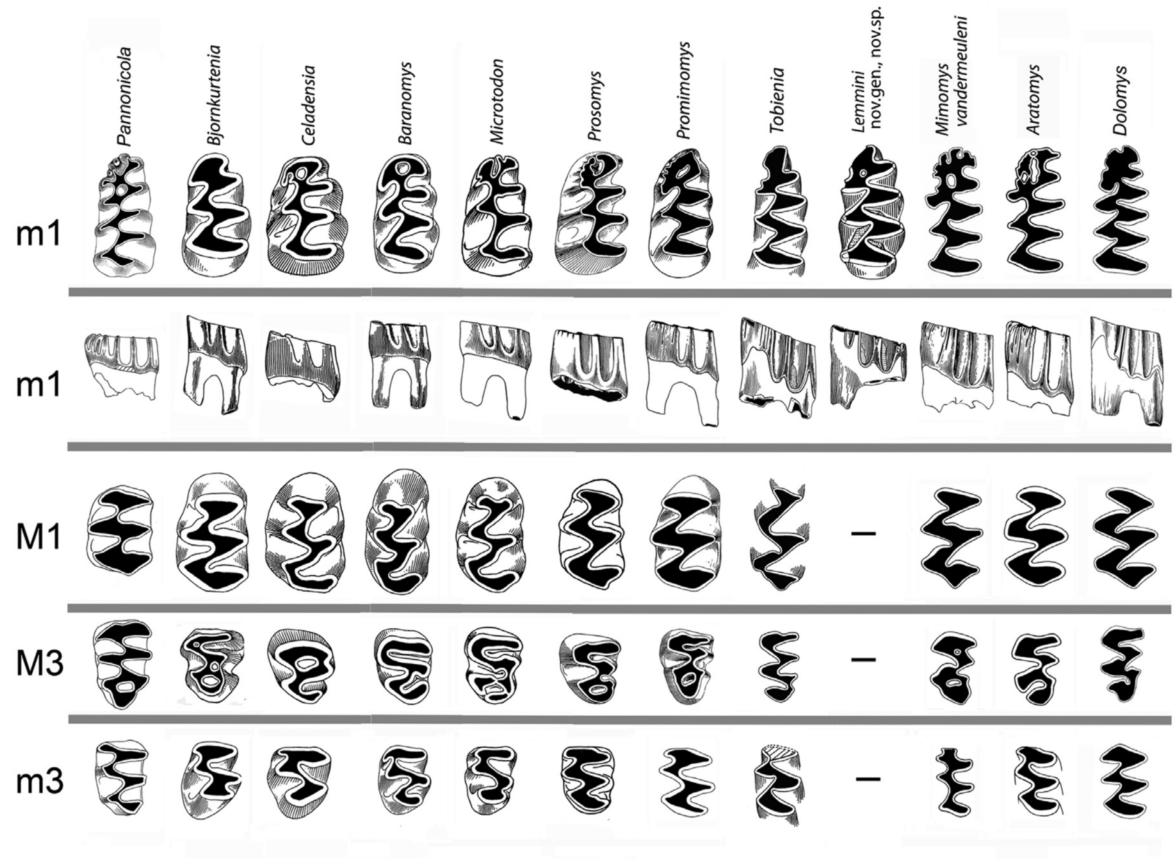

FIGURE 1 (continued).

Baodean, NMU 8), the age of which correlates probably to the early Vallesian (MN 9) of the European mammalian Neogene chronology (Qiu and Wang 1999; Qiu and Li 2003; Qiu et al. 2003). According to data given by Lindsay (1994), Qiu and Qiu (1995), Qiu et al. (1999), Qiu and Li (2003), and Qiu et al. (2003), *Megacricetodon* apparently disappeared in China during the late Middle Miocene (late Tunggurian, late Astaracian, MN 8), followed by *Democricetodon* in the early Late Miocene (early Baodean, early Vallesian, MN 9) (Mein 2003).

The early dispersal history of *Democricetodon* and *Megacricetodon* in Europe and in the northern and eastern parts of Asia appears to be roughly concordant with the fossil record of Asia Minor (Anatolia). *Democricetodon* seems to appear there for the first time during the early Agenian (MN 1), followed by *Megacricetodon* during the Early Orleanian (MN 3) (Ünay et al. 2003). However, these early occurrences remain to be confirmed by further material and study. Both genera apparently survived in this region until the Late Astaracian (MN 8) (Sümengen et al. 1990; de Bruijn et al. 2003; Ünay et al. 2003). Based on the cricetid record, the fauna from Pasalar, Anatolia, Turkey (Peláez-Campomanes and Daams 2002), containing *Megacricetodon andrewsi* and *Democricetodon brevis* can be correlated with the late European mammal zone MN 6 (Early Astaracian). *Democricetodon* dispersed during the Early Miocene through Saudi Arabia into North Africa prior to about 14 Ma (Jebel Zelten, Libya: Savage 1990; Winkler 1994. However, this record is considered "Cricetidae gen. et sp. indet." by Wessels et al. (2003). Democricetines are also known from the Early Miocene of East Africa and Namibia (Mein 2003) and the Middle Miocene of East Africa (Winkler 1994; Mein 2003).

As in Europe, *Kowalskia* appears in the fossil record of eastern Asia distinctly later than *Megacricetodon* and *Democricetodon*. One of the earliest species, *Kowalskia hanae*, is from the middle Late Miocene Shihuiba site in southern China (middle Baodean, NMU 10), a possible equivalent of the Middle Turolian (MN 12) in Europe (Qiu and Li

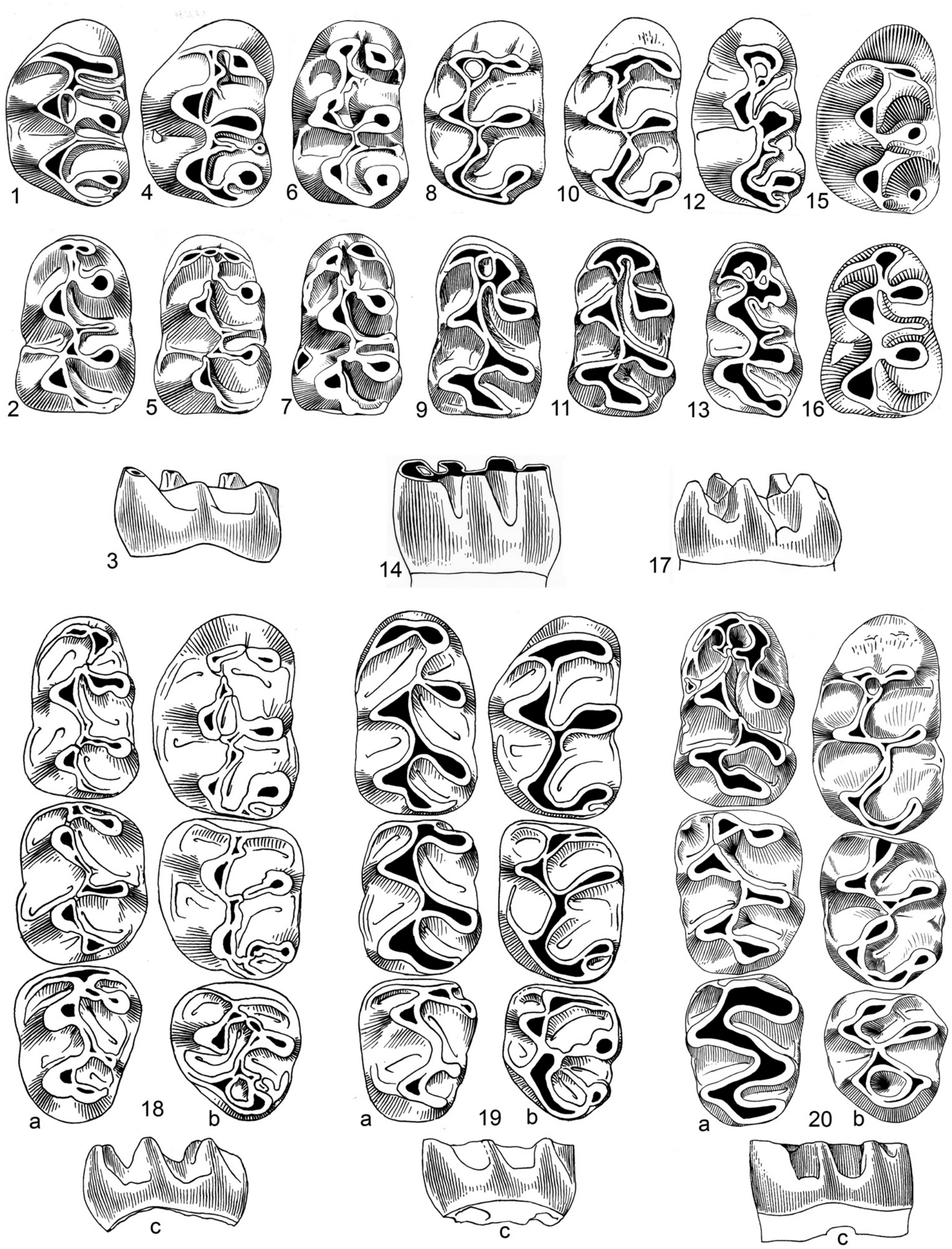

FIGURE 2. Examples of Late Miocene Cricetids I: potential ancestors of the microtoid adaptation. 1-3: *Democricetodon gaillardi* (Schaub, 1934) from Sansan, middle Miocene, MN 6, France; 4, 5: *Democricetodon* cf. *freisingensis* Fahlbusch, 1964 from Rudabanya, early Vallésian, MN 9, Northeast Hungary; 6, 7: *Kowalskia intermedia* Fejfar, 1970 from Ivanovce at Trenčín, late Ruscinian, MN 15, Western Slovakia; 8-11, 20: *Rotundomys bressanus* Mein, 1975 from Soblay (Ain), middle Turolian, upper level of MN 10, Southeast France; 12-14: *Anatolomys teilhardi* (Schaub, 1934) from Ertemte 2, inner Mogolia, late Turolian MN 13, China; 15: *Copemys tenuis* Lindsay, 1972 and 16: *Copemys barstowensis* Lindsay, 1972 from the Barstow Formation, middle Miocene, California, USA; 17: *Copemys esmeraldensis* Clark, Dawson and Wood, 1964 from the upper part of the Barstow sequence, Barstovian, California, and the Esmeralda Formation, Clarendonian, Nevada, both middle Miocene,USA; 18: *Rotundomys sabadelliensis* (Hartenberger, 1966) from Can Llobateres, early Vallésian, upper level MN 9, Spain; 19: *Rotundomys montisrotundi* (Schaub, 1944) from the lignites of Montoulieres, Hérault, middle Turolian, lower level of MN 10, France. – 1-16, 18ab, 19ab, 20ab: occlusal views of the M1 (1, 4, 6, 8, 10, 12, 15), M1-3 (18b, 19b, 20b), m1 (2, 5, 7, 9, 11, 13, 16) and m1-3 (18a, 19a, 20a); 3, 14, 17, 18c, 19c, 20c: buccal views. All figured as left molars; not to scale.

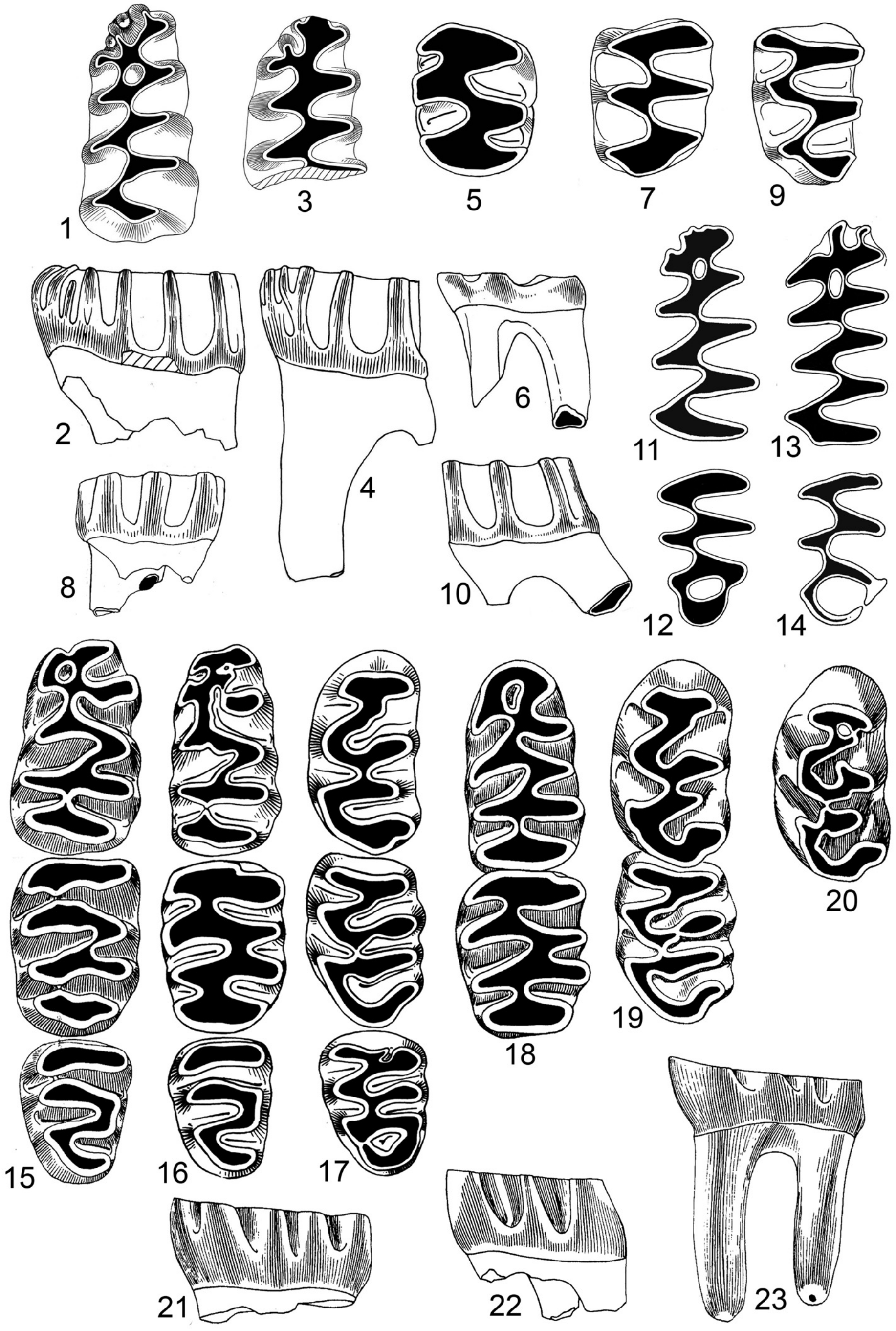

FIGURE 3. Examples of late Miocene Cricetids II: the earliest records of microtoid-prismatic morphology in molars. 1-14: *Pannonicola* Kretzoi, 1965 (= *Ischymomys* Topachevskij et al., 1978): 1-12: *Pannonicola brevidens* Kretzoi, 1965 from Sümegprága (1-4, 9-10), from from Jászladány (5, 6, the Type) and Nyárád (7, 8), all late Pannonian, Turolian, MN 11, N. Hungary; 11 - 12: *Pannonicola brevidens* Kretzoi, 1965 from Frunzovka 2 at Odessa, late Pannonian, Turolian, MN 11, Ukraine; 13, 14: *Pannonicola quadriradicatus* (Zazhigin, 1972) from Ishim strata, on the right bank of the Ishim River, Petropavlovsk, late Pannonian, Turolian, MN 12, Kazakhstan; 15 - 23: *Microtocricetus molassicus* Fahlbusch and Mayr, 1975 from Hammerschmiede, Bavarian freshwater molasse, early Vallésian, MN 9, Southeast Germany (15-17) and Rudabanya, early Vallésian, MN 9, Northeast Hungary, (18-23). – 1, 3, 5, 7, 9, 11-14, 15-20: occlusal views, 2, 4, 6, 10, 21-23: buccal views, 8: lingual view; 1, 3, 11, 13: m1; 20: M1; 12, 14: M3; 15-16: m1-3; 18: m1-2: 17: M1-3; 19: M1-2. All figured as left molars; not to scale.

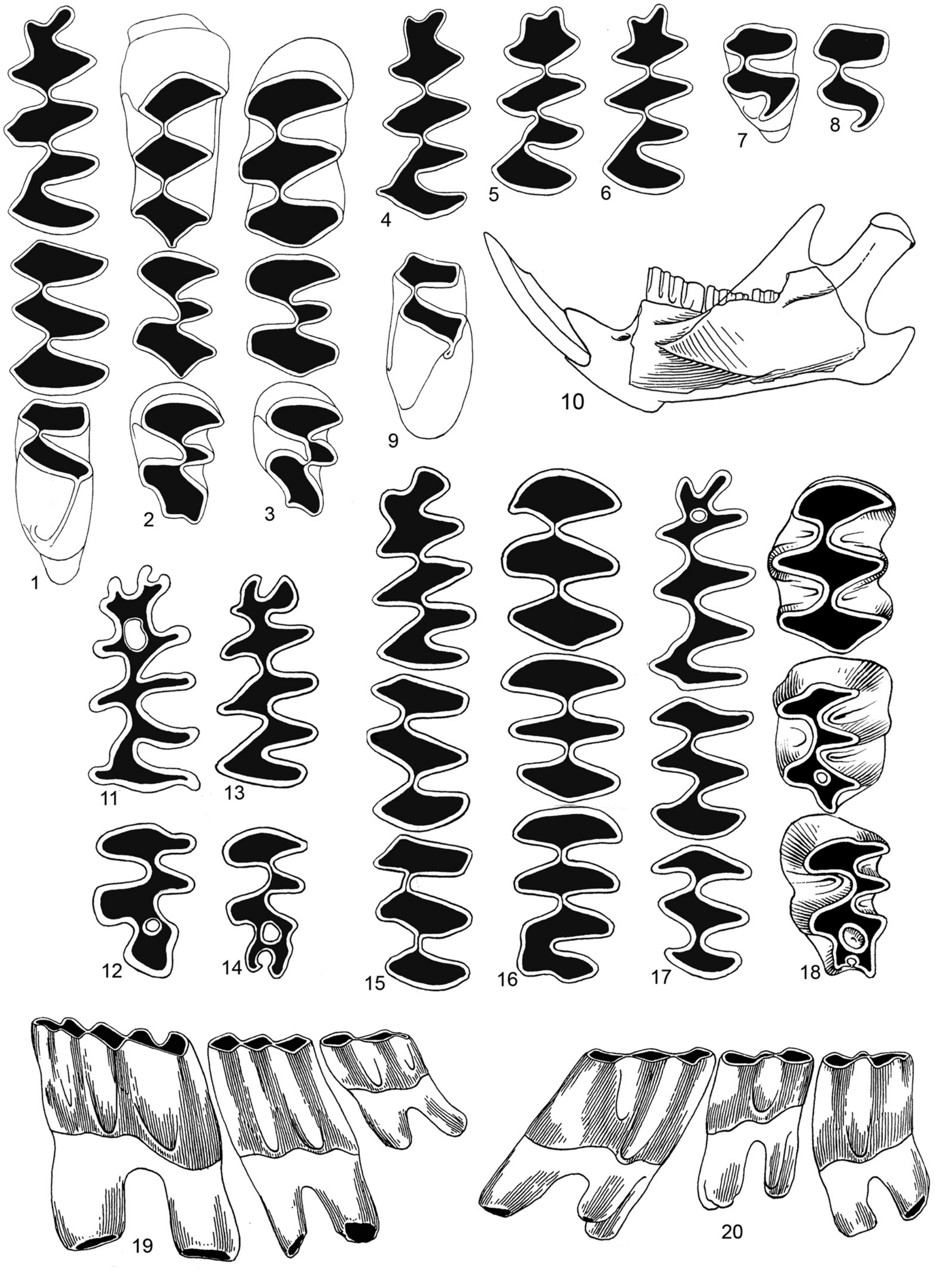

FIGURE 4. Members of subfamily Microtoscoptinae. 1-9, 19, 20: *Microtoscoptes praetermissus* Schaub, 1934 from Ertemte 2, Inner Mongolia (Nei Mongol), late Turolian MN 13, China; 10, 15, 16: *Goniodontomys disjunctus* Wilson, 1937 from USGS Cenozoic locality 20766, Kelly Road local fauna at Jackson Hole, Teton County, Wyoming (13), Strout Claime, Gooding County, Idaho (12) and combination of two jaws from Kelly Road local Rome (Repenning 1968, text.fig. 8) and Malheur County, Oregon, USA (10), USA; 11-14, 17, 18: *Paramicrotoscoptes hibbardi* Martin, 1975 from Barlett Mt., Harney County, Oregon, (17, 18) and Lemoyne, Ash Hollow Formation, Ogallala Group, Keith County, Nebraska, USA (11-14); all North American records of microscoptines: early Hemphillian. 1, 15, 17: m1-3; 2, 3, 16, 18: M1-3; 4-6, 11, 13: m1; 7-9: m3; 12, 14: M 3; 19: m1-3; 20: M1-3. 1-9, 12-18: occlusal views; 10, 19: buccal views, 20: lingual view. All figured as left molars; not to scale.

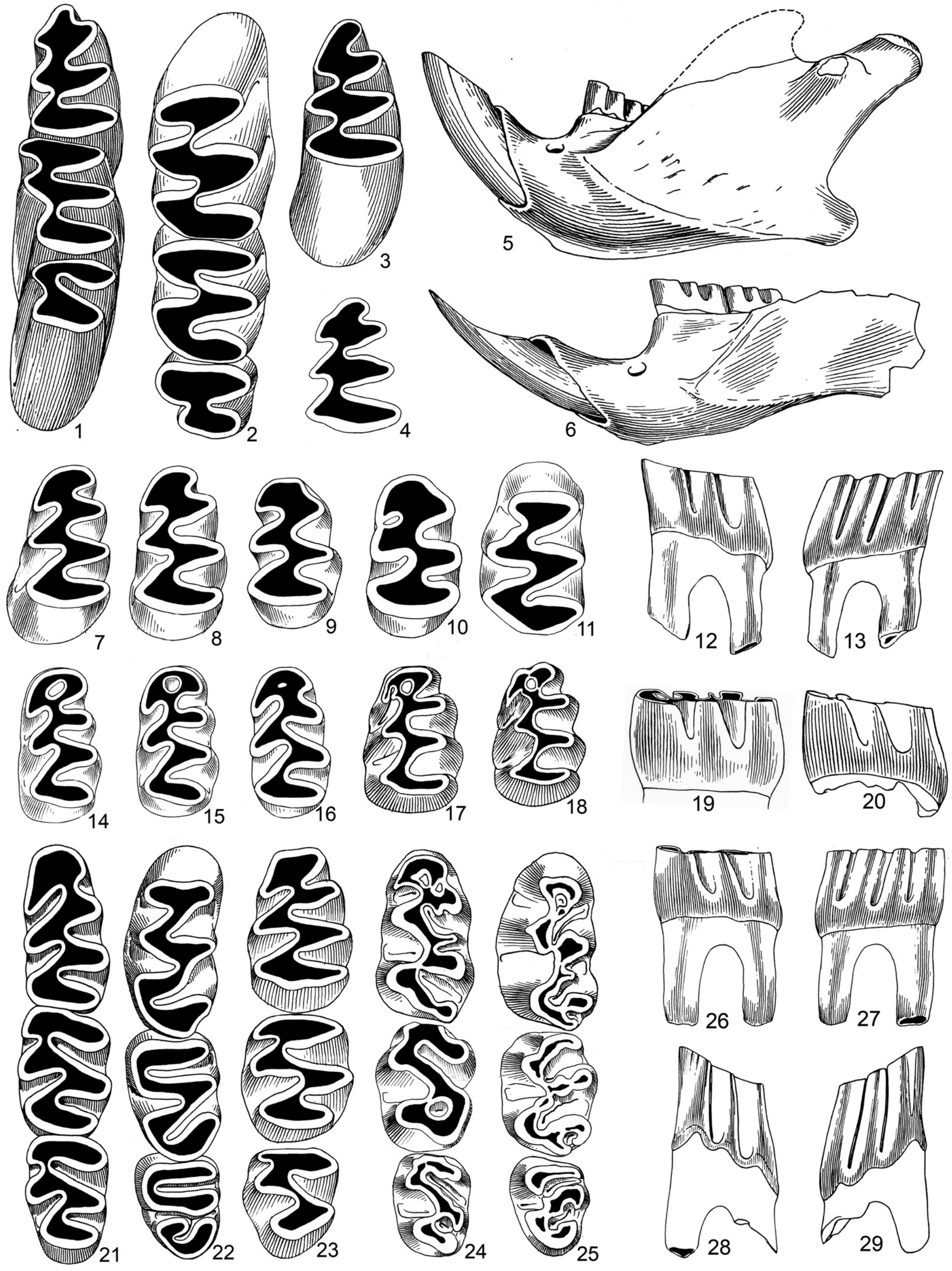

FIGURE 5. 1, 2, 4, 5: *Trilophomys depereti* Fejfar, 1961 from Ivanovce at Trenčín, late Ruscinian, MN 15, Western Slovakia; 3, 28, 29: *Trilophomys schaubi* Fejfar, 1961 from Ivanovce at Trenčín, late Ruscinian, MN 15, Western Slovakia; 7-13: *Bjornkurtenia canterranensis* (Michaux, 1976) from Gundersheim near Worms, late Ruscinian, MN 15, Western Germany; 6, 14-16, 21, 22, 26, 27: *Baranomys longidens* (Kowalski, 1960) from Gundersheim 2 near Worms, Western Germany (14-16, 26, 27) and Ostramos 7, N. Hungary, late Ruscinian, MN 15 (21, 22, 6); 17, 18, 20, 23: *Celadensia nicolae* Mein, Moissenet et Adrover, 1983 from Celadas 8, late Turolian (MN 13, eastern Spain; 19, 24, 25: *Anatolomys teilhardi* Schaub, 1934 from Ertemte 2, Inner Mongolia (Nei Mongol), late Turolian MN 13, China. - 1, 21, 23, 24: m1-3; 2, 22, 25: M1-3; 3, 4, 7-13, 14-20, 26-29: m1; 5, 6: lower right jaws, buccal views. 12, 19, 20, 26, 28: buccal views; 13, 27, 29: lingual views. All figured as left molars; not to scale.

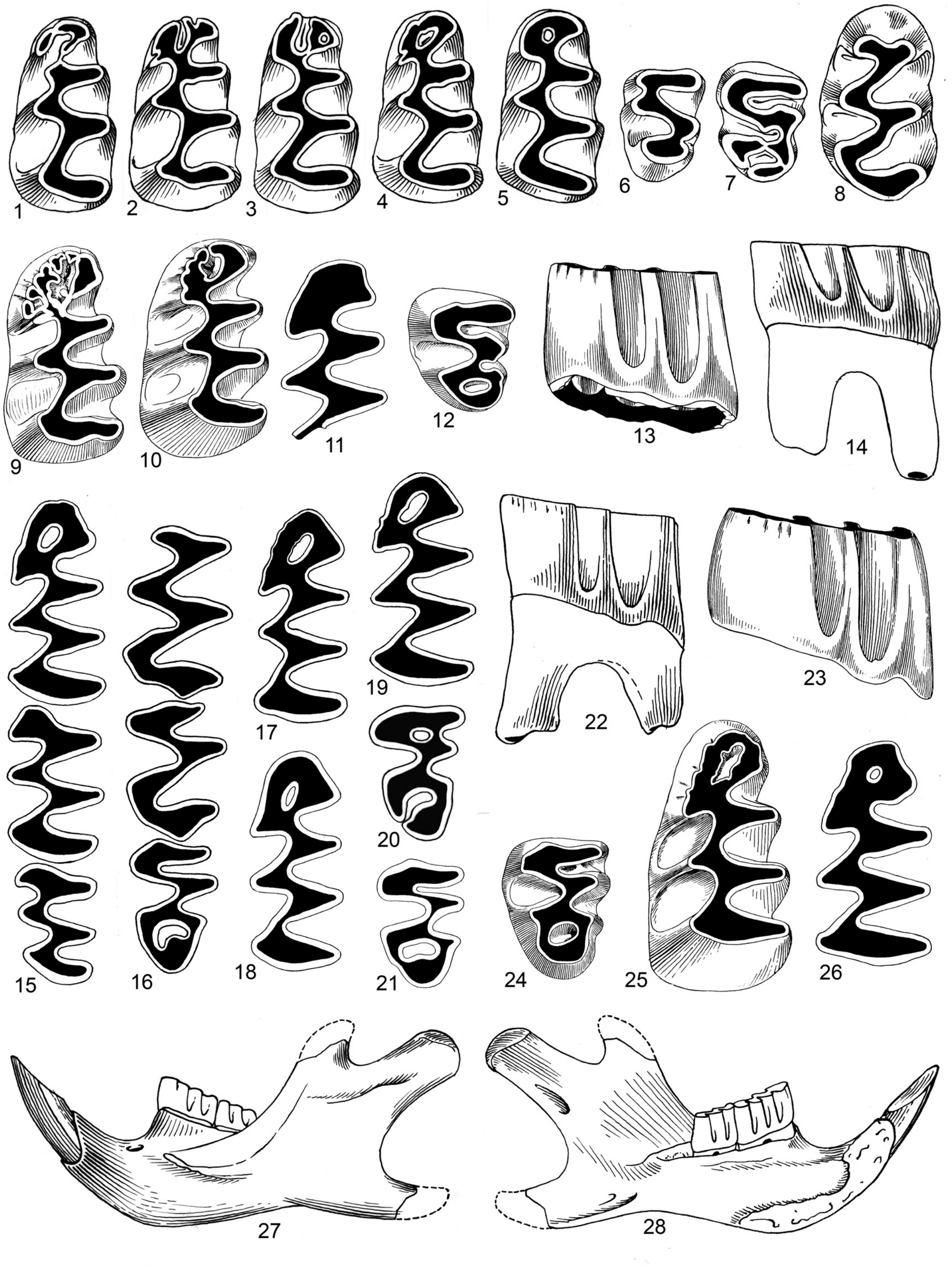

FIGURE 6. 1-7: *Microtodon atavus* Schlosser, 1924 from Ertemte 2, Inner Mongolia (Nei Mongol), late Turolian MN 13, China; 8-13: *Prosomys mimus* Shotwell, 1956 from Christmas Valley, Lake County, Eastern Oregon, late Hemphillian, USA; 14-18, 20, 24, 25: *Promimomys insuliferus* (Kowalski) from Podlesice, early Ruscinian, MN 14, Southern Poland (15-16, 22, 27, 28) and from Antipovka, the Central Russian Plain, South Ural, early Ruscinian, MN 14, Russia (17,18,20,21); 19, 23-26: *Promimomys cor* Kretzoi from Vendargues, early Ruscinian, MN 14a, southern France. - 1-5, 9-11, 13, 14, 17-18, 22, 23, 25, 26: m1; 6, 7, 12, 24: M3; 15: m1-3; 16: M1-3; 27, 28: lower left jaw with m1-2; 1-12, 15-21, 24-26: occlusal views; 13, 14, 22, 23, 27: buccal views, 28: lingual view. All figured as left molars; not to scale.

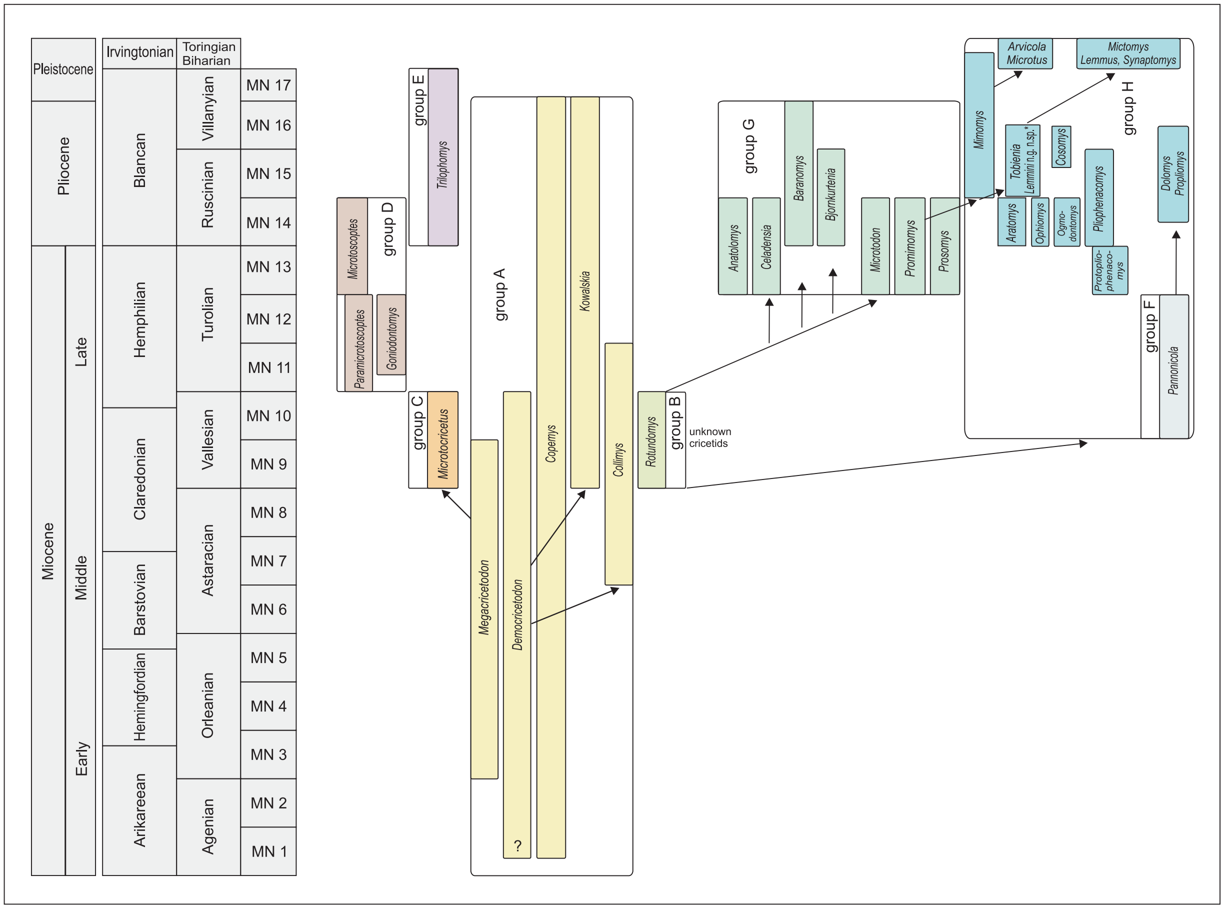

FIGURE 7. Stratigraphic distribution and possible phylogenetic relationships of taxa mentioned in the text. See text for tooth group definitions - according to Fejfar and Repenning (1998).

2003), as is *Kowalskia gansunica* from Songshan (Lindsay 1994; Qiu and Li 2003). Possibly slightly older records of *Kowalskia* are from Shala (Qiu and Wang 1999) that is middle Baodean (early NMU 10) in age, possibly early Turolian (MN 11). *Kowalskia neimengensis* and *Kowalskia similis* are known from the famous late Late Miocene (late Baodean, NMU 11) local fauna from Ertemte, correlated with the late Turolian (MN 13). In the Late Miocene to Early Pliocene section locality 93002; Lingtai, Gansu, range *Kowalskia* cf. *similis* from the middle Baodean (approximately Middle Turolian, MN 12) to the early Yushean (Early Ruscinian, MN 14), and *Kowalskia neimengensis* from the middle Baodean (Middle Turolian, MN 12) to later Yushean (approximately Late Ruscinian, MN 15) (Zhang and Zheng 2000; Zheng and Zhang 2001). The Early Pliocene (early Yushean, NMU 12) site of Bilike, coeval with the Early Ruscinian (MN 14), has produced *Kowalskia zhengi* and *Kowalskia* cf. *similis* (Qiu and Storch 2000). *Kowalskia neimengensis* from Harr Obo (Wu 1991; Qiu and Storch 2000) is similar in age (MN 14). *Kowalskia* sp. has been reported from the late Pliocene (late Yushean, MNU 13) deposits of the Laowogou section near Daodi in northeastern China (Zhang et al. 2003). This site was correlated with the MN 16 zone (Qiu and Li 2003) indicating that *Kowalskia* survived in China into the Early Villanyian, as in Europe. *Kowalskia* sp. has recently been reported from the Udunga site (level 2, 3) located in the Transbaikal area and considered Early Villanyian (MN 16a) in age (Erbajeva et al. 2003).

The earliest appearance of the cricetid *Copemys* in North America coincides with the beginning of the Hemingfordian or somewhat before (Lindsay, 2008), which roughly correlates to the early Orleanian (Prothero 2006) in Europe, and ranged into the early Pliocene. The lower jaw morphology and the tooth crown pattern of *Copemys* are very similar to that of of the Eurasian *Democricetodon*. Therefore, *Copemys* is considered to be very near to *Democricetodon* (Fahlbusch 1967), but it is not justified to make *Democricetodon* a junior synonym of *Copemys* (Freudenthal 2006).

According to Fejfar et al. (1996), *Copemys pagei* from the Middle Miocene Barstow Formation (California) is one of the earliest North American taxa and could have been derived from Eurasian cricetids (Democricetinae), as formerly suggested by Fahlbusch (1967). Slaughter and Ubelaker (1984) proposed an origin of Neotropical cricetine rodents and North American peromyscines from *Copemys*. In contrast, Jacobs and Lindsay (1984) considered *Copemys* to be an immigrant and suggested a non-copemyine ancestor for the Neotropical cricetine rodents: the Late Hemphillian *Bensonomys*, derived from a separate Miocene Old World lineage of *Megacricetodon* that would have dispersed to North America. More recently, Lindsay (2008) reports the range of Copemys as Late Arikareean – Late Blancan. Unlike Eurasian Miocene cricetids, *Copemys* never developed hypsodont molars.

Tooth group B: Brachyodont molars with lophodont dental pattern and planar occlusal surface

Rotundomys bressanus Mein, 1966
Figures 1, 2.8-11, 20

Rotundomys is known only from the Vallesian (late MN 9 - MN 10) of western Europe (Mein 1966; 1975; Kälin 1999; Sesé 2006). *Rotundomys bressanus* is the last member of a line: *R. sabadelliensis – R. hartenbergeri – R. montisrotundi*; the species *R. montisrotundi* and *R. bressanus* are equipped with brachyodont molars, but they clearly display further tendencies toward a lophodont tooth crown pattern and a planar occlusal surface without interlocking cusp (Pineda-Muñoz et al. 2010). The absence of both mesolophs and mesolophids is typical, as is the lack of a posterior transverse loph, formed by the “äußeren Quersporn” (sensu Fahlbusch 1964) and the entoconid. The anteroconid is broad and both protoconid and metaconid are longitudinally offset and medially connected with the cusps of the anteroconid. During evolution, the molars became relatively narrower. In *R. bressanus* both broad anteroconid and anterocone (anteroloph) include symmetrically a circular enamel islet that rapidly disappears with wear. Both species were recovered from paludal lignites at the sites of Montredon, district of Montoulieres, Hérault (*R. montisrotundi*, lower level of MN 10), and in Soblay, district of Ain, France (*R. bressanus*, upper level of MN 10) (Mein 1975).

Rotundomys is a derivative of *Cricetulodon* (Freudenthal 1967; Kälin 1999). The specific molar crown pattern of *Rotundomys bressanus* shows remarkable similarities to that of early arvicolids (*Microtodon*, *Promimomys*). This affinity could favor the idea that *Rotundomys bressanus* or a still unknown closely related species restricted to a relatively small region in Western Europe during the Vallesian could have given rise to this rodent group. The solution to this question requires further material and study.

Tooth group C: Mesodont molars with tendencies towards a prismatic dental pattern

Microtocricetus Fahlbusch and Mayr, 1975
Figures 1, 3.15-23

Only one species has been reported for this genus: *Microtocricetus molassicus* (Fahlbusch and Mayr 1975; Bachmayer and Wilson 1984; Wellcomme et al. 1991; Rögel et al. 1993; Kowalski 1993; Fejfar 1999; Hír and Kókay 2010). *Sarmatomys podolicus* (Topachevskij and Skorik 1988, 1992) is likely a junior synonym of *Microtocricetus molassicus*. The members of this taxa differ from other groups of microtoid cricetid rodents in having rooted mesodont molars (higher than in *Rotundomys bressanus*) with flat chewing surfaces and an aberrant occlusal pattern. Behind the anterior cusp of the m1, there are three buccal and four lingual anticlines as well as three buccal and four lingual synclines; the same number of synclines and anticlines is seen in the m2 (Fahlbusch and Mayr 1975; Fejfar 1999; Kretzoi and Fejfar 2005). The upper molars display three buccal and four lingual anticlines as well as three buccal and two lingual synclines (Fahlbusch and Mayr 1975; Fejfar 1999; Kretzoi and Fejfar 2005). The synclines lack cementum. Both narrow triangles (anticlines) and reentrants (synclines) are more or less transverse with an irregular alternation. Roots in molars of adult individuals are well developed. The thickness of the enamel walls increases distinctly with wear. The presence of the posterior transverse ridge (“äußerer Quersporn"; Äqs, fig. 1:17), which is an important feature of advanced species of *Democricetodon*, suggests a possible ancestry from these Miocene cricetids.

Microtocricetus molassicus is the oldest recorded cricetid rodent with mesodont prismatic molars. It apparently represents an isolated lineage of microtoid cricetids of the Vallesian (MN 9, MN 10) (Fahlbusch and Mayr 1975; Fejfar 1999). Its unique molar structure excludes affinities with other microtoid cricetids that developed similar prismatic molars, such as *Pannonicola* (= *Ischymomys*) *pontica* (MN 11) and *Microtoscoptes praeter-*

missus (MN13, MN 14). Most likely, *Microtocricetus* inhabited moist riparian or paludal environments where it fed on reed leaves, as did *Microtoscoptes* and *Goniodontomys*. *Microtocricetus molassicus* appears to have been distributed throughout southeastern, central and western Europe. It is as old as or older than the records of *Goniodontomys* and *Paramicrotoscoptes* from the Early Hemphillian in North America.

Microtocricetus can be considered an "early experiment" of microtoid cricetids to develop high-crowned prismatic molars. However, success was not forthcoming and *Microtocricetus* became extinct without descendants.

Tooth group D: Mesodont and hypsodont molars with prismatic dental pattern and opposing and slightly alternating triangles

Microtoscoptes Schaub, 1934
Figures 1, 3.1-9, 19, 20

Microtoscoptes is a medium-sized advanced cricetid rodent with rooted hypsodont molars. The occlusal surface is flat, and the reentrants lack cementum. The buccal and lingual reentrants and triangles of the prisms have sharp apices and are opposing, they typically form rhomboid dentine fields, except for M2 and M3 (cf. Figure 4). The thickness of the enamel walls is not differentiated in the prismatic folds of the occlusal surface. The apices of the opposing reentrants touch each other, and the dentine fields of adjacent lophs are not confluent even with well worn molars. Although the opposition of the reentrants and triangles of the teeth is close to being exact in all lower teeth and in the first upper tooth, it is not true of the second and third upper teeth. This feature distinguishes *Microtoscoptes* from the very similar *Goniodontomys*, in which the reentrants and triangles of all teeth are directly opposite.

The m1 has 3 buccal and 4 lingual salient angles and 3 buccal and 4 lingual reentrants. The anteroconid complex ("Vorderlobus"), as in arvicolids, has one lingual and one labial reentrant; posterior to these are the most anterior two salient angles; behind the anteroconid complex there are two lingual and one labial triangles exactly analogous to the three basic alternating triangles of the arvicolid m1, the most posterior labial triangle never has an opposing triangle but is confluent with the "posterior loop" of Hinton (1926, p. 106). Triangles T2 and T3 make a rhombus, a typical trait of the Microtoscoptinae not seen in true arvicolids and other branches of arvicolid-like cricetids rodents. The m3 of *Microtoscoptes* is bilophed with one pair of opposing reentrants and a posterior ridge that is the remnant of the third (posterior) loph in contrast to the two other genera of Microtoscoptinae and to the older species of *Paramicrotoscoptes* from North America. M2 and M3 have 3 buccal and 2 lingual dentine fields ("triangles") with 2 buccal and 1 lingual reentrants. The M3 and m3 in *Microtoscoptes* are distinctly reduced.

The Eurasians species *Microtoscoptes praetermissus* was first described from the sites of Ertemte and Olan Chorea, Inner Mongolia (Nei Mongol), China (Schaub 1934, 1950; Jacobs et al. 1985; Fahlbusch 1987). The Ertemte local fauna is considered Late Miocene (late Baodean, NMU 11) in age correlated with the European mammalian zone MN 13 (Qiu and Qiu 1995; Flynn et al. 1997; Qiu and Wang 1999; Qiu et al. 1999; Qiu et al. 2003; Qiu and Li 2003). Additional remains come from Harr Obo, also Inner Mongolia (Nei Mongol, China) (Fahlbusch 1987), the age of which was previously also equated with that of Ertemte (Late Turolian, MN 13). However, the occurrence of *Rhagapodemus* and *Hypolagus* at the site of Harr Obo suggests that this locality is slightly younger than Ertemte, early Yushean (Early Ruscinian, MN 14) (Qiu and Qiu 1995; Qiu and Li 2003; Qiu et al. 2003). *Microtoscoptes praetermissus* is also known from fluvio-limnic deposits (Sasin Formation, Odonin Member) exposed at Olchon Island, Lake Baikal, Irkutsk (Russia) (Mats et al. 1982). These *Microtoscoptes praetermissus*-bearing strata are assigned to the late Turolian (MN 13).

There are other imperfectly known Eurasian species of *Microtoscoptes*, not yet fully described or sufficiently figured in literature, such as as "*Microtoscoptes tjuvanensis"* (Zazhigin in Gromov and Polyakov 1977) and "*Microtoscoptes sibiricus"* (Zazhigin and Zykin 1984). The latter is larger and apparently more advanced than the previous species. Both species seem to be Late Turolian (MN 13) in age, like *Microtoscoptes praetermissus*. At the present stage of knowlege it cannot be excluded that "*Microtoscoptes tjuvanensis"* and "*Microtoscoptes sibiricus"* are possibly junior synonyms of *Microtoscoptes praetermissus*. Note, however, that the known measurements of "*Microtoscoptes tjuvanensis"* (Zazhigin in Gromov and Polyakov 1977, p. 101) might indicate another Eurasian *Microtoscoptes* species, that is distinctly larger and slightly younger than *Microtoscoptes praetermissus* (Fahlbusch 1987). The distribution of *Microtoscoptes* is confined to Eurasia.

Paramicrotoscoptes Martin, 1975
Figures 1, 4.11-14, 17, 18

The North American *Paramicrotoscoptes hibbardi* is a medium-sized cricetid species with rooted, hypsodont molars and flat occlusal surface. There is no cementum in the reentrants. Thickness of the enamel walls is not differentiated. Buccal and lingual reentrants have rounded apices (more so in worn molars) that are not exactly opposite each other, showing slight alternation so that the rhomboid dentine areas are less symmetrical, and the apices of the opposing reentrants do not touch each other in some worn teeth as they do in *Goniodontomys*. Therefore, the dentine fields may be slightly confluent with those anterior or posterior to them. An islet may be present in the anteroconid of the m1.

Paramicrotoscoptes hibbardi is distinguished from Eurasian species of *Microtoscoptes* and from the North American *Goniodontomys disjunctus* (see below) by having the posterior loop of M3 reduced (from the condition in *Goniodontomys*) to an "r", but it is less reduced than in *Microtoscoptes praetermissus* and other Eurasian species in which it is reduced to a simple oblique oval. In addition, the posterior loop of m3 is reduced to a narrow crest in *Microtoscoptes praetermissus*.

The pattern of the enamel on the occlusal surface of the M3 of *Paramicrotoscoptes hibbardi* closely matches that of the very late Miocene prometheomyine North American genus *Protopliophenacomys* (= *Propliophenacomys*, see Martin 2003a), which is about the age of *Microtoscoptes praetermissus;* however the triangles in *Propliophenacomys* have become completely alternating.

The structure of the mandible of *Paramicrotoscoptes*, lacking an arvicoline groove, is also primitive and shows the anterior edge of the ascending ramus leading straight to the upper masseteric crest and to its anterior union with the lower masseteric crest, in the pattern that is typical of low-crowned cricetid rodents; apparently propalinal mastication developed before the musculature that aided it did. The temporal muscles with well=developed deep temporal fossa appear to be extremely typical of arvicolines. By comparison with representatives of the subfamily Microtodontinae (*Microtodon*, *Prosomys*, *Promimomys*), *Paramicrotoscoptes* has twice the dental specialization in hypsodonty and enamel complication, while having half of the specializations in masticator musculature (Repenning 1968).

The genus *Paramicrotoscoptes* was introduced by Martin (1975). Repenning (1987, in litt.) considered *Paramicrotoscoptes* a junior synonym of *Microtoscoptes* and listed *Paramicrotoscoptes hibbardi* as a species of *Microtoscoptes*. The palaeogeographic and stratigraphic range of *Paramicrotoscoptes hibbardi* is confined to North America and the Early Hemphillian (Shotwell 1970; Hibbard 1970; Repenning 1987), beginning at about 9 Ma (Woodburne and Swisher 1995). Records of *Paramicrotoscoptes hibbardi* are known from Idaho, Oregon, Nevada and Nebraska (Repenning 1987; Bell 2000).

Goniodontomys Wilson, 1937
Figures 4.10, 15, 16

Goniodontomys is known only from a single North American species: *Goniodontomys disjunctus* (Wilson 1937; Schaub 1940; Hibbard 1959, 1970; Repenning 1987). The hypsodont molars are rooted, with flat occlusal surface, but without cementum. The enamel walls of the prismatic triangles are not differentiated. In *Goniodontomys*, the anteroconid complex has two very strong and directly opposing wings and a strongly doubled anteroconid, the lingual one more prominent and extending farther anteriorly. Buccal and lingual triangles of the prisms have sharp apices and are exactly opposing. Buccal and lingual reentrants are directly opposing with apices solidly appressed and usually flattened against each other along the midline of the tooth. They are never slightly offset as in *Microtoscoptes*. The rhomboid dentine areas are well expressed, and the fields of different lophs are not confluent (with the same exception at the posterior loop of m1 as in *Microtoscoptes*).

As discussed above, the conspicuous differences that separate *Goniodontomys disjunctus* from the species of *Microtoscoptes* and *Paramicrotoscoptes* are: (1) in *Goniodontomys* the structure of the M2 shows three symmetrical rhomboid dentine fields that are closed by the contact between the opposing reentrants, whereas in *Microtoscoptes* the lingual half of the middle rhomboid loph has been lost; (2) the structure of M3 of *Goniodontomys* is most complex, somewhat reduced in *Paramicrotoscoptes hibbardi,* and is further reduced in Eurasian *Microtoscoptes praetermissus* where the posterior loop is practically lost (see Shotwell 1970, text-fig. 32 J to O; Martin 1975, Figure 3D and F, and Fahlbusch 1987, text-fig 1 and 28-30). (3.) The m3 is not reduced in *Goniodontomys disjunctus* or *Paramicrotoscoptes hibbardi* but was conspicuously reduced in the younger *Microtoscoptes praetermissus* from Asia.

Goniodontomys occurred in the Hemphillian of North America, probably aequivalent to Early Turolian (MN 11) or possibly closer to MN12 (according to the data given by Agusti et al. 2001).

Goniodontomys disjunctus is known from localities in Wyoming and Oregon (Repenning 1987; Bell 2000). Both *Goniodontomys* and *Paramicrotoscoptes* are likely North American natives (Repenning 1987; Repenning et al. 1990). As with *Paramicrotoscoptes*, the distribution of Goniodontomys is restricted to North America. Martin (2008) excludes the north American Microtoscoptes and Goniodontomys from the Arvicoilidae (see also Lindsay 2008).

Tooth group E: Mesodont and hypsodont molars with prismatic dental pattern and opposing triangles; M1, m1, and m2 trilophodont

Trilophomys Depéret, 1892
Figures 1, 5.1-5, 28, 29

Trilophomys is a medium-sized advanced cricetid rodent with simply formed hypsodont prismatic molars. The M1, m1, and m2 are trilophodont with two lingual and two buccal reentrants; the M3 is reduced, bilophodont, with one lingual and one buccal reentrant. The occlusal pattern reveals that the reentrants of the lower cheek teeth are basically opposing, those of the upper molars basically alternating, except for the M2, which is equipped with a pair of opposing triangles that are prominently confluent. All reentrants lack cementum. The relatively thick enamel walls are distinctly differentiated. In lower molars the posterior walls of the triangles or lophs are thicker than the anterior ones, and the reverse true for the upper cheek teeth. The tooth crown base (linea sinuosa) is moderately sinuous. It curves slightly up on the salient angles (triangles) and slopes down below the reentrants. There is a trend in *Trilophomys* to increase the height of the tooth crowns.

The very massive and short lower jaw of *Trilophomys* shows a strong lower masseteric crest that terminates far anteriorly beneath the anterior end of the first lower molar; it is, however, positioned very high on the buccal side of the ramus. The massiveness of the jaw results largely from the stout lower incisor, which has a short radius of curvature so that at first glance the jaw appears more sciurid than cricetid. These features, combined with stout and upward-directed incisors, suggest arboreal or fossorial habits of *Trilophomys*.

As with *Baranomys*, the temporal and palaeogeographical range of *Trilophomys* was confined to the Early Ruscinian (MN 14) to Early Villanyian (MN 16) of Europe (Mein 2003) and possibly MN17. *Trilophomys pyrenaicus* is a large species with relatively broad molars (Schaub 1940; Adrover 1986). A distinct additional lingual reentrant on the anteroconid of the m1 persists during wear. In occlusal view the reentrants and triangles are opposing, not alternating, and the dentine fields were less confluent than in other species of *Trilophomys*. *Trilophomys pyrenaicus* was dispersed in Western Europe during the Ruscinian (MN 14, MN 15) (Schaub 1940; Adrover 1986; Kowalski 1990).

Trilophomys schaubi (Fejfar 1964; Adrover 1986) is smaller than *Trilophomys pyrenaicus*. In addition, it possesses relatively narrow molars. The narrow anteroconid of the m1 has a deep additional lingual reentrant that persists during wear for a long time. The buccal reentrants are shallower than the lingual ones. In occlusal view, the reentrants are slightly alternating, not directly opposing as in *Trilophomys pyrenaicus*, and the dentine fields are less confluent than those of the adjacent lophs in *Trilophomys depereti*. *Trilophomys schaubi* is known from numerous sites in Western and Central Europe. Stratigraphic range: Ruscinian (MN 14, MN 15).

Trilophomys depereti (Fejfar 1961, 1964; Adrover 1986; Popov 2004) also is smaller than *Trilophomys pyrenaicus*. The molars are relatively narrow, the lower cheek teeth less hypsodont but strongly trilophodont. The m1 (resembling that of *Epimeriones*) displays a narrow anteroconid, with shallow additional lingual reentrant seen only in juvenile individuals. In occlusal view the reentrants are weakly alternating, particularly in the upper cheek teeth. In contrast to other species of *Trilophomys*, the dentine fields are distinctly confluent between the lophs. In lower molars, the buccal reentrants are shallower than the lingual ones. Like the two *Trilophomys* species described above, *Trilophomys depereti* was distributed in Western and Central Europe during the Ruscinian (MN 14, MN 15).

Trilophomys vandeweerdi (Brandy 1979; Adrover 1986) is the most advanced species of *Trilophomys* known so far. It differs from other *Trilophomys* species in having unmistakably greater hypsodonty. Moreover, the m1 possesses especially well-developed dentine tracts, which, however, do not interrupt the enamel walls of the chewing surface before the cheek tooth is about half worn. *Trilophomys vandeweerdi* ranges in Spain from the Late Ruscinian (MN 15) to the Early Villanyian (MN 16) (Sesé 2006).

The youngest records of *Trilophomys* are in Rebielice Krolewskie (MN 16b), Poland (Nadachowski 1989) and in Osztramos 3 (MN 17) (Jánossy 1970).

Tooth group F: Mesodont molars with prismatic dental pattern and opposing or alternating triangles

Pannonicola Kretzoi, 1965 (= *Ischymomys* Zazhigin 1982)
Figures 1, 3.1-14

Pannonicola brevidens is based on two rooted molars, a heavily worn left m2 and a left M3, also deeply worn (Kretzoi 1965). Both molars, possibly representing a single individual, were recovered from a deep core near Jászladány, North Hungary (Kretzoi 1965). The specimens were tentatively assigned to Middle Turolian (MN 12). Although heavily worn, the short and broad molars of *Pannonicola brevidens* display an arvicolid-like occlusal pattern. The dentine fields are broadly confluent owing to advanced abrasion.

More recently, additional records of *Pannonicola* have been reported from the Hungarian sites Nyárad and Sümegprága (Kordos 1994), which have not yet been fully described. The available data suggest a Late Vallesian (MN 10) to Early Turolian (MN 11) age for these findings (Kordos 1994). Kordos (1994) argues that, *Ischymomys* Zazhigin 1982 is a junior synonym of *Pannonicola*, and the present authors agree.

Outside Central Europe, two additional species of *Pannonicola* (= *Ischymomys*) have been reported from Turolian deposits in Eastern Europe and Western Asia. The younger species *Pannonicola (= Ischymomys) quadriradicatus* was recovered from Middle Turolian (MN 12) Ishim strata exposed on the right bank of the River Ishim, Petropavlovsk, Kazakhstan in Western Asia (Zazhigin 1982, Zazhigin in Gromov and Polyakov 1977); the older one, *Pannonicola* (= *Ischymomys*) *ponticus*, known from Frunzovka 2 near Odessa, Ukraine (Topachevskij et al. 1978) is referred to the EarlyTurolian (MN 11).

Pannonicola (= *Ischymomys*) *ponticus* is a medium-sized cricetid with subhypsodont, prismatic, cementless, and rooted molars; similar to the preceding species. Enamel walls of molars are relatively thin and not differentiated; the triangles are slightly alternating with tendency to form a dentine rhomboid across the occlusal surface; the apices of the reentrants touch the opposing apices near the center of the tooth as in the Microtoscoptini. Enamel islets are present in the central anteroconid of m1 and in the posterior lobe of M2 and M3, persisting with deeper wear. One specimen illustrated by Topachevski et al. (1978, text-fig. 1:3) clearly shows that the islet in the anteroconid complex derives from the most anterior lingual reentrant of the tooth. If consistent, this differs with the derivation from the most anterior buccal reentrant in the arvicolines and with derivation from a reentrant at the anterior end of the anteroconid complex, called the “cricetine islet” by Repenning (1968, text-fig. 10) and apparently is characteristic of the prometheomyines and possibly the ondatrines (Hinton 1926, text-figs 58 and 62). The mesial/buccal wall of the anteroconid in M1 is variably undulated but less so than in the younger and more advanced *Pannonicola* (= *Ischymomys*) *quadriradicatus*.

Pannonicola (= *Ischymomys*) *quadriradicatus* is a large advanced cricetid with slightly hypsodont, prismatic, cementless, and rooted molars. The M2 and M3 have four roots (hence the specific name). The enamel walls of molars are relatively thin and not differentiated; the reentrants and triangles slightly alternating with tendency to form rhombic, lophate dentine fields across the occlusal surface. The apices of the reentrants touch medially in many individuals, similar to the Microtoscoptini. Prominent enamel islets are present in the anteroconid of m1 in some individuals as well as in the posterior loop of the m3 and M3 (M2?), persisting during considerable wear. The mesial wall of the anteroconid in m1 is variably undulated.

The origin of *Pannonicola* is unknown. A close affinity with the genus *Microtocricetus* is excluded because of the non-homologous molar structure. However, all Turolian/Hemphillian microtoid cricetid genera (*Goniodontomys*, *Microtoscoptes*, *Microtocricetus*, and *Pannonicola*) invariably occur in paludal/fluviatile sediments, which suggest a wet habitat. In many respects (e.g., the tendency to have rhomboid dentine fields showing little or no alternation of the triangles, and contact of opposing reentrant apices near the midline of the tooth) the younger *Pannonicola* (= *Ischymomys*) *quadriradicatus* and the older *Pannonicola* (= *Ischymomys*) *ponticus* both resemble the Microtoscoptini. The species of *Pannonicola* (= *Ischymomys*) could represent a lineage of “Old World” microtoscoptines during the Turolian, more advanced in the offset of its dental triangles but less advanced in the development of hypsodonty.

Owing to the advanced molar structure already developed during the Late Vallesian (MN 10) or Early Turolian (MN11) (Kordos 1994), *Pannonicola* cannot be derived from *Microtodon*, a younger taxon that displays a more primitive molar pattern, although it appeared distinctly later in the fossil record of Asia for the first time (Late Turolian, MN 13). Most probably, *Pannonicola* gave rise to *Dolomys* and *Propliomys* represented first in the Late Ruscinian record (MN 15) of Europe as well as possibly to *Dicrostonyx*, which made its first appearance during the Biharian.

Tooth group G: Mesodont molars with prismatic dental pattern and alternating triangles

Anatolomys Schaub, 1934
Figure 1, 2.12-14

Small microtoid cricetid with rooted, cementless, mesodont molars; occlusal outline is longer than wide. Both unworn M1 and m1 display a broad and inflated anteroconid with shallow islet(s) that soon disappear with wear, and with variably short mesoloph/id. The axes of the inner (in upper molars) and the outer (in lower molars) reentrants are transverse, as in *Microtodon* or *Promimomys*. The axes of the outer (in upper molars) and inner (in lower molars) reentrants are oblique. The relatively thick enamel walls are not differentiated. There are mainly three roots in upper and two roots in lower molars.

The general pattern of the mandible and molars of *Anatolomys* suggests similarities with the Ruscinian genus *Baranomys* described by Kormos (1933). However, the genera probably are unrelated. *Anatolomys* likely was adapted for a digging lifestyle.

The only known species *Anatolomys teilhardi w*as originally described from the late Late Miocene site of Ertemte, Inner Mongolia (Nei Mongol), China (Schaub 1934; Jacobs et al. 1985; Fahlbusch and Moser 2004), and referred to the late Baodean (NMU 11) (Qiu et al. 2003) that is considered approximately equivalent in age to the European Late Turolian (MN 13) (Qiu and Li 2003). The localities Harr Obo and Bilike, also Inner Mongolia (Nei Mongol), China, that have produced *Anatolomys* cf. *teilhardi* (Qiu and Storch 2000; Fahlbusch and Moser 2004) are younger than Ertemte and can be assigned to the early Yushean (NMU 12), regarded equivalent to the Early Ruscinian (MN 14) in Europe (Qiu and Li 2003; Qiu et al. 2003).

Celadensia Mein, Moissenet and Adrover, 1983
Figures 1, 5.17-18, 20, 23

In occlusal view the mesodont, cementless molars have a barrel-like outline, because the cheek teeth become conspicuously wider toward the crown base (Aguilar et al. 1982; Mein et al. 1983). The small anteroconid of the m1 retains a circular islet during wear. Unlike other microtoid cricetids (e.g., *Microtoscoptes*, *Trilophomys*, and *Baranomys*), the M1 retains two buccal reentrants. Only one species has been recognized so far (Mein et al. 1983), *Celadensia nicolae*. Records were recovered from a few Late Miocene and Early Pliocene sites of the Iberian Peninsula and in France (e.g., Aguilar et al. 1982; Mein et al. 1983). *Celadensia nicolae* ranges from the Late Turolian (MN 13) to Early Ruscinian (MN 14) (Fejfar 1999; Mein 1999, 2003; Sesé 2006).

Baranomys Kormos, 1933
Figures 1, 5.6, 14-16, 21, 22, 26, 27

The molars of *Baranomys* are rooted, mesodont, and initially prismatic. The helmet-like anteroconid complex of the m1 is very short, and an enamel islet is present. The molars of *Baranomys* are, as in *Microtodon*, very small (length of the m1 about 1.5 mm), and the reentrants (synclines) are distinctly asymmetrical. There is no cementum in the reentrants. The dentine fields are confluent. The number of reentrants in *Baranomys* corresponds to that in *Microtodon* and *Promimomys* (or *Prosomys* of some authors). There is an important feature in the dentition of *Baranomys* that is worth mentioning: The anterior edges of the lower molars and the posterior edges of the upper molars are curved backward in *Baranomys*, a distinct contrast to the condition in arvicolids and arvicolid-like rodents where these edges are always straight.

The chewing surface of the cheek teeth displays some similarities to those of *Microtodon* (e.g., Kowalski 1960; Kretzoi 1962; Sulimski 1964; Repenning 1968; Fahlbusch and Moser 2004), the taxonomic, and status of *Baranomys* has been discussed for a long time. Some authors (e.g., Kretzoi 1955a, Fejfar and Storch 1990) accept *Baranomys* and *Microtodon* as two distinct genera, whereas others (e.g., Fahlbusch and Moser 2004) regard the separation as unjustified and consider *Baranomys* and *Microtodon* as identical taxa.

All fossil remains of *Baranomys* are from Europe. The three species of *Baranomys* range from Early Ruscinian (MN 14) to Early Villanyian (MN 16), like *Trilophomys*. The oldest species, *Baranomys kowalskii*, was first reported from the Early Ruscinian (MN 14a) locality Podlesice at Kroczyce, south Poland (Kretzoi 1962). *Baranomys loczyi* (Kowalski 1956; Kretzoi 1962) ranges from the late Ruscinian (MN 15) to the Early Villanyian (MN 16). *Baranomys longidens* is known from a series of localities in Europe (Kowalski 1960; Sulimski 1964; Repenning 1968; Fejfar and

Storch 1990; Fejfar et al. 2006) confined to the late Ruscinian (MN 15).

Bjornkurtenia Kowalski, 1992
Figures 1, 5.7-13

The rooted and cementless molars of *Bjornkurtenia* are small, brachyodont, and massive. The enamel band is very thick and undifferentiated. The thickness of the enamel walls increases progressively during wear. Dentine tracts are not developed. The short anteroconid complex of the m1 displays a simple design. The reentrants alternate and the dentine fields are typically broadly confluent. On the chewing surface of the m1 there are no islets in the AC, the lingual reentrants of which disappear with wear. A striking feature is the extremely thick enamel band that reaches with *Bjornkurtenia* its maximum thickness for the Baranomyinae. The molars of *Bjornkurtenia* recovered from sites in Central Europe are smaller then those from the type locality La Jasse at Terrats in France (Michaux 1976). The single species described so far, *Bjornkurtenia canterranensis* (Michaux 1976; Kowalski 1992; Popov 2004), appeared in the Early Ruscinian (MN 14) and became extinct during the Late Ruscinan (MN 15). Most likely, the lifestyle of *Bjornkurtenia canterranensis* was fossorial.

Microtodon Miller, 1927
Figures 1, 6.1-7

The molar crown pattern of *Microtodon* is rather similar to that of *Promimomys*. The molars are mesodont and low prismatic-lophodont. They have alternating reentrants and triangles. The apices of the triangles are sharp and V-shaped in moderately worn molars, and U-shaped in heavily worn cheek teeth. The enamel band is of more or less equal width, but distinctly thicker in heavily worn molars than in unworn or moderately worn cheek teeth. The dentine fields are confluent, especially with increasing wear. The relatively deep and long existing enamel islet of the anteroconid complex is a true “cricetine islet”, derived from the medial groove of the anteroconid which was originally bilobed (Fahlbusch and Moser 2004).

The mandible shows some arvicoline features. A distinct but nascent “arvicoline groove” (Repenning 1968) is present in some members, but rudimentary (or unknown) in others, there is a prominent and anteriorly placed lower masseteric crest, and a deep internal temporal fossa separates the row of lower molars from the ascending ramus. In all respects the masticatory musculature obviously must have been proto-arvicoline (Repenning 1968).

Microtodon is known from the Late Baodean (MNU 11, Late Turolian, MN 13) Ertemte (Nei Mongol, China) and from early Yushean (MNU 12, Early Ruscinian, MN 14) Harr Obo and Bilke (described as *Microtodon* cf. *atavus*), also Inner Mongolia, China (Schlosser 1924; Schaub 1934; Jacobs et al. 1985; Qiu and Storch 2000; Fahlbusch and Moser 2004). Other records of *Microtodon* that are slightly larger than those from Ertemte have been recovered at the localities of Kirgiz Nur 2 and Pavlodar in western Asia also correlated with the European Late Turolian (MN 13) (Fejfar et al. 1997).

Recently, *Microtodon* was recorded at Komanos 1 in Greece (MN 13-14) (Hordijk and de Bruijn 2009).

An important fauna including *Microtodon* sp. has been collected more recently from Gaotege, central Nei Mongol, China (Li et al. 2003). The Gaotege mammalian assemblage is thought to be stratigraphically younger than that from Bilike. It was assigned to the Early Pliocene (early Yushean) and tentatively correlated with the Early (MN 14) or early Late Ruscinian (early MN 15) of Europe (Li et al. 2003). If correctly assessed, this Chinese record suggests that *Microtodon* passed the Miocene/Pliocene (Turolian/Ruscinian) boundary in East Asia.

Baranarviomys Nesin, 1996

Baranarviomys admirabilis was recovered from a sequence of fluvio-limnic deposits exposed at the site Vinogradovka 1, Ukraine (Nesin 1996a). It is Late Turolian (MN 13) in age. The lower jaw and the molars of *Baranarviomys admirabilis* display a primitive arvicolid-like condition. The cheek teeth are mesodont and low prismatic-lophodont. In the m1, the reentrants are alternating, U-shaped in faintly worn molars and sharply V-shaped in heavily worn molars. The broad dentine fields are confluent. In the overall morphology of the molars, *Baranarviomys admirabilis* is rather similar to *Microtodon atavus* known from the Late Turolian (MN 13) of Central Asia. Possibly, *Baranarviomys admirabilis* is a junior synonym *Microtodon atavus*.

Promimomys Kretzoi, 1955
Figures 1, 6.14-18, 19, 20, 23-28

This genus is a member of the *Microtodon*-*Promimomys*-*Mimomys*-*Arvicola* lineage and has a far-reaching importance for understanding the evolution of arvicolids. *Promimomys* entered the fossil record for the first time in Eastern Europe

(Mugureny, Vinogradovka: *Promimomys* sp. 1 and 2) during the late Turolian (MN 13) (Fejfar et al. 1997). In contrast to its dental similarity to *Baranomys (*Figures 1, 5, 7), the mandible of *Promimomys* shows several characteristic arvicoline features. The arvicoline groove is well developed and the lower masseteric crest is prominent, especially anteriorly where it and the higher arvicoline groove meet and run forward to the anterior termination of the insertion of the masseter muscle. The internal temporal fossa (separating the lower molars from the ascending ramus) is deep and broad, and the entire mandiblar ramus is deeper and more robust, like an arvicoline, while that of *Baranomys* is more slender with a procumbent incisor as in many low-crowned cricetids. The lower jaw has a short diastema and a lower masseteric crest relative to the alveolar margin. The arvicoline groove and lower masseteric crest merge at a low angle rather far behind the anterior termination of the masseteric insertions, a conspicuous character of most arvicolines. The symphyseal insertion for the digastric muscle is moderately strong. In all respects the masticatory musculature was obviously arvicoline (Repenning 1968).

The massive lower incisor passes below the posterior root of m2 and continues on the buccal side of m3. The basal part of the lower incisor ascends far above the level of the occlusal surfaces of the molars and forms a distinct elevation on the lateral side of *processus articularis*. The anteroconid has a deep, persistent enamel islet. In worn molars the occlusal surface is much broader than in juvenile teeth.

The first lower molar of *Promimomys insuliferus*, the index fossil of the early Early Ruscinian (MN 14a), is characterised by a short anteroconid complex that is equipped with an oval enamel islet. The M3 also displays an enamel islet. In juvenile indivduals, the anteroconid complex of the m1 has a typical mesial opening and a moderately undulated, arched anterior margin; a lingual indentation is not developed. The enamel walls are rather thick, the enamel band undifferentiated, and the base of the tooth crown, the so-called linea sinuosa, is almost straight. The mesodont, rooted, and cementless molars correspond in size and height of the tooth crown well with those of *Promimomys mimus* (or *Prosomys mimus* of other authors*)*. However, the lingual reentrants are narrower and more sharply cornered. In worn molars the occlusal surface is much broader than in unworn juvenile teeth. The base of the enamel crown is nearly straight.

Promimomys insuliferus was originally described from Podlesice, Poland, and other important eastern Europe sites are Novaya Andriashevka, Antipovka, and Chugunovka (Fejfar et al. 1997). The site Novaya Stanica in western Siberia has yielded *Promimomys* sp. (Zazhigin and Zykin 1984), a form more primitive than *Promimomys insuliferus* from Europe.

The genus *Promimomys* is based on an incomplete left lower jaw with a heavily worn m1, which was recovered at the MN 14b site of Csarnóta 2 (Hungary) and later described as *Promimomys cor* by Kretzoi (1955b). More recently, *Promimomys cor* was reported from Early Pliocene lignitic mudstone deposits of the Haltipasa Formation in Anatolia, Turkey (Kaya et al. 2004) and at Komanos 1 and Vorio in Greece (Hordijk and de Bruijn 2009)

. *Promimomys cor*, the index fossil of the late Early Ruscinian (MN 14b), has mesodont prismatic, cementless, and rootless molars. The enamel band is relatively thin, but not differentiated; it becomes slightly thicker during wear. The reentrants of m1 are distinctly alternating, U-shaped in unworn molars and sharply V-shaped in worn molars. The dentine fields are confluent but usually prominently constricted. There is a high and broad anteroconid in the m1 with oval shaped islet becoming circular and disappearing during wear. The linea sinuosa is almost straight.

Promimomys asiaticus, described from early Yushean (early Pliocene) cave deposits of Dajushan Hill (Hainan, Anhui Province, China) is said to be more primitive than *Promimomys cor* from western Eurasia (Jin and Zhang 2005).

The stratigraphic range of *Promimomys* in Eurasia is confined to the Late Turolian (MN 13) and Early Ruscinian (MN 14) (Fejfar et al. 1997; Sesé 2006). *Promimomys* gave rise to *Mimomys*. The interval during which *Mimomys* appeared for the first time is poorly understood and needs further study. According to the fossil arvicolid record in Western and Southern Europe *Mimomys vandermeuleni* which was reported from the early Late Ruscinian (MN 15a) site Villalba Alta Rio (VAR 2a), Spain, is among the most primitive *Mimomys* species known so far (Fejfar et al. 1990). An even more primitve species was described from the late Early Ruscinian (MN 14b) in Western Asia as *Mimomys antiquus* (Zazhigin et Zykin, 1984).

Prosomys Shotwell, 1956
Figures 1, 6.8-13

The North American records of *Promimomys* were described as *Prosomys* by Shotwell (1956).

According to Repenning (1968, 1987) *Prosomys* Shotwell, 1956 is a junior synonym of *Promimomys* Kretzoi, 1955. Records of *Promimomys* (or *Prosomys*) approximately equivalent in age to the Late Turolian (MN 13) and Early Ruscinian (MN 14) in Eurasia are reported from the Late Hemphillian in North America (Repenning 1987, 2003; Bell 2000; Martin 2003a). According to Tedford et al. (1987, 2004), the immigration of *Promimomys* as well of *Agriotherium*, *Felis*, *Megantereon*, *Ochotona, Plesiogulo* and Odocoileini cervids defines the beginning of the Late Hemphillian. Records of *Promimomys* (or *Prosomys*) in North America are known from two sites in Oregon (McKay, Christmas Valley) and from one locality in Nebraska (Mailbox) (Repenning 1987; Bell 2000; Martin 2003a). *Promimomys mimus* is the index fossil for the first central Great Plains rodent zone (Rz 1, Martin 2003a).

Tooth group H: Hypsodont molars with prismatic dental pattern and alternating triangles

Mimomys Forsyth Major, 1902
Figure 1

Among known early arvicolid taxa, the fossil representatives of the genus *Mimomys* have been the main focus of research for a long time. Many extant arvicolid taxa, such as *Microtus* and *Arvicola*, are derived from *Mimomys*. Both genera are important side branches of the main stream of *Mimomys* evolution that can be traced over approximately three million years since the end of the Turolian (MN 13). All species of *Mimomys* have only three basic alternating triangles on the m1. Diagnostic features are the structure of the anteroconid in m1, the height of the dentine tracts (linea sinuosa), presence or absence of cementum within the reentrants, the thickness of the enamel band (the Schmelzmuster), and others.

Among the oldest and most primitive species are *Mimomys antiquus* from the late Early Ruscinian (MN 14 b) of Peshniovo in western Asia (Zazhigin and Zykin 1984), and *Mimomys vandermeuleni* and *Mimomys davakosi* reported from the early Late Ruscinian (MN 15a) of western and southern Europe (Fejfar et al. 1990; Van de Weerd 1979). *Mimomys vandermeuleni* and *Mimomys davakosi* are more advanced than *Mimomys antiquus* from Siberia. Heavily worn molars recovered from fluviolimnic deposits at the site of Malusteni, Roumania (Kormos 1932), and previously described as *Mimomys moldavicus* (or *Promimomys moldavicus* of some authors) belong most probably to *Mimomys davakosi* (Fejfar et al. 1998).

All these early species of *Mimomys* have an m1 with a highly complicated anteroconid. In the m1 of juvenile individuals, the mesial portion of the anteroconid is variably undulated. An enamel islet is positioned within the anteroconid of the m1 and in the posterior portion of the M3 as well. On the buccal side of the anteroconid, a *Mimomys* ridge (*Mimomys*-Kante) is developed, which is progressively reduced in later species of the Villanyian and Biharian. Moreover, also in contrast to later species of the Villanyian and Biharian (e.g., *Mimomys pliocaenicus*, *Mimomys savini*), (1) the enamel band is thick and undifferentiated, (2) the linea sinuosa (base of the tooth crown) of the m1 is faintly undulated, (3) the dentine fields of the m1 triangles T1 and T4 are still more or less confluent, and (4) the reentrants (synclines) lack cementum, which later appeared in the *Mimomys* lineage, as in the late Late Ruscinian (MN 15) *Mimomys hassiacus* from Gundersheim or the earliest Villanyian (MN 16a) *Mimomys stehlini*.

The early history of *Mimomys* in eastern Asia is poorly known. Early Pliocene records described as *Mimomys* sp. were reported from the early Yushean Gaozhuang assemblage (Yushe fauna, NMU 12), China (Lindsay 1994; Flynn et al. 1997; Qiu and Li 2003) that possibly correlates to the Early (MN 14) or Late Ruscinian (MN 15). *Mimomys irtyshensis* from the late Yushean Mazegou assemblage (Yushe fauna) (Flynn et al. 1997; Qiu and Li 2003) is also notable. It belongs most likely to the Early Villaniyan (MN 16) (Qiu and Li 2003). *Mimomys orientalis* recovered from the upper part of the Daodi Formation (Nihewan Basin), China, seems to be of the same age (Qiu and Li 2003; Zhang et al. 2003). Late Yushean *Mimomys youhenicus* also would belong to the Early Villanyian (Qiu and Qiu 1995).

The early Yushean (Early Pliocene, MN 14) Bilike site (Inner Mongolia, China) produced a primitive arvicolid species originally called *Mimomys* sp. (Qiu 1988; Lindsay 1994; Qiu and Qiu 1995). The size and dental pattern of this species that are not described in Qiu and Storch (2000) displays similarities with *Mimomys* (*Cseria*) *gracilis* from Central Europe (Repenning, in litt.). It is assumed to represent the earliest and most primitive record of Mimomys in China (Qiu and Qiu 1996).

Mimomys has an extensive fossil record in Eurasia, dating back to at least to the Early Pliocene (*Mimomys antiquus*, Ruscinian, MN 14b; Fejfar et al. 1997; Repenning 2003). However, in contrast to Eurasia, there is no consensus on the origin and dispersal history of *Mimomys* in North America. Many authors (e.g., Repenning 1968, 1987, 2003; Repenning et al. 1990; Woodburne and Swisher 1995) consider *Mimomys* to be an immigrant from Eurasia, whereas von Koenigswald and Martin (1984) assumed that it had never reached North America because the Schmelzmuster patterns do not match that of the Eurasian *Mimomys* (see also Martin 2003b; Martin et al. 2002, 2006). If so, the North American *Mimomys* must have evolved directly from a *Promimomys* grade arvicolid in North America (or possibly in Asia?), a conclusion that agrees with earlier suggestions by Lindsay et al. (1984: 483): "If North America species of Mimomys evolved from a different species of *Promimomys* than did the Eurasian species of *Mimomys*, as we propose, then separate North American and European lineages of *Mimomys* should be distinct."

Aratomys Zazhigin, in Gromov, 1972
Figure 1

Aratomys has originally been reported from the early Pliocene of Mongolia (Schaub 1934). The molars are rooted and cementless. The m1 of *Aratomys* is relatively short and broad, and displays three alternating basic triangles. The stucture of the anteroconid is distinctly more complex than that in *Promimomys*, which also occured in the Pliocene (Early Ruscinian) of Eurasia.

The species *Aratomys multifidus* is based on material collected at the site of Chono-Khariak 2 in western Mongolia. The deposits that produced the remains of *Aratomys multifidus* were referred to the late Early Ruscinian (upper MN 14b) by Zazhigin (Qiu and Storch 2000). *Aratomys bilikensis* was described from Bilike, Inner Mongolia, China (Qiu and Storch 2000), also early Yushean (Early Ruscinian, MN 14) in age (Qiu and Storch 2000; Qiu and Li 2003). According to Qiu and Storch (2000), *Aratomys bilikeensis* seems to be slightly more primitive than *Aratomys multifidus*.

Aratomys is larger than typical *Mimomys*. The molar pattern of *Aratomys multifidus* and *Aratomys bilikeensis* could suggest relations to the *Mimomys* branch (Fejfar et al. 1998), and comparison with early species of *Mimomys* (e.g., *Mimomys vandermeuleni*, *Mimomys davakosi*) reveals little differences in the occlusal pattern and the developmental stage of the tooth crown base (linea sinuosa).

Aratomys multifidus and *Aratomys bilikeensis,* as well *as Kilarcola kashmirensis* from Kilar, Kashmir (Kotlia 1994; Kotlia and von Koenigswald 1992), were assigned to *Mimomys (Aratomys*) by Repenning (2003), who considered this taxon a possible Oriental faunal region subgenus.

Dolomys Nehring, 1898
Propliomys Kretzoi, 1959
Figure 1

Dolomys is characterised by relatively large rooted hypsodont prismatic molars. As a representative of the tribe Ondatrini, *Dolomys* has five basic triangles on m1. In lateral view, all molars display a conical shape that resulted in a typical increase of the length and width of the cheek teeth in advanced stages of wear. The enamel base of the tooth crown (linea sinuosa) is faintly undulated. In moderately worn m1 of juvenile individuals, the mesial walls of the anteroconid are variably undulated; in heavily worn m1 of adult to senile individuals, however, the shape of the anteroconid is mushroom-like. The chewing surface displays a striking asymmetry: the lingual triangles and synclines are larger than the buccal ones. The triangles of the m1 are alternating, as they are in M1. The apices of the triangles are sharp in juvenile individuals, but rounded in adult and senile individuals. The enamel band is not differentiated; the reentrants lack cementum. A typical trait of the m1 is the deeply inserted reentrant (syncline) BRA 3 that distinguishes *Dolomys* from *Mimomys* where BRA 3 is always distinctly shallower (for details see Maul 1996; Popov 2004).

Dolomys species were present throughout the southern parts of western, central and eastern Europe during the Ruscinian (MN 14b and MN 15); it became extinct in the Villanyian (MN 16a), since the probable latest record is from Beremend 15, where *Dolomys milleri* co-occurs with *Mimomys* cf. *hajnackensis* and *Mimomys* cf. *pitymyoides* (Jánossy 1990). Important early species are *Dolomys adroveri* reported from Orrios 3, 9 and from Villalba Alta Rio 3, Escorihuela B, and Tollo Chiclana (TCH1), Spain (Fejfar et al. 1990; Minwer-Barakat 2004), *Dolomys milleri* (Nehring 1898) (e.g., Beremend 5, Hungary, Kretzoi 1956), *Dolomys nehringi* (e.g., Csarnóta 2, Hungary, Kretzoi 1959), as well as *Dolomys occitanus* from Sète, France, which was first described as *Mimomys occitanus* by Thaler (1955). Except for Csarnóta 2 (MN 14b), all these localities are Late Ruscinian (MN 15) in age. According to Fejfar et al. (1990), *Dolomys milleri* and *Dolomys nehringi* are more derived than *Dolomys adroveri* from Teruel basin, Spain. In the western Mediterranean *Dolomys* gave rise to the large rootless genus *Kislangia*.

It is worth mentioning, that a poorly preserved m1 found in Blancan 2 deposits of the Kettleman Hills of southern California and tentatively assigned to *Dolomys* indicates that muskrats possibly entered the North American fossil record earlier than previously thought (Repenning et al. 1995; Bell 2000).

The hypsodont prismatic molars of *Propliomys* are smaller than those of *Dolomys*. As revealed by *Propliomys hungaricus* from the late Early Ruscinian (MN 14b) of Csarnóta 2 (Hungary), the anteroconid is elongated, the so-called Vorderkappe sharply edged and inclined medially. *Propliomys* shares with *Dolomys* the asymmetry of the alternating synclines and the deep buccal syncline BRA 3. Moreover the lingual triangles are larger than the buccal ones, as in *Dolomys*.

Cosomys Wilson, 1932
Ophiomys Hibbard and Zakrzewski, 1967
Ogmodontomys Hibbard, 1941

The overall molar morphology of these three taxa shows such striking similarities with the cheek teeth of the Eurasian *Mimomys* that an allocation to this genus and the subgenus status of *Cosomys*, *Ophiomys*, and *Ogmodontomys* has been widely accepted for many years (e.g., Repenning 1987, 2003). However, this taxonomical assignment has been challenged, based on the molar enamel structure of these taxa (von Koenigswald and Martin 1984; for *Ogmodontomys* see also Martin et al. 2002; Martin et al. 2006). These authors suggest that *Cosomys*, *Ophiomys*, and *Ogmodontomys* did not evolve from the *Mimomys* stock (see above) but belong to a North American vole clade with its own history derived from a *Promimomys* grade arvicolid.

Ophiomys and *Cosomys* mark the beginning of the Blancan in North America (Repenning 1987). *Ophiomys mcknighti*, a small form, and *Cosomys sawrockensis (*or *Ogmodontomys sawrockensis*, see Hibbard 1957; Martin 2003a) a large form, are the hallmarks of the Blancan I (Repenning 1987). According to Martin (2003a – there referred to as *Ogmodontomys*), *Cosomys sawrockensis* is the index fossil for the central Great Plains rodent zone 4. It appeared by about 4.8 Ma for the first time (Repenning 2003). The m1 is characterised by three basic triangles, very low dentine tracts, persistent islet on the anteroconid complex, gradual loss of the *Mimomys*-Kante, and a primitve Schmelzmuster that consists apparently entirely of radial enamel (Repenning 2003).

Ophiomys mcknighti (Blancan I), known from localities of the western U.S. faunal region (Fejfar and Repenning 1992; Repenning et al. 1990) is also rather primitive because it has only low undulations of its linea sinuosa on the m1, indicating an early stage in the development of dentine tracts. *Ophiomys mcknighti* evolved through an intermediate form (*Ophiomys "mcknighti -taylori"*) (Blancan II) into *Ophiomys taylori* (Blancan III) (Repenning 1987).

In the western U.S. faunal region, *Cosomys* (or *Ogmodontomys* of some authors) *sawrockensis* or a closely related species gave rise during the Blancan to (Repenning 1987; Bell 2000) *Cosomys primus* as well as to *Ogmodontomys poaphagus*, the index fossil for the central Great Plains rodent zone 6 (Martin 2003a) Cosomys disappears at the middle/ late Bancan boundary at about 3.0 Ma (Martin 2008).

In contrast to early members of *Mimomys* in Eurasia such as the Early Pliocene (Villanyian, MN 16) *Mimomys hassiacus* or *Mimomys stehlini*, the North American members of *Cosomys*, *Ophiomys*, and *Ogmodontomys* never developed cementum. *Mimomys (Cromeromys) virginianus* from the Cheetah Room fauna of West Virgina represents, according to Repenning (2003, in litt.), an independent immigration of *Mimomys* to North America, about at the beginning of the Pleistocene.

Protopliophenacomys Martin, 1975
(= *Propliophenacomys* Martin, 1975)
Pliophenacomys Hibbard, 1937

Protopliophenacomys is an endemic North American arvicolid taxon that appeared with *Protopliophenacomys parkeri* during the Late Hemphillian for the first time (Repenning 1987; Martin 2003a). It is the index fossil for the central Great Plains rodent zone 2 (Martin 2003a). *Pliophenacomys* is apparently a derivative of *Protopliophenacomys*. *Protopliophenacomys* displays a dental pattern that is intermediate between *Promimomys mimus* and *Pliophenacomys* (Martin 2003a). The oldest record of *Pliophenacomys* was described as *Pliophenacomys wilsoni* and comes from the Concha fauna of the site of Chihuahua near Yepomera (Lindsay and Jacobs 1985). It is Blancan I in age (Repenning 1987). In the eastern U.S. faunal region, *Pliophenacomys wilsoni* evolved into *Pliophenacomys finneyi* during the Blancan II, followed by *Pliophenacomys primaevus* in the Great Plains of Blancan III (central Great Plains rodent zone 9, Martin 2003a) (Repenning et al. 1990; Bell 2000).

Tobienia Fejfar and Repenning, 1998
Lemmini nov. gen. nov. sp. Fejfar and Repenning,

1998

Figure 1

Two potential ancestors of lemmings with rooted molars (A, B) were recorded in sandy lenses below the lignite seam in the lignite quarry at Wölfersheim near Frankfurt/M., Rheinhessen, Germany; the age of the fossilferous layer is the Latest Ruscinian, MN zone 15b (Fejfar and Repenning, 1998).

A. The first record: the molars of the genus *Tobienia* are rooted; the occlusal surface is simple „*Mimomys*-like“, relatively narrow. The longitudinal tooth axis is shifted slightly to the labial side (in lower molars) and to the lingual side side (in upper molars); this shifting of the longitudinal axis is best visible in the first lower and upper molars. Enamel bands are relatively thin; the anterior and posterior enamel edges of the prisms-triangles (lingual of the lower molars; buccal of the upper molars) are mostly straight The cementum in the reentrant folds is present.The nearest comparable taxon to *Tobienia* is the rootless and about 2,5 - 1,5 Ma years younger *Mictomys vetus* (Wilson, 1933) from the North American Late Pliocene. *Tobienia* represents an ancestral “*Mimomys*-like“ stage when the lemming type of enamel was not yet fully developed. B. The second record: Lemmini nov. gen., nov. sp. in Wölfersheim: one rooted deeply worn first lower molar - with the occlusal pattern gennerally shaped as a “smaller *Mimomys*-like“ arvicoline. The anteroconid complex (ACC) is short, narrow and simple without *Mimomys*-Kante but with a circular, long, persisting islet that is not present in more advanced lemmings without rooted teeth; the interruptions of the buccal enamel wall are due to the distinct high dentine tracts on the posterior loop. The longitudinal occlusal axis of the deep alternating reentrants is slightly buccally shifted. The buccal enamel edges of the triangles are slightly differentiated in thickness: the anterior ones are thinner than the posterior ones; the lingual edges are equally thick. The buccal enamel crown base is strongly undulated similar to *Tobienia.* Fejfar and Repenning, 1998 stated that *Tobienia* belongs in the affinity of the tribe Synaptomyini whereas the second record of Lemmings - the Lemmini nov. gen. nov. sp. – represents the Lemmini tribe. Both are the first record of the Lemmings with rooted molars. Both tribes appear to have evolved from early *Mimomys* and thus belong to the subfamily Arvicolinae of the family Cricetidae; the subfamily Lemminae is no longer recognized.

DISCUSSION

In response to changing herbivorous feeding habits, cricetid rodents developed an enormous variability of cheek teeth patterns during the Miocene. The molars of the primitive cricetid rodents and arvicolids considered here represent only limited insight into the immense diversity of molar patterns and offer no more than a small window into the dental history of this extremely successful group of rodents. Based on the comments on the considered taxa, the following conclusions can be drawn.

Cricetini with brachyodont-bunodont molars and a primitive dental pattern (**tooth group A)** appeared in the late Early Miocene (Late Orleanian, MN 4) of Europe, among them *Democricetodon* and *Megacricetodon* (Mein 2003). In Anatolia, *Democricetodon* appeared apparently earlier (Agenian - MN 1) and *Megacricetodon* during the Early Orleanian (MN 3) (Ünay et al. 2003). However, the validty of these occurrences remains to be confirmed. Both genera retained low-crowned molars and disappeared from the European fossil record during the Early Vallesian (MN 9) (*Megacricetodon*) and Late Vallesian (MN 10) (*Democricetodon*), respectively (Mein 2003; Sesé 2006). *Kowalskia* appeared in the Early Vallesian (MN 9) and survived until the Early Villanyian (MN 16), and is fairly specialised in its own direction but no tendencies toward hypsodonty are seen in its European representatives. *Collimys* (MN 7 – MN 11), the first European member of the Cricetini that increased the height of the tooth crowns, was followed by *Cricetulodon* (MN 9 – MN 10) and *Rotundomys bressanus* (MN 10) (**tooth group B**).

The oldest Eurasian microtoid cricetid is *Microtocricetus* from the Vallesian (MN 9 – MN 10) of Central Europe. It is characterised by mesodont molars that display an initial prismatic dental pattern (**tooth group C**).

Microtoid cricetids with mesodont-hypsodont prismatic molars that have opposing or alternating triangles (**tooth group D**) appeared first with *Paramicrotoscoptes* in the Early Hemphillian of North America considered to be equivalent of Early to Middle Turolian (MN 11, MN 12) of Europe. Eurasian records of *Microtoscoptes* have only been reported from the Late Turolian (MN 13) to Early Ruscinian (MN 14) so far.

Mesodont-hypsodont prismatic molars characterised by opposing triangles and trilophodont upper (M1) and lower molars (m1, m2) are traits of *Trilophomys* (**tooth group E**), a microtoid rodent, which was distributed in Europe during the Ruscinian (MN 14 – MN 16).

The first microtoid cricetid having mesodont molars and a true prismatic dental pattern with opposing and alternating triangles is *Pannonicola* (= *Ischymomys*), known from the Late Vallesian (MN 10) and the Turolian (MN 11 - MN 12) of Eurasia (**tooth group F**). Members of **tooth group G** are characterised by mesodont molars with alternating triangles. They were reported from the Late Turolian (MN 13) to Early Ruscinian (MN 14) (e.g., *Anatolomys*, *Microtodon*, *Promimomys*, *Celadensia*) of Eurasia, the Late Hemphillian of North America (*Promimomys*, or *Prosomys* of some authors) as well as from the Ruscinian (MN 14–MN 15) (e.g., *Bjornkurtenia*) and Ruscinian (MN 14–MN 15) to Villanyian (MN 16) (e.g., *Baranomys*,) of Eurasia. The recent proposal that *Microtodon* and *Anatolomys* are synonyms of *Baranomys* (Fahlbusch and Moser 2004) appears to be unjustified, since the occlusal patterns and overall shape can be rather clearly distinguished (Figure 1, descriptions above).

Hypsodont prismatic molars with alternating triangles (**tooth group H**) are first known from *Aratomys* in the Early Ruscinian (MN 14) of Asia. Further early true arvicolids included in this tooth group are, for instance, *Mimomys vandermeuleni* (early Late Ruscinian, MN 15a) and *Dolomys adroveri* (Late Ruscinian, MN 15), *Propliomys hungaricus* (late Early Ruscinian (MN 14 b to Early Villanyian, MN 16) of Eurasia as well as *Protopliophenacomys parkeri* (Late Hemphillian), *Ophiomys mcknighti* (Blancan I), and *Cosomys taylori* (Middle Blancan) of North America; all of which are characterised by increasing height of crowns, enlargement of the anteroconid in m1, enlargement of the posterior portion of M3, and the development of dentine tracts.

Megacricetodon and *Democrocricetodon* display dental features indicating that these Miocene cricetids might have given rise to microtoid cricetids and extant cricetids as well. The origin of *Megacricetodon* and *Democricetodon* is far from clear, but *Shamalina* from the Early Miocene of Saudi Arabia (Whybrow et al. 1982) may have given rise to *Megacricetodon* (Lindsay 1994) and *Spanocricetodon* might be ancestral to *Democricetodon* (Mein 2003). *Megacricetodon* and *Democrocricetodon* appeared as Asian immigrants in Europe already in the late Early Miocene (late Orleanian, MN 4) for the first time and reached their highest point of evolutionary development and maximum abundance during the late Middle Miocene (Late Astaracian, MN 8) and early Late Miocene (Early Vallesian, MN 9). *Kowalskia*, a descendant of *Democricetodon*, made its first appearance in Europe during Late Miocene (Early Vallesian, MN 9) and survived until the Late Pliocene (Villanyian, MN 16).

During the Vallesian (MN 9 to 10) and possibly again at the Pliocene transition (MN 13 to 14) drastic ecological changes can be observed with the spread of more dry open habitats supporting grasslands, which is concluded from the increase of large and small mammal taxa with hypsodont teeth (Fortelius et al. 2002, 2006). At this time also the spread of prairies in North America with an increase of C4 plants has been recorded (Retallack 1997). This is also a period of many other changes in micromammals, like the MN 9 decline of glirids, the radiation of Murinae, the MN 10 appearance of *Hystrix*, *Pliopetaurista*, *Apodemus* etc., and the extinction of seven cricetine genera. Hypsodont forms were not only deveolped in cricetines, but also in murines (e.g., *Microtia*).

During the Late Miocene some cricetids with brachyodont-bunodont molars developed a more complex tooth crown pattern by the acquisition of more or less transverse ridges (lophs). Moreover, the molars became gradually high-crowned. A typical representative of this stage of cricetid evolution is *Rotundomys bressanus* known from the Late Vallesian (MN 10) in Western Europe. It seems that the basic lophodont tooth crown pattern of *Rotundomys bressanus* must have been quite similar to that of the forerunner of early arvicolid forms like *Microtodon* that is still to be discovered.

During the Late Vallesian (MN 10) *Pannonicola* (= *Ischymomys*) appeared in Eurasia for the first time and survived until the mid-Turolian (MN 12). The molar pattern of *Pannonicola* (= *Ischymomys*) is distinctly more derived than that of *Rotundomys* because its particular molar specialization resulted in the development of prismatic cheek teeth with opposing and alternating triangles. *Pannonicola* (= *Ischymomys*) belongs to the so-called Ischymomyini (Topachevskij and Nesin 1992), which were mostly considered an aberrant side branch of “micotoid cicetids” that became extinct during the Turolian without descendants. Therefore, closer relationship between *Pannonicola* (= *Ischymomys*) and true arvicolids met with disapproval (e.g., Nesin and Topachevskij 1991). However, this rejection is not justified because the relatively modern molar pattern of *Pannonicola* (= *Ischymomys*) (e.g., mesodont prismatic cheek teeth, the deep BRA 3 syncline, overall pattern of chewing surface) indicates closer relationships to *Dolomys* (Repenning et al. 1990) and possibly to *Dicrostonyx*. If so, *Pannonicola* (= *Ischymomys*) must be considered as one of the most important starting points of arvicolid evolution leading to the Ondatrinae (*Dolomys*, *Propliomys*) and probably to the Dicrostonychini (*Predicrostonyx*, *Dicrostonyx*). In various phylogenetic studies based on mitrochondrial and nuclear DNA e.g., Galewski et al. 2006, Buzan et al. 2008; Robovský et al. 2008, Abramson et al. 2009; Triant and Dewoody 2009) ondatrins and lemmings are sister taxa to all other recent arvicolid genera that might confirm this pattern.

The Microtoscoptinae include two North American genera (*Goniodontomys*, *Paramicrotoscoptes*) and one Eurasian genus (*Microtoscoptes*) and represent an aberrant lineage of advanced microtoid cricetids known from the Late Turolian (MN 13) and Early Ruscinian (MN 14) of Eurasia and the Early Hemphillian of North America.

The molars look rather modern because of the prismatic structure, however, some buccal and lingual triangles and reentrants are still opposing and not strictly alternating, as in true arvicolids. In these chacteristics *Paramicrotoscoptes* from the Early Hemphillian of North America is more derived than *Microtoscoptes* from the Late Turolian (MN 13) and Early Ruscinian (MN 14) of Eurasia. Nesin and Topachevskij (1992) suggest closer relationships between *Microtoscoptes* and *Pannonicola* (= *Ischymomys*), however, this suggestion needs further study.

Because of this unique feature we consider the genera *Microtoscoptes*, *Paramicrotoscoptes*, *Goniodontomys*, and *Pannonicola* as representing primitive microtoid cricetid branches of the first independent hypsodont-prismatic dental adaptation; the first three in Eurasia and North America and the less hypsodont, more primitively rooted but more alternating-triangled and younger *Pannonicola* only in Eurasia.

Along with *Microtocricetus*, the three genera of the subfamily Microtoscoptinae belong to the earliest Late Miocene prismatic cricetid in the Northern Hemisphere; the records of *Goniodontomys* and *Paramicrotoscoptes* in the Early Hemphillian of Idaho, Nevada, Wyoming, Oregon, and Nebraska predate the Old World sites with *Microtoscoptes*. Consequently, the Mongolian, Siberian, and Russian occurrences of *Microtoscoptes* seem to represent North American immigrants that crossed the Bering Land Bridge. This immigration does not preclude the possibility that the unknown ancestor of *Paramicrotoscoptes* and *Goniodontomys* came to North America from Eurasia.

Microtoscoptinae are known earlier in North America than in other parts of the Northern Hemisphere and must have dispersed to Asia during the faunal exchange that took place in the Late Miocene (Repenning 1987). Neither *Paramicrotoscoptes* nor *Goniodontomys* are known from Late Hemphillian faunas of North America (Repenning 1987).

Baranomys, which ranged in Europe from the Early Ruscinian (MN 14) to Early Villanyian (MN 16) and *Anatolomys* from the Late Turolian (MN 13) and Early Ruscinian (MN 14) of Asia share some dental similarities with Eurasian *Microtodon* (MN 13, MN 14). However, in contrast to *Microtodon* and other arvicolid taxa, the Baranomyinae never developed additional prisms (triangles) in the anterior portion of the m1. Therefore, the Baranomyinae are to be considered as an aberrant side branch, like the Trilophomyini, which were widely distributed in Europe during the Ruscinian (MN 14, MN 15) and Early Villanyian (MN 16).

The most successful (in number of taxa and geographic distribution) evolutionary line of arvicolid evolution can be traced through *Microtodon*, *Promimomys*, and *Mimomys* that gave rise first to *Microtus* and later to *Arvicola*. The ancestor of *Microtodon* (MN 13, MN 14) is still unknown. Special attention needs to be given to *Promimomys* sp. from the Late Turolian (MN 13) of eastern Europe and western Asia (Zazhighin and Zykin 1984) because it displays a molar pattern apparently in between *Microtodon* and *Promimomys*. *Mimomys* evolved from *Promimomys*. Among the oldest and larger species are *Mimomys antiquus* from the late Early Ruscinian (MN 14b) of Siberia (Zazhigin 1980), *Mimomys vandermeuleni*, and *Mimomys davakosi* from the early Late Ruscinian (MN 15a) of the Iberian Peninsula and southern Europe, respectively, followed by *Mimomys hassiacus* known primarily from the Late Ruscinian (MN 15b) and Early Villanyian (MN 16) of central Europe.

The Ruscinian was the starting point of two important “directions” of *Mimomys* evolution in Europe (the taxa cited below are not in all cases in ascendant-descendant relation): (1) *Mimomys* with *Mimomys vandermeuleni* (early MN 15a), *Mimomys davakosi* (late MN 15a), *Mimomys hassiacus* (MN 15b/Mn 16a), *Mimomys polonicus* (MN 16b), *Mimomys pliocaenicus* (MN 17), *Mimomys savini* (Biharian), *Arvicola mosbachensis* (early Toringian), *Arvicola terrestris* (late Toringian); and (2)

Mimomys with *Mimomys gracilis* (MN 15), *Mimomys stehlini* (MN 16), *Mimomys reidi* (MN 17), *Mimomys pusillus* (Biharian). Later on *Pusillomimus*, *Pliomys*, *Clethrionomys*, *Borsodia*, *Villanyia* etc. appeared. Further investigations are expected to solve the question whether these sequences represent true lineages or merely Stufenreihen with members that invaded successively from Asia.

It has been suggested (Kotlia and Koenigswald 1992; Kotlia 1994) that *Mimomys* (*Cseria*) dispersed to southern Asia where it evolved to *Kilarcola* prior to 2.5 Ma. The immigration of *Mimomys* (*Cseria*) was correlated with the megafaunal turnover in southern Asia that took place about 2.5 Ma (Kotlia and Koenigswald 1992). *Kilarcola* that existed in geographic isolation south of the Himalaya and gave rise to the following lineage (Kotlia 1994): *Kilarcola indicus – Kilarcola indicus sahni – Kilarcola kashmiriensis*. Note that *Kilarcola kashmiriensis* was referred to *Mimomys* (*Aratomys*) *kashmiriensis* by Repenning (2003, p. 484). Prior to these discoveries, *Mimomys* (*Cseria*) cf. *gracilis* and *Mimomys* sp. were reported from Hadji Rona (Sarobi Basin) in Afghanistan (Sen et al. 1979), likely of Ruscinian age.

The center of origin of *Promimomys* was located in the northern parts of Asia. According to Repenning (1987), a Late Hemphillian dispersal event introduced *Promimomys*, which was first described as *Prosomys mimus* (Shotwell 1963) to North America. The North American *Promimomys mimus* seems to be slightly more primitve than *Promimomys insuliferus* from the Early Ruscinian of Europe (Repenning et al. 1990).

Also Nesin and Nadachowski (2006) consider evolutionary centers of early arvicolids in both Eurasia and N-America.

It has been suggested that *Promimomys* became extinct in North America, but gave rise to *Mimomys* in Asia (Repenning 1980, 1987). A dispersal framework established by Repenning (1980, 1987, 2003; see also Repenning et al. 1990) proposes that *Mimomys* entered North America via the Bering land bridge during Blancan I for the first time, followed by further immigration waves from the Eurasian continent. This model was challenged by von Koenigswald and Martin (1984) who argued, based on their studies of Schmelzmuster, that early *Mimomys* never immigrated to North America. According to these authors it is more likely that the North American *Cosomys*, *Ophiomys*, and *Ogmodontomys* (considered as subgenera of *Mimomys* by Repenning 1987) and the Eurasian *Mimomys* developed in parallel from the *Promimomys* basic stock (von Koenigswald and Martin 1984). In contrast to von Koenigswald and Martin (1984), Martin (2003b) has recently suggested that *Mimomys* occurred in North America but was limited to the early Pleistocene (early Irvingtonian) species *Mimomys virginanus* and *Mimomys dakotaensis*. We agree that *Promimomys* gave rise to *Mimomys* and its long history with extended diversification of several subgenera and many species in Eurasia. Nevertheless, we think that the fossil record in North America may suggest a more complicated iterative dispersal pattern of immigration and endemic evolution followed by diversification, and that the solution of the *Mimomys* question is a topic requiring more material and extensive further study.

The fossil record of microtoid cricetids and early arvicolids in Eurasia is remarkably complex. The discussed fossil record and the complete lack of hypsodont species of the American *Copemys* indicate that the place of origin and the primary evolutionary centre for arvicolids were situated in the northern parts of Asia. The present large arid/semiarid areas indicate extensive grass plains – the suitable habitat for both microtoid and arvicolid ancestors.

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REFERENCES

Abramson, N.I., Lebedev, V.S., Bannikova, A.A., and Tesakov, A.S., 2009. Radiation Events in the Subfamily Arvicolinae (Rodentia): Evidence from Nuclear Genes. *Doklady Biological Sciences,* 428: 458-461.

Abdul Aziz, H., Böhme, M., Rocholl, A., Zwing, A., Prieto, J., Wijbrans, J. R., Heissig, K. and Bachtadse, V. 2007. Integrated stratigraphy and 40Ar/39Ar chronology of the Early to Middle Miocene Upper Freshwater Molasse in eastern Bavaria (Germany). *International Journal of Earth Sciences* (*Geologische Rundschau*), doi:10.1007/s00531-006-0166-7 (online version).

Adrover, R. 1986. *Nuevas faunas de roedores en el Mio-Plioceno continental de la región de Teruel (España). Interés biostratigráfico y paleoecológico*. Unpublished Ph.D. Thesis, Publicaciones del Instituto de Estudios Turolenses, Teruel.

Agadjanian, A.K., 2009. Small mammals of the Plio-Pleistocene of the Russian Plain, Moskva, 1-676 pp.

Aguilar, J.-P., Dubar, M., and Michaux, J. 1982. Nouveaux gisements à Rongeurs dans la formation de Valensole: La Tour près Brunet, d'âge Miocène supérieur (Messinian) et le Pigeonnier de l'Ange près de Villeneuve, d'âge Pliocène moyen. Implications stratigraphiques. *Comptes rendus de l'Académie des Sciences Paris*, 295:745-750.

Agustí, J., Cabrera, L., Garcés, M., Krijgsman, W., Oms, O., and Parés, J.M. 2001. A calibrated mammal scale for the Neogene of Western Europe. State of the Art. *Earth-Science Reviews*, 52:247-260.

Bachmayer, F. and Wilson, R.W. 1970. Die Fauna der altpliozänen Höhlen- und Spaltenfüllungen bei Kohfidisch, Burgenland (Österreich). *Annalen des naturhistorischen Museums Wien*, 74:533-587.

Bachmayer, F. and Wilson, R.W. 1984. Die Kleinsäugerfauna von Götzendorf, Niederösterreich. *Sitzungsberichte der Österreischischen Akademie der Wissenschaften Mathematisch-Naturwissenschftliche Klass*, *Abteilung 1*, 193:6-10; 303-319.

Bell, C.J. 2000. Biochronology of North American Microtine Rodents, p. 379-406. In Noller, J.S., Sowers, J.M., and Lettis, W.R. (eds.), *Quaternary Geochronology*. *Methods and Applications*. American Geophysical Union, Washington.

Bi, S., Meng, J., and Wu, W. 2008. A new species of *Megacricetodon* (Cricetidae, Rodentia, Mammalia) from the Middle Miocene of northern Junggar Basin, China. *American Museum Novitates*, 3602:1-23.

Brandy, L.D. 1979. Contribution a l'étude du genre *Trilophomys* (Rodentia) du Pliocène d'Europe. *Bulletin de la Société Géologique de France*, 21:105-112.

Buzan, E.V., Krystufek, B., Hänfling, B,. and Hutchinson, W.F. 2008. Mitochondrial phylogeny of Arvicolinae using comprehensive taxonomic sampling yields new insights. *Biological Journal of the Linnean Society*, 94:825-835.

Chaline, J., Brunet-Lecomte, Montuire, S., Viriot, L., and Courant, F. 1999. Anatomy of the arvicoline radiation (Rodentia): palaeogeographical, palaeoecological history and evolutionary data. *Annales zoologici Fennici*, 36:239-267.

Cope, E.D. 1891: Syllabus of lectures on Geology and Paleontology. Part 3 - *Paleontology of the Vertebrata.* Ferris Bros., Philadelphia, 1-90.

Daxner-Höck, G. 1972. Cricetinae aus dem Alt-Pliozän vom Eichkogel bei Mödling (Niederösterreich) und von Vösendorf bei Wien. *Paläontologische Zeitschrift*, 46:133-150.

Daxner-Höck, G. 1995. The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian boundary (Neogene). 9. Some glirids and cricetids from Maramena and other late Miocene localities in Northern Greece. *Münchner Geowissenschaftliche Abhandlungen*, A, 28:103-120.

Daxner-Höck, G., Fahlbusch, V., Kordos, L., and Wu, W. 1996. The Late Neogene cricetid genera *Neocricetodon* and *Kowalskia*, p. 220-226. In Bernor, R.L., Fahlbusch, V., and Mittman, H.-W. (eds.), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University, New York.

de Bruijn, H. and Hussain, S.T. 1984. The succession of rodent faunas from the Lower Manchar Formation, Southern Pakistan and its relevance for the biostratigraphy of the Mediterranean Miocene. *Paléobiologie continentale*, 14:191-204.

de Bruijn, H., van den Hoek Ostende, L., Kristkoiz-Boon, E., Rummel, M., Theocharopoulos, C., and Ünay, E. 2003. Rodents, lagomorphs and insectivores from the middle Miocene hominoid locality of Candir (Turkey). *Courier Forschungsinstitut Senckenberg*, 240:51-87.

Depéret, C. 1892. Note sur la classificatin et le parallélisme du Système miocène. *Bulletin de la Societé Géologique de France*, 3:145-154. (In French)

Doukas, C.S. 2003. The MN 4 faunas of Alivieri and Karydia (Greece). In López-Martínez, N., Peláez-Campomanes, and Hernández Fernández, M. (eds.), *Surrounding Fossil Mammals: Dating*, *Evolution and Palaeoenvironment*, *Volume in Honour of Remmert Daams*. *Coloquios de Paleontologí*, Vol. Extr. 1:127-132.

Erbajeva, M., Alexeeva, N., and Khenzykhenova, F. 2003. Pliocene small mammals from the Udunga site of Transbaikal area, p.133-145. In López-Martínez, N., Peláez-Campomanes, and Hernández Fernández, M. (eds.), *Surrounding Fossil Mammals: Dating*, *Evolution and Palaeoenvironment*, *Volume in Honour of Remmert Daams*. *Coloquios de Paleontologí*, Vol. Extr. 1:133-145.

Fahlbusch, V. 1964. Die Cricetiden (Mamm.) der Oberen Süßwasser-Molasse Bayerns. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse*, N. F. 118:1-136.

Fahlbusch, V. 1967. Die Beziehungen zwischen einigen Cricetiden (Mamm., Rodentia) des nordamerikanischen und europäischen Jungtertiärs. *Paläontologische Zeitschrift*, 41:154-164.

Fahlbusch, V. 1969. Pliozäne und pleistozäne Cricetinae (Rodentia, Mammalia) aus Polen. *Acta zoologica cracoviensia*, 14:99-137.

Fahlbusch, V. 1987. The Neogene Mammalina faunas of Ertemte and Harr Obo in Inner Mongolia (Nei Mongol), China. 5. The genus *Microtoscoptes* (Rodentia, Cricetidae). *Senckenbergiana lethaea*, 67:345-373.

Fahlbusch, V. and Mayr, H. 1975. Microtoide Cricetiden (Mammalia, Rodentia) aus der Oberen Süßwasser-Molasse Bayerns. *Paläontologische Zeitschrift*, 49:78-93.

Fahlbusch, V. and Moser, M. 2004. The Neogene mammalian faunas of Ertemte and Harr Obo in Inner Mongolia (Nei Mongol), China. 13. The genera *Microtodon* and *Anatolomys* (Rodentia, Cricetidae). *Senckenbergiana lethaea*, 84:323-349.

Fahlbusch, V., Qiu, Z., and Storch, G. 1984. Neogene micromammal faunas from Inner Mongolia: Recent investigations on biostratigraphy, ecology and biogeography, p. 697-707. In Whyte, R.O. (ed.), *The Evolution of the East Asian Environment*, *Vol. II: Palaeobotany*, *Palaeozoology and Palaeoanthropology*. Centre of Asian Studies, University of Hong Kong, Hong Kong.

Fejfar, O. 1961. Die plio-pleistozänen Wirbeltierfaunen von Hajnácka und Ivanovce (Slowakei), SR. II. Microtidae und Cricetidae inc. sed. *Neues Jahrbuch für Geologie und Paläontoloige*, *Abhandlungen*, 112:48-82.

Fejfar, O. 1964. The Lower Villafranchian Vertebrates from Hajnácka near Filakovo in Southern Slovakia. *Rozpravy ÚÚG*, 30:1-115.

Fejfar, O. 1970. Die plio-pleistozänen Wirbeltierfaunen von Hajnáčka und Ivanovce (Slowakei, CSSR) VI. Cricetidae (Rodentia, Mammalia). *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie*, 10:277-296.

Fejfar, O. 1999. Microtoid Cricetids, p. 356-371. In Rössner, G.E. and Heissig, K. (eds.), *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München, Germany.

Fejfar, O. and Heinrich, W.-D. 1983. Arvicoliden-Sukzession und Biostratigraphie des Oberpliozäns und Quartärs in Europa. *Schriftenreihe für geologische Wissenschaften*, 19/20:61-109.

Fejfar, O. and Heinrich. W.-D. 1990. Muroid Rodent Biochronology of the Neogene and Quaternary in Europe, p. 91-117. In Lindsay, E.H., Fahlbusch, V., and Mein, P. (eds.), *European Neogene Mammal Chronology*. NATO ASI Series, A, 180, Plenum Press, New York.

Fejfar, O. and Repenning, Ch. A. 1992. Holarctic dispersal of the Arvicolids (Rodentia, Cricetidae). *Courier Forschungsistitut Senckenberg*, 153:205-212.

Fejfar, O. and Repenning, Ch. A. 1998. The ancestors of lemmings (Lemmini, Arvicolidae, Cricetidae, Rodentia) in the early Pliocene of Wölfersheim near Frankfurt am Main; Germany. *Senckenbergia Lethaea,* 77:161-193.

Fejfar O. and Storch, G. 1990. Eine pliozäne (ober-ruscinische) Kleinsäugerfauna aus Gundersheim, Rheinhessen. 1. Nagetiere: Mammalia, Rodentia. *Senckenbergiana lethaea*, 71:139-184.

Fejfar, O., Heinrich, W.-D., and Lindsay E. H. 1998. Updating the Neogene Rodent biochronology in Europe, p. 533-554. In van Kolfschoten, T. and Gibbard, P.L. (eds.), *The Dawn of the Quaternary. Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO*, 60:533-553.

Fejfar, O. and Repenning, Ch. A. 1998. The ancestors of lemmings (Lemmini, Arvicolidae, Cricetidae, Rodentia) in the early Pliocene of Wölfersheim near Frankfurt am Main; Germany. Senckenbergia Lethaea, 77:161-193.

Fejfar, O., Mein, P., and Moissenet, É. 1990. Early arvicolids from the Ruscinian (Early Pliocene) of the Teruel Basin, Spain, p. 133-164. In Fejfar, O. and Heinrich, W.-D. (eds.), *International Symposium Evolution Phylogeny and Biostratigraphy of Arvicolids (Rodentia, Mammalia)*. Geological Survey, Praha.

Fejfar O., Storch, G., and Tobien, H. 2006. Gundersheim 4, a third Ruscinian micromammalian assemblage from Germany. *Palaeontographica*, *Abt. A*, 278:67-111.

Fejfar, O., Heinrich. W.-D., Pevzner, M.A., and Vangengeim, E.A. 1997. Late Cenozoic sequences of mammalian sites in Eurasia: an updated correlation. *Palaeogegraphy*, *Palaeoclimatology*, *Palaeoecology*, 133:259-288.

Fejfar, O., Ficcarelli, G., Mezzabotta, C., Espinosa, M.M., Rook, L., and Torre, D. 1996. First record of a copemyine-peromyscine cricetid (Rodentia, Mammalia) in South America: hypotheses regarding its ancestry in the Palaearctic. *Acta zoological cravoviensia*, 39:137-145.

Flynn, L.J., Wu, W.Y., and Downs, W.R. 1997. Dating vertebrate microfunas in the late Neogene recordof Northern China. *Palaeogegraphy*, *Palaeoclimatology*, *Palaeoecology*, 133:227-242.

Forsyth Major, C.I. 1902. Some jaws and teeth of Pliocene voles (*Mimomys* gen. nov.) from the Norwich Crag at Thorpe, and from the Upper Val d'Arno. *Proceedings of the Zoological Society of London*, 1:102-107.

Fortelius, M., Eronen, J., Liu, L. P., Puskhina, D., Tesakov, A., Vislobokova, I., and Zhang, Z.Q. 2003. Continental-scale hypsodonty pattern, climatic paleobigeography and dispersal of Eurasian Neogene large mammal herbivores, p. 1-11. In Reumer, J.W.F. and Wessels, W. (eds.), *Distribution and Migration of Tertiary Mammals in Eurasia*. *A Volume in Honour of Hans De Brujin*. *DEINSEA*.

Fortelius, M., Eronen, J., Liu, L., Pushkina, D., Tesakov, A., Vislobokova, I., and Zhang, Z. 2006. Late Miocene and Pliocene large land mammals and climatic changes in Eurasia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 238:- 219-227.

Fortelius, M., Eronen, J. Jernvall, J., Liu, L., Pushkina, D., Rinne, J., Tesakov, A., Vislobokova, I., Zhang, Z., and Zhou, L. 2002. Fossil mammals resolve regional patterns in Eurasian climate change over 20 million years. *Evolutionary Ecology Research*, 4:1005-1016.

Freudenthal, M. 1967. On the mammalian fauna of the *Hipparion*-beds in the Calatayud-Teruel Basin. Part 3: *Democricetodon* and *Rotundomys* (Rodentia). *Procedeedings Koninklijie Nederlandse Akademie van Wetenschappen*, 70:298-315.

Freudenthal, M. 2006. The status of *Democricetodon*, *Fahlbuschia*, *Pseudofahlbuschia*, and *Renzimys* (Cricetidae, Mammalia). A reply to van der Meulen et al. (2004). *Geobios*, 39:43-55.

Galewski, T., Tilak, M., Sanchez, S., Chevret, P., Paradis, E., and Douzery, E.J.P. 2006. The evolutionary radiation of Arvicolinae rodents (voles and lemmings): relative contribution on nuclear and mitochondrial DNA phylogenies. *BMC Evolutionary Biology*, 6:80, doi: 10.1186/1471-2148-6-80 (online version).

Gromov, I.M. 1972. Systematic groups above the species level in the vole subfamily (Microtinae) and their possible affinities. *Trudy oologicheskogo Museya Moskovskogo gosudarstvennogo Universiteta*, 13:8-33.

Gromov, V.J. and Polyakov, I.Ya. (eds.) 1977. *Fauna of the SSSR*. *Mammals*, *III*, *8: voles (Microtinae)*. Nauka, Leningrad. (In Russian)

Hartenberger, J.L. 1966. Les Cricetidae (Rodentia) de Can Llobateres (Néogene d'Espagne). *Bulletin de la Societé de France,* 7: 487-498.

Heissig, K. 1990. The faunal succession of the Bavarian Molasse reconsidered – correlation of the MN 5 and MN 6 faunas, p. 181-192. In Lindsay, E.H., Fahlbusch, V., and Mein, P. (eds.), *European Neogene Mammal Chronology*. NATO ASI Series, A, 180, Plenum Press, New York.

Heissig, K. 1995. Die Entwicklung der großen *Democricetodon*-Arten und die Gattung *Collimys* (Cricetidae, Mamm.) im späten Mittelmiozän. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie*, 35:87-108. (in German)

Hibbard, C.W. 1937. A new pitymys from the Pleistocene of Kansas. *Journal of Mammalogy*, 59:235.

Hibbard, C.W. 1941. New mammals from the Rexroad Fauna: Upper Pliocene of Kansas. *American Midland Naturalist,* 26:337-368.

Hibbard, C.W. 1957. Two new Cenozoic microtine rodents. *Journal of Mammalogy*, 38:39-44.

Hibbard, C.W. 1959. Late Cenozoic Microtine Rodents from Wyoming and Idaho. *Papers of the Michigan Academy of Science, Arts and Letters*, 44:1-40.

Hibbard, C.W. 1970. The Pliocene Rodent *Microtoscoptes disjunctus* (Wilson) from Idaho and Wyoming. Contributions from the Museum of Paleontology, University of Michigan, 23:95-98.

Hibbard, C.W. and Zakrzewski, R.J. 1967. Phyletic trends in the Late Cenozoic microtine, *Ophiomys* gen. nov., from Idaho: *University of Michigan, Contributions from the Museum of Paleontology*, 21:255-271.

Hinton, M.A.C. 1926. Monograph of the Voles and Lemmings (Microtinae) living and extinct. British Museum (Natural History), London.

Hír, J., and Kókay, J. 2010. A systematic study of the middle-late Miocene rodents and lagomorphs (Mammalia) of Felsőtárkány 3/8 and 3/10 (Northern Hungary) with stratigraphical relations. *Geodiversitas*.

Hordijk, K., and Bruijn, H. d. 2009. The succession of rodent faunas from the Mio/Pliocene lacustrine deposits of the Florina-Ptolemais-Servia Basin (Greece). *Hellenic Journal of Geosciences,* 44: 21-103.

Jacobs, L.L. and Lindsay, E.H. 1984. Holarctic radiation of Neogene muoid rodents and the origin of South American cricetids. *Journal of Vertebrate Paleontology*, 4:265-272.

Jacobs, L.L., Flynn, L.J., and Li, C-K. 1985. Comments on rodents from the Chinese Neogene. *Bulletin of the Geological Institution of the University of Upsala*, N.S. 11:59-78.

Jánossy, D. 1970. Ein neuer Eomyide (Rodentia, Mammalia) aus dem Ältestpleistozän ("Oberes Villafrankium", Villányium) des Osztramos (Nordostungarn). *Annales historico-naturales Musei nationalis Hungarici*, *Pars Mineralogica et Palaeontologica*, 62:99-113.

Jánossy, D. 1990. Arvicolids from the Lower Pleistocene sites at Beremend 15 and Somssich-hegy 2, Hungary, p. 223-232. In Fejfar, O. and Heinrich, W.-D. (eds.), *International Symposium Evolution Phylogeny and Biostratigraphy of Arvicolids (Rodentia, Mammalia)*. Geological Survey, Praha.

Jin, Ch. and Zhang, Y. 2005. First discovery of *Promimomys* (Arvicolidae) in East Asia. *Chinese Science Bulletin*, 50:327-332.

Kälin, D. 1999. Tribe Cricetini, p. 373-385. In Rössner, G.E. and Heissig, K. (eds.), *The Miocene Land Mammals Of Europe*. Verlag Dr. Friedrich Pfeil, München.

Kälin, D., and Engesser, B. 2001. Die jungmiozäne Säugetierfauna von Nebelbergweg bei Nunningen (Kanton Solothurn, Schweiz). *Abhandlungen Schweizerische Paläontologische Gesellschaft*, 121:1-61.

Kaya, O., Ünay, E., Sarac, G., Eichhorn, S., Hassenrück, S., Knappe, A., Pekdeger, A., and Mayda, S. 2004. Haltipasa transgressive zone: Implications for an Early Pliocene compressional phase in central Wesern Anatolia, Turkey. *Turkish Journal of Earth Sciences*, 13:1-13.

Kordos, L. 1994. *Pannonicola* and *Ischimomys*, p. 35. In *Neogene and Quaternary Mammals of the Palaearctic, Conference in Honour of Professor Kasimierz Kowalski*, May 17-21, 1994, Kraków, Poland, conference volume.

Kormos, T. 1932. Neue pliozäne Nagetiere aus der Moldau. *Paläontologische Zeitschrift*, 14:198-200. (In German)

Kormos, T. 1933. *Baranomys* lóczyi n. g. n. sp., új rágcsáló a magyarországi felső pliocénből (Baranomys lóczyi n. g. n. sp. ein neues Nagetier aus dem Oberpliocan Ungarns). *Állattani Közlemények*, 30:45-54. (In Hungarian)

Kotlia, B.S. 1994. Evolution of Arvicolidae in South Asia, p. 157-171. In Tomida, Y., Li, C.K., and Setoguchi, T. (eds.), *Rodent and Lagomorph Families of Asian Origins and Diversification*. *National Science Museum Monographs*, 8.

Kotlia, B.S. and von Koenigswald, W. 1992. Plio-Pleistocene arvicolids (Rodentia, Mammalia) from Kashmir intermontan basin, northwestern India. *Palaeontographica*, *Abt. A*, 223:103-135.

Kowalski, K. 1956. Insectivores, bats and rodents from the early Pleistocene bone breccia of Podlesice near Kroczyce (Poland). *Acta Palaeontologia Polonica*, 1:331-394.

Kowalski, K. 1960. Cricetidae and Microtidae from the Pliocene of Weze (Poland). *Acta zoologica cracoviensia*, 5:447-505.

Kowalski, K. 1990. Stratigraphy of Neogene mammals of Poland, p. 193-209. In Lindsay, E.H., Fahlbusch, V., and Mein, P. (eds.), *European Neogene Mammal Chronology*. NATO ASI Series, A, 180, Plenum Press, New York.

Kowalski, K. 1992. *Bjornkurtenia*, a new genus of primitive voles of Europe (Rodentia, Mammalia). *Annales zoologici Fennici*, 28:321-327.

Kowalski, K. 1993. *Microtocricetus molassicus* Fahlbusch and Mayr, 1975 (Rodentia, Mammalia) from the Miocene of Belchatów (Poland). *Acta zoologica cracoviensia*, 36:251-258.

Kowalski, K. 2001. Pleistocene rodents of Europe. *Folia Quaternaria*, 72:3-389.

Kretzoi, M. 1941. Die unterpleistozäne Säugetierfauna bei Nagyvárad. *Foldtani Közlöny*, 71:308-335.

Kretzoi, M. 1955a. *Dolomys* and *Ondatra*. *Acta Geologica Hungarica*, 3:347-355.

Kretzoi, M. 1955b. *Promimomys cor* n.g. n.sp. ein altertümlicher Arvicolide aus dem ungarischen Unterpliozän. *Acta Geologica Hungarica*, 3:89-94.

Kretzoi, M. 1956. Die altpleistozänen Wirbeltierfaunen des Villányer Gebirges. *Geologica Hungarica*, *Ser. Paleontologia*, 27:1-264.

Kretzoi, M. 1959. Insectivoren, Nagetiere und Lagomorphen der jüngstpliozänen Fauna von Csarnóta im Villanyer Gebirge (Südungarn). *Vertebrate Hungarica Musei historico-naturalis Hungarici*, 1/2:237-246.

Kretzoi, M. 1962. Fauna und Faunenhorizont von Csarnóta. *Magyar Állami Földtani Intézet évi jelentése*, az 1959:344-395.

Kretzoi, M. 1965. *Pannonicola brevidens* n.g n.sp., ein echter Arvicolide aus dem ungarischen Unterpliozän. *Vertebrate Hungarica Musei historico-naturalis Hungarici*, 7:131-139.

Kretzoi, M. 1969. Skizze einer Arvicoliden-Phylogenie – Stand 1969. *Vertebrate Hungarica Musei historico-naturalis Hungarici*, 11:155-193.

Kretzoi, M. 1990. History of research of fossil arvicolids, p. 305-312. In Fejfar, O. and Heinrich, W.-D. (eds.), *International Symposium Evolution Phylogeny and Biostratigraphy of Arvicolids (Rodentia, Mammalia)*. Geological Survey, Praha, Czech Republic.

Kretzoi, M. and Fejfar, O. 2005. Sciurids and Cricetids from Rudabánya. *Palaeontographia Italica*, 90:113-148.

Lazzari, V., Charles, C., Tafforeau, P., Vianey-Liaud, M., Aguilar, J.-P., Jaeger, J.-J., Michaux, J., and Viriot, L. 2008. Mosaic Convergence of Rodent Dentition. *PLoS ONE,* 3(10): 1-13.

Li., Q., Wang, X.-M., and Qiu, Z. 2003. Pliocene mammalian fauna of Gaotege in Nei Mongol (Inner Mongolia), China. *Vertebrata PalAsiatica*, 41:104-114.

Lindsay, E.H. 1972. Small mammals from the Barstow Formation, southern California. University of California, *Publications in Geological Sciences,* 93:1-104.

Lindsay, E.H. 1987. Cricetids rodents of lower Siwalik deposits, Potwar Plateau, Pakistan, and Miocene mammal dispersal events. Proc. Ann. Inst. Geol. Publ. Hung., 70:438-488, Budapest.

Lindsay, E.H. 1988. Cricetid rodents from Siwalik deposits near Chinji village, part I. Megacricetodontinae, Mycricetodontidae ans Dendromurinae. *Palaeovertebrata*, 18: 95-154.

Lindsay, E.H. 1994. Fossil record of Asian Cricetidae with emphasis on Siwalik cricetids, p. 131-147. In Tomida, Y., Li, C.K., and Setoguchi, T. (eds.), *Rodent and Lagomorph Families of Asian Origins and Diversification*. *National Science Museum Monographs*, 8.

Lindsay, E.H. 2008. Cricetidae, p. 456-479. In Janis, C.M., Gunnell, G.F., and Uhen, M.D. (eds.), *Evolution of Tertiary Mammals of North America, Vol. 2: Small Mammals, Xenarthrans, and Marine Mammals*. Cambridge University Press, Cambridge, UK.

Lindsay, E.H. and Jacobs, L.L. 1985. Pliocene small mammal fossils from Chihuahua, Mexico. *Paleontologias Mexicana*, 51:1-62.

Lindsay, E.H., Fahlbusch, V., and Mein, P. (eds.) 1990. *European Neogene Mammal Chronology*. NATO ASI Series, A, 180, Plenum Press, New York and London.

Lindsay, E.H., Opdyke, N.D., and Johnson, N.M. 1984. Blancan-Hemphillian land mammal ages and late Cenozoic mammal dispersal events. *Annual Review of Earth and Planetary Sciences*, 12:445-488.

Lindsay, E.H., Opdyke, N.D. and Fejfar, O. 1997. Correlation of selected late Cenozoic European mammalian faunas with the magnetic polarity time scale. *Palaeogegraphy, Palaeoclimatology, Palaeoecology,* 133, 205-226, 12 text.-figs., Amsterdam.

Lungu, A.N. 1981. The Hipparion fauna of the Middle Sarnatina of Moldavia (Insectivora, Lagomorpha, Rodentia). *State Tiraspol Institut Pedagogiki Publ.*, 1557:1-137. (In Russian)

Martin, L.D. 1975. Microtine Rodents of the Ogallala Pliocene of Nebraska and the early Evolution of the Microtinae in North America, p. 101-110. In Smith, G.R. and Friedland, N.E. (eds.), *Studies on Cenozoic Paleontology and Stratigraphy – Claude W. Hibbard Memorial Volume 3*. *University of Michigan Papers on paleontology*, 12.

Martin, R.A. 2003a. Biochronology of latest Miocene through Pleistocene arvicolid rodents from the Central Great Plains of North America, p. 373-383. In López-Martínez, N., Peláez-Campomanes, and Hernández Fernández, M. (eds.), *Surrounding Fossil Mammals: Dating, Evolution and Palaeoenvironment, Volume in Honour of Remmert Daams*. *Coloquios de Paleontologí*, Vol. Extr.

Martin, R.A. 2003b. The status of *Mimomys* in North America revisited, p. 399-406. In Reumer, J.W.F. and Wessels, W. (eds.), *Distribution and Migration of Tertiary Mammals in Eurasia*. *A Volume in Honour of Hans De Brujin*. *DEINSEA*, 10.

Martin, R.A. 2008. Arvicolidae, p. 480-497. In Janis, C.M., Gunnell, G.F., and Uhen, M.D. (eds.), *Evolution of Tertiary Mammals of North America, Vol. 2: Small Mammals, Xenarthrans, and Marine Mammals.* Cambridge University Press, Cambridge, UK.

Martin, R.A. Crockett, Ch., and Marcolini, F. 2006. Variation of the Schmelzmuster and other enamel characters in molars of the primitive vole *Ogmodontomys* from Kansas. *Journal of Mammalian Evolution*, 13:223-241.

Martin, R. A., Honey, J- G., Peláez-Campomanes, P., Goodwin, H. Th., Baskin, Ho. A., and Zakrewski, R.J. 2002. Blancan lagomorphs and rodents of the Deer Park assemblage, Meade County, Kansas. *Journal of Vertebrate Paleontology*, 76:1072-1090.

Mats, V.D., Pokatilov, S.M., Popova, A.J., Kranchynsky, N.V., Kulagina, N.V., and Shymaraeva, M.K. 1982. *Pliocene And Pleistocene Of Middle Baikal*. 1-192. Academy of Sciences of the USSR, Siberian Branch, Novosibirsk. (in Russian)

Maul, L. 1996. A discussion of the referral of *Mimomys occitanus* Thaler, 1955 (Rodentia: Arvicolidae to the genus *Mimomys*. *Acta zoologica cracoviensia*, 39:343-348.

Mayr, H. and Fahlbusch, V. 1975. Eine unterpliozäne Kleinsäugerfauna aus der oberen Süßwasser-Molasse Bayerns. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie*, 15:91-111.

Mein, P. 1966. *Rotundomys*, nouveau genre de Cricetidae (Mammalia, Rodentia) de la faune Neogène de Montredon. *Bulletin de la Société Géologique de France*, *7 Sér.*, 8:421-425.

Mein, P. 1975. Une forme de transition entre deux Familles de Rongeurs, p. 759-763. In Hofstetter, R. (ed.), *Problemes Actuels de Paléontologie. Evolution des Vertebres*. C.N.R.S., Paris, France.

Mein, P. 1990. Updating of MN Zones, p. 73-90. In Lindsay, E.H., Fahlbusch, V., and Mein, P. (eds.), *European Neogene Mammal Chronology*. NATO ASI Series, A, 180, Plenum Press, New York.

Mein, P. 1999. European Miocene mammal biochronology, p. 25-38. In Rössner, G.E. and Heissig, K. (eds.), *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München, Germany.

Mein, P. 2003. On Neogene rodents of Eurasia: distribution and migrations, p. 407-418. In Reumer, J.W.F. and Wessels, W. (eds.), *Distribution and Migration of Tertiary Mammals in Eurasia*. *A Volume in Honour of Hans De Brujin*. *DEINSEA*, 10.

Mein, P., Moissenet, E., and Adrover, R. 1983. L'extension et l'âge des formations continentales pliocènes du fosse de Teruel (Espagne). *Comptes Rendus de l' Académie des Sciences Paris*, *sér. II*, 296:1603-1610.

Michaux, J. 1976. Découverte d'une faune petits Mammifères dans le Pliocène continental de la vallée de la Canterrane (Roussillon); ses conséquences stratigraphiques. *Bulletin de la Société Géologique de France*, 17:165-170.

Miller, G.S. 1896. Genera and subgenera of voles and lemmings. *North America Fauna*, 12:1-86.

Miller, G.S. 1927. Revised determination of some Tertiary mammals from Mongolia. *Paleontologica Sinica*, 2:5-20.

Minwer-Barakat, R., García-Alix, A., Martin-Suárez, E., Freudenthal, M. 2004. Arvicolidae (Rodentia) from the Pliocene of Tollo de Chiclana (Granada, Southeast Spain). *Géobios*, 37:619-629.

Musser, G.G. and Carleton, M.D. 1993. Family Muridae, p. 501-753. In Wilson, D.E. and Reeder, D.M. (eds.), *Mammal species of the World*. Smithsonian Institution Press, Washington, London.

Nadachowski, A. 1989. 7.5 Rodentia, p. 151-176. In Kowalski, K. (ed.), *History and Evolution of the terrestrial fauna of Poland*. *Folia Quaternaria* 59-60.

Nehring, A. 1898. Über *Dolomys* nov. gen. foss. *Zoologischer Anzeiger*, 549:13-16.

Nesin, B.A. 1996a. An ancient fossil vole species (Rodentia, Cricetidae) from the Lower Pontian South Ukraine *Vestnik zoologii*, 3:74-75. (In Russian)

Nesin, B.A. and Topachevskij, V.A. 1991. The ancient phases of evolution of arvicolids (Rodentia, Microtinae). *Vestnik zoologii*, 6:41-46. (In Russian)

Nesin, V.A. and Nadachowski, A., 2006. Origin and early stages of evolution of voles (Arvicolinae) in the Holarctic, Problemy paleontologii ta biostratigrafii proterozoyu i fanerozoyu Ukraini. Natsional'naya Akademiya Nauk Ukraini, Kiev, pp. 287-290. (In Russian)

Niethammer 1982. Familie Arvicolidae Gray, 1821 – Wühlmäuse, p. 51-59. In Niethammer, J. and Krapp, F. (eds), *Handbuch der Säuegetiere Europas, Band 2/1, Rodentia II (Cricetidae. Arvicolidae. Zapodidae, Spalacidae, Hystricidae, Capromyidae)*. Akademische Verlagsgesellschaft, Wiesbaden.

Peláez-Campomanes, P. and Daams, R. 2002. Middle Miocene rodents from Pasalar, Anatolia, Turkey. *Acta palaeontologica Polonica*, 47:125-132.

Pineda-Muñoz, S., Casanovas-Vilar, I., Miguel, D. d., Karme, A., Evans, A. R., and Fortelius, M. 2010. Evolution of hypsodonty in a cricetid (Rodentia) lineage: preliminary results using patch analysis. *Cidaris,* 30: 247-252.

Popov, V.V. 2004. Pliocene small mammals (Mammalia, Lipotyphla, Chiroptera, Lagomorpha, Rodentia) from Muselievo (North Bulgaria). *Geodiversitas*, 26:403-491.

Pradel, A. 1988. Fossil hamsters (Cricetinae, Rodentia) from the Pliocene and Quaternary of Poland. *Acta zoologica cracoviensia*, 31:235-296.

Prieto, J., Böhme, M., and Gross, M. 2010. The cricetid rodents from Gratkorn (Austria, Styria): a benchmark locality for the continental Sarmatian sensu strictu (late Middle Miocene) in the Central Paratethys. *Geologica Carpathica,* 61(5), 419-436.

Prothero, D.R. 2006. *After the Dinosaurs*. *The Age of Mammals*. Indiana University Press, Bloomington and Indianapolis.

Qiu, Z. 1988. Neogene micromammals of China, p. 834-848. In Chen, E.K.Y. (ed.), *The Palaeoenvironment of East Asia from the Mid-Tertiary*. University of Hong Kong, Hong Kong.

Qiu, Z. 1990. The Chinese Neogene mammalian biochronology – Its correlation with the European Neogene mammalian zonation, p. 527-556. In Lindsay, E.H., Fahlbusch, V., and Mein, P. (eds.), *European Neogene Mammal Chronology*. NATO ASI Series, A, 180, Plenum Press, New York.

Qiu, Z. and Li, Ch. 2003. Rodents from the Chinese Neogene: Biogeographic relationships with Europe and North America. *Bulletin of the American Museum of Natural History*, 279:586-602.

Qiu, Z. and Qiu, Z. 1995. Chronological sequence and subdivision of Chinese Neogene mammalian faunas. *Palaeogeeography, Palaeoclimatology, Palaeoecology*, 116:41-70.

Qiu, Z. and Storch, G. 2000. The Early Pliocene micromammalian fauna of Bilike, Inner Mongolia, China (Mammalia: Lipotyphla, Chiroptera, Rodentia, Lagomorpha). *Senckenbergiana lethaea*, 80:173-229.

Qiu, Z.-D. and Wang, X.-M. 1999. Smal mammal faunas and their ages in Miocene of central Nei Mongol (Inner Mongolia). *Vertebrata PalAsiatica*, 37:120-139.

Qiu, Z., Li, Ch., and Wang, Sh. 1981. Miocene mammalian fossils from Xining Basin, Qinghai. *Vertebrata PalAsiatica*, 19:156-163.

Qiu, Z., Li, Ch., and Wang, X.-M. 1999. Small mammal faunas and their ages in Miocene of Central Nei Mongol (Inner Mongolia). *Vertebrata PalAsiatica*, 37:120-139. (In Chinese, with English summary)

Qiu, Z., Wu, W., and Qiu, Z 1999. Miocene mammal faunal sequence of China: paleozoogeography and Eurasien relationships, p. 443-445. In Rössner, G.E. and Heissig, K. (eds.), *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München, Germany.

Qiu, Z., Zheng, S.H., Sen, S., and Zhang, Z.Q. 2003. Late Miocene micromammals from the Bahe Formation, Lantian, China, p. 443-453. In Reumer, J.W.F. and Wessels, W. (eds.), *Distribution and Migration of Tertiary Mammals in Eurasia*. *A Volume in Honour of Hans De Brujin*. *DEINSEA*, 10.

Rabeder, G. 1981. Die Arvicoliden (Rodentia, Mammalia) aus dem Pliozän und älteren Pleistozän von Niederösterreich. *Beiträge zur Paläontologie von Österreich*, 8:1-343.

Repenning, Ch.A. 1968. Mandibular Musculature and the origin of the Subfamily Arvicolinae (Rodentia). *Acta zoologica cracoviensia*, 13:29-72.

Repenning, Ch.A. 1980. Faunal exchanges between Siberia and North America. *Canadian Journal of Anthropology*, 1:37-44.

Repenning, Ch.A. 1987. Biochronolgy of the Microtine Rodents of the United States, p. 236-268. In Woodburne, M.O. (ed.), *Cenozoic Mammals of North America: Geochronology and Biostratigraphy*. Berkeley University of California Press, Berkeley, Los Angeles, London.

Repenning, Ch.A. 2003. *Mimomys* in North America. *Bulletin of the American Museum of Natural History*, 279:469-512.

Repenning, Ch.A., Fejfar, O., and Heinrich, W.-D. 1990. Arvicolid rodent Biochronology of the Northern Hemisphere, p. 358-418. In Fejfar, O. and Heinrich, W.-D. (eds.), *International Symposium Evolution Phylogeny and Biostratigraphy of Arvicolids (Rodentia, Mammalia)*. Geological Survey, Praha.

Repenning, Ch.A., Weasma, T.R., and Scott, G.R. 1995. The early Pleistocene (latest Blancan – earliest Irvingtonian) Froman Ferry fauna and history of the Glenns Ferry, southwestern Idaho. *U.S. Geological Survey Bulletin*, 2105:1-86.

Retallack, G.J. 1997. Neogene expansion of the North American prairie. *Palaios*, 12:380-390.

Robovský, J., Řičánková, V., and Zrzavý, J. 2008. Phylogeny of Arvicolinae (Mammalia, Cricetidae): utility of morphological and molecular data sets in a recently radiating clade. *Zoologica Scripta,* 37(6): 571-590.

Rögl, F., Zapfe, H., Bernor, R.L., Brzobohaty, R., Daxner-Höck, G., Draxler, I., Fejfar, O., Gaudant, J., Herrmann, P., Rabeder, G., Schultz, O., and Zetter, R. 1993. Die Primatenfundstelle Götzendorf an der Leitha (Obermiozän des Wiener Beckens, Niederösterreich). *Jahrbuch der Geologischen Bundesanstalt*, 136:503-526.

Savage, R.J.G. 1990. The African dimension in European Early Miocene mammal faunas, p. 587-599. In Lindsay, E.H., Fahlbusch, V., and Mein, P. (eds.), *European Neogene Mammal Chronology*. NATO ASI Series, A, 180, Plenum Press, New York.

Schaub, S. 1934. Über einige Simplicidentaten aus China und Mongolei. *Abhandlungen der schweizerischen Paläontologischen Gesellschaft*, 54:1-40.

Schaub, S. 1940. Zur Revision des Genus *Trilophomys* Deperet. *Verhandlungen der Naturforschenden Gesellschft Basel*, 51:56-75.

Schaub, S. 1944 - Cricetodonten der Spanischen Halbinsel. *Eclogae Geologicae Helvetiae,* 37: 453-457.

Schlosser, M. 1924. Tertiary vertebrates from Mongolia. *Palaeontologica Sinica*, *Ser. C*, 1:1-119.

Sen, S., Brunet, M., and Heintz, E. 1979. Découverte de Rongeurs "africains" dans le Pliocène d'Afghanistan (Bassin de Sarobi): implications paléobiogéographiques et stratigraphiques. *Bulletin du Muséum National d'Histoire Naturelle Paris*, *4th ser.*, *Sec. C*, 1 :65-75.

Sesè, C. 2006. Los roedores y lagomorphs del Neógene de Espana. *Estudios Geologicos*, 62:429-480.

Shotwell, J.A. 1956. Hemphillian mammalian assemblage from northeastern Oregon. *Bulletin of the Geological Society of America*, 67:717-738.

Shotwell, J.A. 1963. Mammalian Fauna of the Drewsey Formation, Barlett Montain, Dirkwater and Otis Basin local faunas. *Transactions of the American Philosophical Society*, N.S., 53:70-77.

Shotwell, J.A. 1970. Pliocene mammals of southeastern Oregon and adjancent Idaho. *Bulletin of the Museum of Natural History, University of Oregon,* 17:1-103.

Slaughter, B. H. and Ubelaker, J.E. 1984. Relationships of South American cricetines to rodents of North America and the Orld World. *Journal of Vertebrate Paleontology*, 4:255-263.

Sulimski, A. 1964. Pliocene Lagomorpha and Rodentia from Weze 1 (Poland). *Acta Palaeontologica Polonica*, 9:149-241.

Sümengen, M.E., Ünay, E., Sarac, G., de Bruijn, H., Terlemez, I., and Gurbuz, M. 1990. New Neogene rodent assemblages from Anatolia (Turkey), p. 61-72. In Lindsay, E.H., Fahlbusch, V., and Mein, P. (eds.), *European Neogene Mammal Chronology.* NATO ASI Series, A, 180, Plenum Press, New York.

Thaler, L. 1955. Sur l'âge pliocène de la faune des grottes du Lazaret (Sète, Hérault). *Comptes Rendus de l'Académie des Sciences Paris*, 420:433-435.

Tedford, R.H., Skinner, M.F., Fields, R.W., Rensberger, J.M., Whistler, D.P., Galusha, T., Taylor, B.E., MacDonald, J.R., and Webb, S.D. 1987. Fauna succession and biochronology pf the Arikareean through Hemphillian interval (late Olicocene through earliest Pliocene epochs) in North America, p. 123-210. In Woodburne, M.O. (ed.), *Cenozoic Mammals of North America: Geochronology and Biostratigraphy.* Berkeley University of California Press, Berkeley, Los Angeles, London.

Tedford, R.H., Albright III, L.B., Barnosky, A.D., Ferrusquia-Villagranca, I., Hunt Jr., R.M., Storer, J.E., Swisher III, C.C., Voorhies, M.R., Webb, S.D., and Whistler, D.P. 2004. Mammalian biochronology of the Arikareean through Hemphillian interval (late Oligocene through early Pliocene epochs), p. 169-231. In Woodburne, M.O. (ed.), *Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology.* 2004. Columbia University Press, New York.

Topachevskij, V.A. and Nesin, V.A. 1992. A New Tribe of Extinct Cricetids Ischymomyini (Rodentia, Cricetidae). *Vestnik zoologii*, 1992/1:28-32. (In Russian, English summary)

Topachevskij, V.A. and Skorik, A.F. 1988. The vole-toothed Cricetodontidae (Rodentia, Cricetidae) from Vallésian of Eurasia and some questions of supergeneric systematics of the subfamily. *Vestnik zoologii*, 1988/ 5:37-45. (In Russian, English summary)

Topachevskij, V.A. and Skorik, A.F. 1992. *The Neogene and Pleistocene lower Cricetids of SE Europe*. Akademiya Nauk Ukrainy, Institut Zoologii, Naukova Dumka, Kiev. (In Russian)

Topachevskij, V.A., Skorik, A.F. and and Rekovets, L.I. 1978. The most ancient Voles of the Microtini tribe (Rodentia, Microtidae) from the South of the Ukrainian SSR. *Vestnik Zoologii*, 1978:35-41, Moscow. (In Russian)

Topachevskij, V.A., Skorik, A.F., and Rekovets, L.I. 1987. *The Late Neogene and Early Antropogene Rodents of the Chadzhibei Liman*. Naukova Dumka, Kiev. (in Russian)

Triant, D.A. and Dewoody, J.A. 2009. Integrating numt pseudogenes into mitochondrial phylogenies: comment on 'Mitochondrial phylogeny of Arvicolinae using comprehensive taxonomic smapling yields new insight'. *Biological Journal of the Linnean Society*, 97:223-224.

Ünay, E., de Brujin, H., and Sarac, G. 2003. A preliminary zonation of the continental Neogene of Anatolia based on rodents, p. 539-547. In Reumer, J.W.F. and Wessels, W. (eds.), *Distribution and Migration of Tertiary Mammals in Eurasia*. *A Volume in Honour of Hans De Brujin*. *DEINSEA*, 10.

van der Meulen, A.J. 1973. Middle Pleistocene smaller mammals from the Monte Peglia (Orvieto, Italy) with special reference to the phylogeny of *Microtus* (Arvicolidae, Rodentia). *Quaternaria* 17:1-144.

van de Weerd, A. 1979. Early Ruscinian rodents and lagomorphs (Mammalia) from the lignites near Ptolemais (Macedonia, Greece). *Koninklijke Nederlandse Akademie van Wetenschapen, Proceedings, Ser. B*, 82:127-180.

von Koenigswald, W. 1980. Schmelzstruktur und Morphologie in den Molaren der Arvicolidae (Rodentia). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, 539:1-129.

von Koenigswald, W. and Martin, L.D. 1984. The status of the genus *Mimomys* (Arvicolidae, Rodentia, Mamm.) in North America. *Neues Jahrbuch für Geologie und Paläontologie*, *Abhandlungen*, 168:108-124.

Wellcomme, J.L., Aguilar, J.P., and Ginsburg L. 1991. Découverte d'un nouveau Pliopitheque (Primates, Mammalia) associé à des rongeurs dans les sables du Miocène supérieur de Priay (Ain, France) et rémarques sur la paléogeographie de la Bresse au Vallesian. *Comptes Rendus de l' Académie des Sciences*, 313:723-729.

Wessels, W., de Bruijn, H., Hussain, S.T., and Leinders, J.J.M. 1982. Fossil rodents from the Chinji Formation, Banda Daud Shah, Kohat, Pakistan. *Koniklijke Nederlandse Akademie van Wetenschappen*, *Proceedings, Ser. B*, 85:337-364.

Wessels, W., Fejfar, O., Peláez-Campomanes, van der Meulen, A., and de Bruijn, H. 2003. Miocene small mammals from Jebel Zelten, Libya, p. 699-715. In López-Martínez, N., Peláez-Campomanes, and Hernández Fernández, M. (eds.), *Surrounding Fossil Mammals: Dating, Evolution and Palaeoenvironment, Volume in Honour of Remmert Daams*. *Coloquios de Paleontologí*, *Vol. Extr.* 1.

Whybrow, P.J., Collinson, M.E., Daams, R., Gentry, A.W., and McClure, H.A. 1982. Geology and fauna (Bovidae, Rodentia) from the early Miocene of eastern Saudi Arabia. *Tertiary Research*, 4:105-120.

Wilson, R.W. 1932. Cosomys, a new genus of vole from the Pliocene of California. *Journal of Mammalogy*, 13:150-154.

Wilson, R.W. 1937. New Middle Pliocene Rodent and Lagomorph faunas from Oregon and California. *Carnegie Institution of Washington Publication*, 487:1-19.

Winkler, A.J. 1994. The Middle/Upper Miocene dispersal of major rodent groups between Southern Asia and Africa. p. 173-184. In Y. Tomida, Li, C.K., and Setoguchi, T. (eds), *Rodent and Lagomorph Families of Asian Origins and Diversification, National Science Museum Monographs*, 84.

Wood, A.E. 1936. The cricetid rodents described by Leidy and Cope from the Tertiary of North America. *American Museum Novitates*, 822:1-8.

Woodburne, M.O. and Swisher, C.C. III. 1995. Land mammal high-resolution geochronology, intercontinental overland dispersals, sea level, climate, and vicariance, p. 335-364. In Berggren, W.A., Kent, D.V., Aubry, M.-P., and Hardenbol, J. (eds.), *Geochronology, Time Scales and Global Stratigraphic Correlations, SEPM Special Publication No. 54*. Tulsa, Oklahoma, USA.

Wu, W. 1991. The Neogene mammalian faunas of Ertemte and Harr Obo in Inner Mongolia (Nei Mongol), China. 9. Hamsters: Cricetinae (Rodentia). *Senckenbergiana lethaea*, 71:257-305.

Zazhigin, V.S. 1980. Late Pliocene and Anthropogene Rodents of the South of Western Siberia. *Transactions of the Geological Institute*, 339:1-156. (In Russian)

Zazhigin, V.S., 1982. Order Rodentia-rodents. In: Shanzer E.V. (ed.) *Stratigraphy of the USSR: The Quaternary system.* Nedra, Moscow, 294-305 (in Russian).

Zazhigin, V.S. and Zykin V.C. 1984. New data on the Pliocene stratigraphy of the south west Siberian Plain, p. 29-53. In Arkhipov, S.A. (ed.), *Stratigraphy of the Neogene-Anthropogene Boundary Sediments in Siberia*. Acadademy of Sciences of the USSR, Siberian Department, Novosibirsk. (In Russian)

Zhang, Z.-Q., and Zheng, S. 2000. Late Miocene-Early Pliocene biostratigraphy of Loc. 93002 Section, Lingtai, Gansu. *Vertebrata PalAsiatica*, 38:274-286. (In Chinese, with English summary)

Zhang, Z.-Q., Zheng, S.-H., and Liu, J.-B. 2003. Pliocene mammalian biostratigraphy of Nihewan basin, with comments on the stratigraphic division. *Vertebrata PalAsiatica*, 41:306-313. (In Chinese, with English summary)

Zheng, S.-H. and Zhang, Z.-Q. 2001. Late Miocene-Early Pliocene biostratigraphy of the Leijiahe area, Lingtai, Gansu. *Vertebrata PalAsiatica*, 39:215-228. (In Chinese, with English summary)