COMMENTS ON THE AGE AND DISPERSAL OF MICROTOSCOPTINI (RODENTIA: CRICETIDAE)

We can know only that we know nothing.
And that is the highest degree of human wisdom.

Lev Nikolayevich Tolstoy, War and Peace

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Abstract: The tribe Microtoscopini, comprising the genera Microtoscopites from Eurasia and Paramicrotoscopites and Goniodontomys from North America, is an enigmatic group of microtoid cricetids, which was widespread during the Late Miocene. Although fossil remains have been reported from 33 localities, their evolutionary and dispersal history is still poorly understood.

Here we give an overview of sites and records and discuss temporal ranges and some aspects of the dispersal history. The branch of cricetids that gave rise to the Microtoscopini is still unknown. The currently oldest records are those of Microtoscopites from Shala in China, considered 8 to 9 Ma and correlated with MN 10 or MN 11. All other remains from Eurasia are distinctly younger (MN 11 – MN 13). The earliest North American records of Paramicrotoscopites and Goniodontomys are from the early Hemphillian beginning at 9.0 Ma (approximately MN 10 – MN 11 transition). Whether Microtoscopites from Shala actually indicates the origin of Microtoscopini in Asia and subsequent dispersal to North America is still unclear. The presence of Microtoscopini in both Central Asia and North America during the Late Miocene does suggest dispersal through Beringia. The Microtoscopini inhabited probably open grasslands locally differentiated by shrubs, tree patches and water bodies. It is far from clear why the Microtoscopini became extinct even though they had developed an efficient arvicoline-like cheek-tooth pattern.

Key words: Microtoscopites, Paramicrotoscopites, Goniodontomys, Late Miocene records, dispersal

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Introduction

Tolstoy’s phrase, the epigraph of this paper, previously supposed to be taken from Socrates (who, however, probably never said this), or from a thousand other wisemen, seems particularly appropriate with regard to our knowledge of the Microtoscopini, the enigmatic extinct tribe of so-called microtoid cricetids or “vole-toothed hamsters” (Fahlbusch and Mayr 1975, Fahlbusch 1996, Fejfar 1999, Fejfar et al. 2011). Judging from the number of Microtoscopini-bearing localities (33), this group seems to be a well-known one. However, considering our knowledge of its fossil history, there are still a lot question marks.

There is a considerable similarity between the cheek-teeth of the Microtoscopini and those of arvicolines (voles) owing to similar adaptations (for a summary, see Fejfar et al. 2011). Also the molars of the Microtoscopini are hypsodont, and they display a prismatic molar shape with opposing or slightly alternating dental triangles. However, at the first lower molar the second and third triangles (counted from distal side of the tooth) form a distinct rhombus – the “trademark” of the Microtoscopini that is not seen in true arvicolids or other branches of microtoid cricetids.

Microtoscopites, confined to Eurasia and the first described genus of Microtoscopini, comes from the Late Miocene
(Turolian) of Ertemte in northern China (Schaub 1934), and it has been reported since then from several regions of Central Asia and Eastern Europe (e.g., Topachevskiy 1971, Zazhigin in Gromov et Polyakov 1977, Zazhigin in Pevzner et al. 1982, Savinov 1982, Zazhigin and Zykin 1984). *Goniodontomys* and *Paramicrotuscoptes* were exclusively distributed in North America during the Late Miocene (Hemphillian) (e.g., Wilson 1937, Hibbard 1970, Repenning 1987, Repenning et al. 1990).

Because *Microtuscoptes* Schaub, 1934, *Goniodontomys* Wilson, 1937, and *Paramicrotuscoptes* Martin, 1975 are morphologically rather similar, they seem to be closely related (Schaub 1940) and were grouped in one taxon: first at subfamily level as Microtuscoptinae (Kretzoi 1955), then as a family Microtuscoptidae (Kretzoi 1969), and later as tribe Microtuscoptini (Gromov and Polyakov 1977), the still commonly accepted taxonomic rank (Fejfar et al. 2011).

Although three genera with seven species have been named so far (*Microtuscoptes praetermissus* Schaub, 1934, *M. tjuvanensis* Zazhigin in Gromov et Polyakov, 1977, *M. pristinus* Savinov, 1982, *M. sibiricus* Zazhigin et Zykin, 1984, *M. mongolicus* Zazhigin in Pevzner et al., 1982, *Goniodontomys disjunctus* Wilson, 1937 and *Paramicrotuscoptes hibbardi* Martin, 1975), the fossil record of the Microtuscoptini is far from being satisfactorily documented. Some of these species mentioned have not yet been adequately described and illustrated. Therefore, many aspects of the phylogeny, biostratigraphy and paleoecobiogeography of these microtoid cricetids have been remained obscure until today.

For a long time the Microtuscoptini were to many European paleontologists strange small mammals from the Far East. This view changed in the early 1970s, when a single tooth of *Microtuscoptes* was unearthed from Late Miocene deposits exposed at the Ukrainian site Cherevychne 3 (Topachevskiy 1971), which showed for the first time that Microtuscoptini were distributed also in Eastern Europe. Since then further sites have been discovered in the Ukraine that yielded numerous finds of *Microtuscoptes* that are currently under investigation (Fejfar and the authors of the present paper). There are also further recent discoveries from Asia (e.g., locality Shala – Qiu et al. 1999, Li et al. 2003, Qiu Zhuding et al. 2013) that require modifications of some previous conclusions about Microtuscoptini (Fejfar et al. 2011).

The purpose of this paper is to summarise and discuss current information on the available records and ages of the finds and the dispersal of Microtuscoptini known so far. It is complementary to the studies on new material of *Microtuscoptes* from the Ukraine, the description of which is in preparation. The present paper is devoted to Oldrich Fejfar and Rudolf Musil with thanks for many years of fruitful co-operation.

**Abbreviations**

AEO – Appearance Event Ordination (a biochronological method of ordering the appearance of fossil mammal genera by multivariate analysis; see Alroy 1994), BI – Blancan, CI – Clarendonian, CLMA – Chinese Land Mammal Ages, ELMA – European Land Mammal Ages, FAD – First appearance datum, Hh – Hemphillian, LAD – last appearance datum, MN – Neogene Mammal Age Zone, NALMA – North American Land Mammal Ages, NMU – Neogene Mammal Unit.

**Records of Microtuscoptini**

The records are listed in geographical order of the countries from east to west in Eurasia: China – Russia – Mongolia – Kazakhstan – Ukraine and in North America. The numbers of the sites (loc. nr.) refer to those in Text-figs 1 and 4. In the morphological descriptions, lower case denotes lower teeth and upper case denotes upper teeth. The maps in Text-figs 1 and 4 were created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Copyright © Esri. All rights reserved. For more information about Esri® software, please visit http://www.esri.com.

**China**

**Ertemte 1 and 2 (loc. nr. 1)**

Location of the site: Northern China, Inner Mongolia (= Nei Mongol) Autonomous Region, Huade county, 4 km SE of the town of Huade, outskirts of village of Ertemte (Storch and Zazhigin 1996). According to Fahlbusch et al. (1983b), Ertemte 1 refers to the classical site excavated in the 1920s (Andersson 1923, Schlosser 1924, Schaub 1934), from where of *Microtuscoptes* was described (Schaub 1934), and Ertemte 2 refers to the site of the later rich material unearthed and investigated by Fahlbusch (Fahlbusch et al. 1983b, Fahlbusch 1987, Qiu Zhuding et al. 2013: 184).


**Abbreviations**

AEO – Appearance Event Ordination (a biochronological method of ordering the appearance of fossil mammal genera by multivariate analysis; see Alroy 1994), BI – Blancan, CI – Clarendonian, CLMA – Chinese Land Mammal Ages, ELMA – European Land Mammal Ages, FAD – First appearance datum, Hh – Hemphillian, LAD – last appearance datum, MN – Neogene Mammal Age Zone, NALMA – North American Land Mammal Ages, NMU – Neogene Mammal Unit.

Remarks: Olan Chorea is the type locality of the species Microtosscoptes praetermissus. Faubus (1987) provided a detailed history of the views on Microtosscoptes praetermissus in the literature up to 1987.

Olan Chorea (loc. nr. 2)

Location of the site: Northern China, Inner Mongolia (= Nei Mongol) Autonomous Region, Huade county, 2 km south of Ertemte (Faulhubsch et al. 1983b, Qiu and Li 2016).


Age: Previously Harr Obo was referred to MN 13 (early Ganzhuangian, Early Ruscinian – Qiu and Qiu 1995, Qiu and Li 2003, Qiu et al. 2003, Faulhubsch and Moser 2004) because of the occurrence of Rhagapodemus and Hypolagus (Fejfar et al. 2011). However, in fact both taxa are recorded already also in MN 13 sites: Hypolagus in Rasdorskaya/Russia (Averianov 1996), and Rhagapodemus in Vinogradovka 1/ Ukraine (Nesin and Storch 2004, Nesin 2013). Therefore Harr Obo might belong also to MN 13. The assignment to MN 13 is in accordance with the FAD of Pliopetaurista in MN 10, of Dipoides in MN 11, of Alilepus and Pseudomeriones in MN 12, and of Sorex and Micromys in MN 13 (Mein 1999). Sorex is recorded in China since MN 11 (Storch et al. 1998). Moreover, the range of Ochotona lagreli and of O. minor (MN 9 – MN 13) (Erbaeva et al. 2015) would confirm the age of MN 13.

Shala (loc. nr. 4)

Location of the site: Northern China, Inner Mongolia (= Nei Mongol) Autonomous Region, Jurh county.


Age: Currently, Qiu and Li (2016) estimate the age of Shala 8 to 9 Ma. It is considered of Late Bahean age (8 to 9.5 Ma), correlated with MN 10 or MN 11, and younger

Age: Early Baodean, equivalent of MN 12 (Wang et al. 2009, Qiu Zhuding et al. 2013), because *Dipoides*, *Hansdebruijina*, *Allepus* made their first appearance during the Baodean, and *Democricetodon*, *Proscipheus*, *Leptodontomys*, *Microdyromys*, and *Miodyromys* had their last appearance there (Qiu Zhaxiang et al. 2013: 65).

**Baogeda Ula** (loc. nr. 5)

Location of the site: Northern China, Inner Mongolia (= Nei Mongol) Autonomous Region, Jurh county.

Other name: Baogedawula.


Age: Early Baodean, equivalent of MN 12 (Wang et al. 2009, Qiu Zhuding et al. 2013), because *Dipoides*, *Hansdebruijina*, *Allepus* made their first appearance during the Baodean, and *Democricetodon*, *Proscipheus*, *Leptodontomys*, *Microdyromys*, and *Miodyromys* had their last appearance there (Qiu Zhaxiang et al. 2013: 65).

**Kholu** (loc. nr. 7)

Location of the site: southeast Russia, southern part of the Republic of Tuva (part of the Russian Federation), right bank of the Kholu River, northern slope of the Ubsunur Depression at the foot of the Tannu Ola mountain (Devyatkin et al. 1968, Zazhigin and Lopatin 2001).

Other names: Southern Tuva (Gromov and Polyakov 1977).


Age: Devyatkin et al. (1968) compared *Microtus* cf. *atavus* (small) from bed 5 of Kholu with *Microtus* from Ertemte which corresponds to MN 13 (see above). Zazhigin et al. (2002) referred the site to MN 13/14 based on the range of *Lophocricetus perpusillus* given by them as MN 13 – MN 14. However, the MN 14 record used by them is from Hyargas-nuur 2, which is actually of MN 13 age.

Remarks: Southern Tuva was considered as the type area of **Microtus tjuvanensis** Zazhigin in Gromov et Polyakov, 1977, also named by some authors (Mats et al. 1982) *M. tjuvanensis*. The species name is a nomen nudum because the statement in Gromov and Polyakov (1977) is: "Size larger than preceding species: Islands absent on M1 in material available". In our opinion, this cannot be considered as a diagnosis. *M. tjuvanensis* is so far neither described nor figured in literature.

**Sarayskoe** (loc. nr. 8)

Location of the site: in the literature also as Olkhon Island; south east Russia, Irkutsk region, Olkhon district, Saray Bay of Baikal Lake.
There are two faunas considered, one in the upper part of the sequence: Odonim member = member B in Mats et al. (1982) = Olkhon 2 in Zazhigin and Zykyn (1984), and one in the lower part: Saray member = member A in Mats et al. (1982) = Olkhon 1 in Zazhigin and Zykyn (1984).

Fauna: 1(Pokatilov in Mats et al. 1982), 2(Erbaeva and Alexeeva 1997):

Odonim member (Odonim Faunistic complex, section 1, horizon 5 – Erbaeva and Alexeeva 1997): Microtoscopes praetermissus2, Microtoscopes cf. tjuvanensis3, associated with Soricomorpha: Soricidae: Sorex sp.1, Lagomorpha: Ochotonidae: Lophocricetus tjuvanensis2, Lophocricetus minuscilus1, Soricidae: Soricidae indet. 3, Lagomorpha: Arvicolinidae: Microtus sp. (Pevzner et al. 1983). However, the age of Cherevychne is well correlated with the Pavlodar material collected by Delinschi 2014 because of the occurrence of Dipoides sp., Lophocricetus cf. grabaudi, Scirtodipus sp. (Pevzner et al. 1982, 1983). Scirtodipus, Lophocricetus, and Microtoscopes are more highly evolved in the younger, upper (24 m) assemblage than in the older layers (18–22 m) (Pevzner et al. 1983).

Remark: Microtoscopes mongolicus Zazhigin in Pavlov et al., 1982 first mentioned from Hyargas-nuur 2/ lower layers (18–22 m), is a nomen nudum, since it was not described, figured, or diagnosed or was a type specimen designated.

Kazakhstan
Petropavlovsk (loc. nr. 10)

Location of the site: North Kazakhstan region, Right bank of the Ishym River near the town of Petropavlovsk (now Petropavl); site with Microtoscopes is named Petropavlovsk 1A by Zazhigin et al. (2002).


Age: Savinov (1982, 1988) assigned Petropavlovsk to the Meotian (= MN 12 + early MN 13). Later, some authors (Zazhigin et al. 2002, Delinschi 2014) referred Petropavlovsk 1A to MN 10 based on the occurrence of Ischymomys. However, Ischymomys, a rare fossil, is dated in sites other than Petropavlovsk to MN 10 and MN 11 (Fejar et al. 2011). Zazhigin et al. (2002) implied a range of Lophocricetus minusculus from MN 10 and MN 11 from its (only) two records: Petropavlovsk and Cherevychne (the latter with L. maeoticus, considered as a synonym of L. minusculus). However, the age of Cherevychne is well constrained by several taxa to MN 12, and therefore the LAD of L. minusculus should be in this zone. Thus a referral of Petropavlovsk to MN 11 (Nicoara 2013) seems to be most reasonable.

Remarks: Petropavlovsk is the type locality of Microtoscopes pristinus Savinov, 1982. According to the description and figures in Savinov (1982, 1988), it clearly differs from M. praetermissus in that m3 and M3 are hardly reduced.

Pavlodar (loc. nr. 11)

Location of the site: North east Kazakhstan, Pavlodar region; several localities in the city of Pavlodar (Zazhigin and Zykyn 1984). The Pavlodar material collected by Savinov in 1970 (here the fauna ‘Pavlodar’) contains small mammals (Savinov 1970), but Microtoscopes had

Mongolia
Hyargas-nuur 2 (loc. nr. 9)

Location of the site: Western Mongolia, Uvs province, Hyargas (or Khargas) district, northern bank of Hyargas-nuur Lake. Small mammal samples originate from different levels of a sequence, where geological and palaeomagnetic investigations were carried out (Pevzner et al. 1982, 1983).

Other names: Khirgis-Nur (Zazhigin and Lopatin 2001).

Fauna: (Pevzner et al. 1982, 1983):

not yet been reported in this 1970 paper. The material of “Pavlodar 1A” was collected by Zazhigin in 1963–1965, and 1976. The faunal remains obtained in 1980 come from a bone-bearing lens in the upper part of middle layers of the Pavlodar Formation on the right bank of the Irtys River, in the outskirts of the city (= Gusinnyj Perelet) (Storch and Zazhigin 1996, Zazhigin and Lopatin 2000, Zazhigin 2006).


Pavlodar: Microtoscopites praetermissus, Microtoscopites sibiricus, associated with Erinaceomorpha: Erinaceidae: Erinaceus sp.1,3,4, Soricomorpha: Soricidae: Similisorex orlovi1,3,4, Crocidura pavlovatica1,3,4, Chirotecta: Chirotecta indet.1, Lagomorpha: Ochotona: Ochotona cf. eximia1,3,4, Rodentia: Sciuridae: Eutamias sp.1,3 (unclear if identical with the record of Tamias sp.1), Gliridae: Gliridae indet.1,3,4, Dipodidae: Prolaactaga sp.1, Sisicista bagajevi1,3,4, Lophocricetinae vinogradovi1,3,4, Brachyctereutes robustus1,3,4, Scirtodipus kazakhstanica1,3,4, Paralactaga variani1,4, Cricetidae: Cricetinae indet. (5 spp.), Kowalskaia aff. magna1,4, Kowalskaia sp.1,4, Ruscinomysinae indet.1,4, Rhinocerodon n. g. (nomen nundinum1, but later re-erected).

Pavlodar 1A (Gusinnyj Perelet): Microtoscopites sp.2, associated with Erinaceomorpha: Erinaceidae: Hemiechinus sp.1, Soricomorpha: Soricidae: Paranoerusorex sp.1, Petenia sp.1, Paenelmnomus sp.1, Lagomorpha: Ochotona: Prochochotona sp.1,3,4, Rodentia: Soricidae: Sciurotaxonomas sp.1, Gliridae: Myomimus sp.2, Dipodidae: Lophocricetinae vinogradovi1, Sisicista bagajevi1,3,4, Scirtodipus kazakhstanica1,3,4, Brachyctereutes robustus1,3,4, Allactaga variani1,4, Cricetidae: Cricetinae indet.1,4, Kowalskaia aff. magna1,4, Kowalskaia sp.1,4, Ruscinomysinae indet.1,4, Rhinocerodon n. g. (nomen nundinum1, but later re-erected).

Age: Pontian (Savinov 1988) (= late MN 13). Later the mammals from Pavlodar 1A (Gusinnyj Perelet) were referred to MN 12 (Zazhigin et al. 2002, Zazhigin 2003), 3(Zazhigin 2006), 4(Microtoscopites sp.1,4, associated with Erinaceomorpha: Erinaceidae: Hemiechinus sp.1,4, Soricomorpha: Soricidae: Desmana sp.1,4, Soricidae: Paranoerusorex selentiensis1,4, Petenia sp.1,4, Sorex sp.1,4, Paenelmnomus sp.1,4, Lagomorpha: Ochotona sp.1,4, Leporidae: Viterilepus sp.1,4, Rodentia: Sciuridae: Sciurotaxonomas sp.1,4, Castoridae: Castoridae indet.1,4, Dipodidae: Lophocricetinae vinogradovi1,4, Lophocricetinae minusculus (= maeoticus1, Sisicista sp.1,4, Pliosiscritopoda antiqua1,4, Jaculus sibiricus1,4, Brachyctereutes sp.1,4, Allactaga variani1,4, Allactaga sp.1,4, Muridae: Hangeidusuijinicae cf. neutrum1,4, Cricetidae: Pseudocricetinae sp.1,4, Stylocricetinae meoticus1,4, Kowalskaia sp.1,4, Anatolomys sp.4, Rhinocerodon selentensis1,4, Epimeriones sp.1.

Age: The association of Lophocricetinae vinogradovi with Paranoerusorex selentiensis allows dating this site as the early part of MN 13 (Storch and Zazhigin 1996, Zazhigin 2003). The referral to MN 13 is consistent with the FAD of Viterilepus (MN 11) and the range of Pseudocricetinae (MN 12 – MN 13) (Mein 1999).

Kedej 1A (loc. nr. 14)

Location of the site: Northwest Kazakhstan, Aqtobe region, on the right bank of Kedej (= Kedej) River downstream of Kzylta, stratotype of Kedej Formation (Zazhigin 2006).


Age: Zazhigin’s (2006) assignment to MN 13 is in agreement with the FAD of Viterilepus (MN 11) and the range of Pseudocricetinae (MN 12 – MN 13) (Mein 1999).

Makovka (loc. nr. 15)

Location of the site: East Kazakhstan region, 40 km east of Qalbatau, near the village Makovka.

Fauna: 1(Savinov 1988), 2(Zazhigin et al. 2002): Microtoscopites praetermissus, associated with Erinaceomorpha: Erinaceidae: Erinaceus sp.1, Soricomorpha: Soricidae indet.1, Beremendia sp.1, Lagomorpha: Ochotona: Ochotona ex gr. eximia1, Ochotona ex gr. eximia-gigas1, Ochotonaoides sp.1, Rodentia: Sciuridae: Tamias sp.1, Gliridae: Dryomys sp.1, Dipodidae: Lophocricetinae afanasiyevi2, Paralactaga sp.1, Scirtodipus kalbica1, Cricetidae: Cricetodon sp.1, Cricetinae

Seley 1A (loc. nr. 13)

Location of the site: Northern Kazakhstan, Akmolinsk region, Akkol’sk district, left bank of Seley River, 4–5 km upstream from village Il’inka. Small mammals were found everywhere, mostly in the upper part (Seley 1A) (Storch and Zazhigin 1996, Zazhigin and Lopatin 2001, Zazhigin et al. 2002, Zazhigin 2006).

Fauna: 1(Savinov 1988), 2(Zazhigin et al. 2002), 3(Zazhigin 2003), 4(Zazhigin 2006): Microtoscopites sp.1,4, associated with Erinaceomorpha: Erinaceidae: Hemiechinus sp.1,4, Soricomorpha: Soricidae: Desmana sp.1,4, Soricidae: Paranoerusorex selentiensis1,4, Petenia sp.1,4, Sorex sp.1,4, Paenelmnomus sp.1,4, Lagomorpha: Ochotona sp.1,4, Leporidae: Viterilepus sp.1,4, Rodentia: Sciuridae: Sciurotaxonomas sp.1,4, Castoridae: Castoridae indet.1,4, Dipodidae: Lophocricetinae vinogradovi1,4, Lophocricetinae minusculus (= maeoticus1, Sisicista sp.1,4, Pliosiscritopoda antiqua1,4, Jaculus sibiricus1,4, Brachyctereutes sp.1,4, Allactaga variani1,4, Allactaga sp.1, Muridae: Hangeidusuijinicae cf. neutrum1,4, Cricetidae: Pseudocricetinae sp.1,4, Stylocricetinae meoticus1,4, Kowalskaia sp.1,4, Anatolomys sp.4, Rhinocerodon selentensis1,4, Epimeriones sp.1.

Age: The association of Lophocricetinae vinogradovi with Paranoerusorex selentiensis allows dating this site as the early part of MN 13 (Storch and Zazhigin 1996, Zazhigin 2003). The referral to MN 13 is consistent with the FAD of Viterilepus (MN 11) and the range of Pseudocricetinae (MN 12 – MN 13) (Mein 1999).
indet., *Ichsymomys kalbica*1, Spalacidae: Myospalacinae: *Prosinphilus sp.*, Muridae: Murinae indet.¹.

Age: The referral of the site to MN 13 (Zazhigin et al. 2002) based on the record of *Lophocricetus afanasievi* is in contradiction to Savinov (1988), who placed the site in the Kimmerian (MN 14 and MN 15). *Ochotona eximia* is known since MN 12 or even MN 11 (Cermák 2010). Problematic is the record of *Ochotonoides*, which appears according to Wu and Flynn (2017a) only in the Pliocene.

Remarks: The species *Ichsymomys kalbica* has only been mentioned in an unpublished thesis (Mos’kina 1973) and is therefore a nomen nudum.

**Ukraine**

**Cherevychna 3 (loc. nr. 16)**

Location of the site: Southwestern Ukraine, Odessa region, Belyaevskii district, near village Cherevychna, in Lower Meotian gravels.

Other names/spellings: Cherevychnia, Cherevychnoe/nizhnii sloj, Cherevichnoe 3, Cherevychna 3, Avgustovka.


Age: Meotian (Topachevskiy 1971), Belkian faunistic complex ¹ (because of the occurrence of *Pseudocricetus, Lophocricetus*), (Topachevskiy et al. 1997), Belkian complex, Novoelizavetovkian subcomplex correlated with MN 12 (Nesin and Nadachowski 2001). The referral to MN 12 is in agreement with the range of *Schizogalerix* (MN 10 – MN 13), of *Amyeleptus* (MN 11 – MN 13), the FAD of *Alilepus* (MN 12) and the range of *Vasseuromys* (MN 11 – MN 12), *Pseudocricetus* (MN 12 – MN 13), and *Byzantinia* (MN 10 – MN 12) (Mein 1999), the range of *Castromys nadachowskii* and *Apodemus barbara* (Nesin and Storch 2004, Nesin 2013). In the opinion of Zazhigin et al. (2002), *Lophocricetus minuscilus* is confined to MN 10 – MN 11, which would indicate an older age of Cherevychna, but would be in disagreement with the occurrence of *Alilepus*, and of *Pseudocricetus* (see above).

**Protopopovka 3 (loc. nr. 17)**

Location of the site: Southwestern Ukraine, Odessa region, Belyaevskij district, south of the village Protopopovka.


Age: Belkian faunistic complex, Belkian subcomplex (terminal part of MN 12) (Nesin 2013). The dating is in agreement with the range of *Vasseuromys* (MN 11 – MN 12) and *Pseudocricetus* (MN 12 – MN 13) (Mein 1999, Sinitsa in litt. 2015).

**Verkhnya Krynynska (loc. nr. 18)**

Location of the site: Southeastern Ukraine, Zaporizhia region, Vasylivka distric.


**Vasylivka 1 (loc. nr. 19)**

Location of the site: Southeastern Ukraine, Zaporizhia region, Vasylivka district.

Fauna: Only *Microtoscopes sp.*

Age: For the moment, a firm age referral is not possible, since no other stratigraphically significant small mammals are known.

**Lobkove (loc. nr. 20)**

Location of the site: Southeastern Ukraine, Zaporizhia region, Vasylivka district.

Age: The age of the Lobkove site is uncertain. Considering the range of *Petenyia dubia* (MN 9 – MN 14: Rzebik-Kowalska and Rekovets 2016), the FAD of *Ochotonata eximia* (MN 11: Čermák and Rekovets 2010), and the range of *Trogotherium minutum* (MN 3 – MN 15: Hugueney 1999), the Lobkove locality belongs into the interval MN 11 to MN 14. Note that the finds of *Trogotherium minutum* were previously referred to as *Trogotherium minus* by Rekovets and Pashkov (2009).

**U.S.A.**

**Rome (loc. nr. 21)**

Location of the site: U.S. State of Oregon, Malheur County (Paleobiology Database = PBDB2).

Other names: CIT 62; USGS M1078 (PBDB op. cit.).


Age: Early Hemphillian (Repennig 1987); late Clarendonian based on AEO results (PBDB op. cit.).

Remarks: Rome is the type locality of *Goniodontomys disjunctus* Wilson, 1937.

**Bartlett Mountain (Loc. 2517) (loc. nr. 22)**

Location of the site: U.S. State of Oregon, Harney County; Tuff Sandstone Member (Drewsey Formation) (PBDB3).

Other names: Bartlett Mountain local fauna (Lindsay 2008, code PN11B), UO 2239 (= CIT 107), 2339, 2355, 2356, 2357, 2358 (PBDB op. cit.).


Age: Early Hemphillian (Repennig 1987); late Clarendonian based on AEO results (PBDB op. cit.).

Remarks: Rome is the type locality of *Goniodontomys disjunctus* Wilson, 1937.

**Bartlett Mountain (General) (loc. nr. 23)**

Location of the site: U.S. State of Oregon, Harney County, from Tuff Sandstone Member (Drewsey Formation) (PBDB4).

Other names: Bartlett Mountain local fauna (Lindsay 2008, code PN11B*), UO 2451 (PBDB op. cit.), PN13 – Juniper Creek Canyon (Lindsay 2008).


Age: Early Hemphillian (Repennig 1987); late Clarendonian based on AEO results (PBDB op. cit.).

Remarks: Taxonomic list cited from PBDB is lightly revised from Shotwell (1963, 1970).

**Juniper Creek (loc. nr. 24)**

Location of the site: U.S. State of Oregon, Malheur County (PBDB5).

Other names: UO 2451 (PBDB op. cit.), PN13 – Juniper Creek Canyon (Lindsay 2008).


Age: Early late Hemphillian (Hh 2) (PBDB op. cit.).

**Little Valley (loc. nr. 25)**

Location of the site: U.S. State of Oregon, Malheur County, from Chalk Butte Formation (PBDB6).


Age: Early Hemphillian (Repennig 1987), late early Hemphillian (Hh 2 – NB previously Hh 1) (Lindsay 2008); K-Ar 1225 of Evernden et al. (1964): 8.9 Ma basalt ca. 180 m below fauna (Repennig 1987).

Remark: Repennig (1987) reported from this site Paramicroscopites hibbardi instead of *Goniodontomys disjunctus*.

**Stroud Claim (loc. nr. 26)**

Location of the site: U.S. State of Idaho, Gooding County, Hole-in-the-wall Diatomite Formation (PBDB7); Stroud Claim (Lindsay 2008, code PN22).

2 http://fossilworks.org/bridge.pl?ia=collectionSearch&collection_no=188006
3 http://fossilworks.org/bridge.pl?ia=collectionSearch&collection_no=18935
4 http://fossilworks.org/bridge.pl?ia=collectionSearch&collection_no=18944
5 http://fossilworks.org/bridge.pl?ia=collectionSearch&collection_no=188007
6 http://fossilworks.org/bridge.pl?ia=collectionSearch&collection_no=18806
7 http://fossilworks.org/bridge.pl?ia=collectionSearch&collection_no=18935

**Age:** Early Hemphillian (Repenning 1987), early – late Hemphillian (Hh 1-2) (Lindsay 2008).

Remarks: According to PBDB (op. cit.), Evernden et al. (1964): sample K-Ar 830 dated at 10.0 (resp. 10.27) Ma on an “associated” volcanic ash, the age of which is dismissed by Repenning (1987) on biochronological grounds, and another sample from a nearby Mount Bennet Hills “Banbury” ash was dated at 13.5 (± 13.86) ± 1.5 Ma by Armstrong et al. (1975), who considered both of these dates unreliable.

**Kelley Road local fauna (loc. nr. 27)**

Location of the site: U.S. State of Wyoming, Teton County, from Teewinot Formation (PBDB8); named as Kelley Road fauna by Hibbard (1970).

Other names: Jackson (Repenning 1987), Kelley Road local fauna (Lindsay 2008, code CP58), Kelley Road local fauna at Jackson Hole (Fejfar et al. 2011), T56-18; USGS 20766 (PBDB op. cit.).


**Age:** Early Hemphillian (Repenning 1987), early Hemphillian (Hh 1) (Lindsay 2008); a K-Ar date of 9.2 Ma ± 1.5 Ma by Armstrong et al. (1975).  

**Moonstone Formation (loc. nr. 28)**

Location of the site: U.S. State of Wyoming. Scott (2002) reported *Goniodontomys disjunctus* from upper Miocene Moonstone Formation in central Wyoming consisting of sandy, generally fine-grained sediments, soils, and air-fall tufts. “These strata yield the diagnostic Late Miocene mammals *Pliocnictis ogygia*, *Copemys pisinus*, *Phelosaccomys hibbardi*, *Promolagus albus*, and *Goniodontomys disjunctus*, indicating late Barstovian to early Hemphillian ages. The biostratigraphic ages of the faunas are supported by two U-Pb zircon radiometric dates of 11.30 ± 0.48 and 8.39 ± 0.24 Ma from interbedded ashes”. *Goniodontomys* occurs only in the upper part of the section; Prothero et al. (2008) discuss the older Barstovian-Clarendonian part of the sequence, which lacks *Goniodontomys*.

**Lemoyne Quarry (loc. nr. 29)**

Location of the site: U.S. State of Nebraska, Keith County from Ash Hollow Formation, Ogallala Group (PBDB9).

Other names: Lemoyne (Repenning 1987), UNSM Kh-101; UW V-69015 (PBDB op. cit.).


**Age:** Early Hemphillian (Repenning 1987).

Remarks: Lemoyne quarry is the type locality of *Paramicrotoscoptes hibbardi* (Martin 1975).

**Feltz Ranch (loc. nr. 30)**

Location of the site: U.S. State of Nebraska, Keith County (PBDB16).

Other names: Feldt Ranch (PBDB op. cit.), CP116C*, Lemoyne local fauna, and Ogallala Beach local fauna (Lindsay 2008).

Age: Early Hemphillian (Hh 1) (Lindsay 2008), overlies ash dated at 8.0 ± 0.7 Ma FT on glass (PBDB op. cit.).


**Cambridge (loc. nr. 31)**

Location of the site: U.S. State of Nebraska, Frontier County, Ash Hollow Formation (PBDB11).

Other name: *Amelobolodon fricki* Quarry (PBDB op. cit.).


Age: Hemphillian.

**Rick Irwin Site (loc. nr. 32)**

Location of the site: U.S. State of Nebraska, Keya Paha County, from “channel”; un lithified sandstone and un lithified conglomerate (PBDB12).

Other names: RIS, Wyman Creek (PBDB op. cit.), Rich Irwin Site, Wyman Creek local fauna (Lindsay 2008, code CP116III).


Age: Early late Hemphillian (Hh 3) (Lindsay 2008).

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8 http://fossilworks.org/bridge.pl?a=collectionSearch&taxon_no=41779&max_interval=Miocene&country=United States&state=Wyoming&is_real_user=1&basic=yes&taxonomy=node&pe=view&match_subgenera=1
9 http://fossilworks.org/bridge.pl?a=collectionSearch&collection_on_no=18225
10 http://fossilworks.org/bridge.pl?a=collectionSearch&collection_on_no=18158
11 http://fossilworks.org/bridge.pl?a=collectionSearch&collection_on_no=18086
12 http://fossilworks.org/bridge.pl?a=collectionSearch&collection_on_no=35430
Rabbit Hole (loc. nr. 33)

Location of the site: U.S. State of Nevada, Pershing County (Repenning 1987), early Hemphillian (Hh 1) (Lindsay 2008).


Age: Early Hemphillian (Repenning 1987).

Discussion

Late Cenozoic deposits with remains of Microtoscopini are widespread in the Northern Hemisphere. So far, the 33 known sites are located in Central Asia (15), Eastern Europe (5), and North America (13) (Text-fig. 1). The northern limitation of records reflects a general absence of Neogene localities in Eurasia north of about 54° N. Also in North America all Late Miocene sites are restricted to latitudes south of about 55° N (Dawson 1999). Microtoscopini do not occur south of 41° in Asia, of 46° in Europe and of 40° in North America. Although there are numerous (>40) Late Miocene – Pliocene sites in China (Qiu Zhanxiang et al. 2013), only localities on the Mongolian Plateau (Inner Mongolia) have yielded Microtoscopites, whereas in Miocene sites of Yushe Basin, Shanxi Province (south of Inner Mongolia) fossils of this genus have not been found (Wu and Flynn 2017b). In Mongolia and Kazakhstan there are no other Late Miocene sites apart from the aforementioned ones with Microtoscopites. In the Ukraine two Microtoscopites-bearing sites occur in the surroundings of Odessa, but others of similar age and in close vicinity to these localities lack this taxon (Nesin 2013). Three other sites with Microtoscopites are situated on the banks of the Kakhovka reservoir of the Dnieper River where no other faunas of this age were found. This distribution pattern could mean that the occurrence of Microtoscopites is linked to particular geographic areas, as well as to special ecological conditions.

Hibbard (1970) recognised that all North American Microtoscopini specimens were associated with beavers, sometimes accompanied by further semiaquatic species, and concluded that these animals preferred aquatic habitats. Fahlbusch et al. (1983a) suggested from the Ertemte fossil assemblage a palaeoenvironment which is different from the recent typical steppe environments of Inner Mongolia. Many of the small mammals recorded in the aforementioned Late Miocene deposits are indicative of larger water bodies and dense vegetation. However, Fahlbusch (1987) hesitated to imply a general adaptation of all Eurasian Microtoscopites to aquatic habitats. Considering the variety of Microtoscopites-bearing sites, Fejfar et al. (2011) suspected that these small mammals inhabited moist riparian or paludal environments where they fed on reed leaves. The faunal lists above – often with beavers, and other animals adapted to moist or even aquatic conditions – seem to confirm that the Microtoscopini indeed required rather moist habitats and proximate water bodies.

Stratigraphically (Text-fig. 2), known Asian records of Microtoscopini are all Late Miocene in age (MN 11, possibly MN 10, to MN 13). The range of Microtoscopites in China is MN 10 or MN 11 – MN 13, in Russia and Mongolia MN 13, and in Kazakhstan possibly MN 11 – MN 13. In the Ukraine, the only European Microtoscopites records seem to be correlated with MN 12, but for some sites (Vasilivka 1 and Lobkove) a younger age cannot be excluded.
**Microtoscopites pristinus** from Petropavlovsk is morphologically more primitive than *M. praetermissus* from Ertemte 2 (Savinov 1982, 1988) which confirms the relative stratigraphic position of the two sites. From the range of the remaining species (disregarding their validity) *M. tjuvanensis*, *M. mongolicus*, and *M. sibiricus* we cannot recognize a temporal significance, since they overlap with the ranges of the type series of *M. pristinus* and of *M. praetermissus* (Text-fig. 2).

The North American genera *Paramicrotoscopites* and *Goniodontomys* (Repenning 1987, Repenning et al. 1990) are also all dated to the Late Miocene, more specifically the Hemphillian. Records of *Paramicrotoscopites* from the Clarendonian have not been confirmed (Repenning 1987). A tooth fragment from the Clarendonian Black Butte local fauna of Oregon, which was originally referred to as *Microtoscopites* sp. (Shotwell 1970) is likely a heteromyid (Repenning 1987). According to Lindsay (2008: 475, fig. 27.3), *Paramicrotoscopites* and its close relative *Goniodontomys* appeared at the beginning of the early Hemphillian (Hh 1) for the first time. *Paramicrotoscopites* became extinct before the early late Hemphillian (Hh 3), whereas *Goniodontomys* survived at least into the early late Hemphillian (Hh 3). This paper (see Text-fig. 2) supports the view of Lindsay (2008). However, following Tedford (1987: 218), *Goniodontomys* did not appear before the late early Hemphillian (Hh 2). This view was maintained, when Tedford et al. (2004) included small mammals to characterise the base of the Hemphillian, for which they used the FADs of *Paramicrotoscopites*, the desmanine *Lemomynea*, the nectogaline shrew *Crusafontia*, the rabbit *Hypolagus vetus*, the beaver *Dipoides*, the comyid *Kansasimys*, the cricetodontine *Plutomodon*, the geomyid *Pliosaccomys*, and the sigmodontine *Paronychomys*. The late early Hemphillian (Hh 2) is defined in Tedford et al.

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**Text-fig. 2.** Stratigraphic ranges of Microtoscopini-bearing sites. Correlation of ELMA and NALMA with earth years is according to Hilgen et al. (2012). Localities of very broad stratigraphic range (e.g., the entire Turolian or Hemphillian, as for Vasilivka 1, Lobkove, Little Valley, Cambridge), do not contribute to detail the range, and are omitted in this figure.
(2004) by the FADs of *Goniodontomys* and *Dipoides stirtoni* and the LADs of *Hystricops* and *Leptodonotomys*.

It is not yet clear, on which continent Microtoscopini originated. No cricetid is known as the potential ancestor of *Microtoscopites* – neither in Eurasia nor in North America. Fahlbusch (1987) considered *Microtoscopites praeterrmissus* as the most primitive form because of its short upper and lower third molars, which, according to a general trend, should have become elongated during evolution. However, Koenigswald (in Fahlbusch 1987) investigated the Schmelzmuster of the three genera of Microtoscopini and found that in *Paramicrotoscopites* this structure is more primitive. In addition, only *Paramicrotoscopites* retains enamel islets (Martin 1975), which also indicate its more primitive state. This would imply an evolutionary trend in Microtoscopini towards length reduction of m3/M3. It is difficult to discern the oldest representative of Microtoscopini. These difficulties are mainly due to uncertainties and inconsistencies of the correlations of European, North American, and Chinese Land Mammal Ages, as well as the Paratethys stratigraphy and geochronology. As Text-fig. 3 shows, considerations of age and correlation vary during the previous decades. Here we use for the comparison of Eurasian and North American faunas the most updated version of the Geological Time Scale (GTS) (Hilgen et al. 2012).

The oldest records of Microtoscopini in Eurasia originate from Shala, which is probably 8 to 9 Ma, MN 10 or MN 11 in age; those in North America, from the beginning of the Hemphillian (Hh 1), roughly correlating to the same age. Only the Kelley Road local fauna and Feltz Ranch are referred exclusively to Hh 1, whereas Rome, Stroud Claim, Rabbit Hole and Lemoynne Quarry are dated to Hh 1 – Hh 2. The lower boundary of MN 10 is at around 9.4 Ma (Steininger 1999), that of Hh 1 at approx. 9 Ma (Repenning 1987, Repenning et al. 1990, Tedford et al. 2004, Woodburne 2004, Lindsay 2008). However, since it is not clear whether the considered records are at or close to the lower boundary of either stage (MN 10 and Hh 1), it is impossible to determine which is the oldest record.

The youngest records of Microtoscopini seem to be those dated to MN 13 (not considering the uncertainties of the ranges of Vasilivka 1 and Lobkove), the upper boundary of which is at 4.9 Ma. Therefore, according to present knowledge, the maximum global range of Microtoscopini is 9.0–4.9 Ma.

Regardless of the question about the oldest finds of Microtoscopini, the very similar morphology of Eurasian *Microtoscopites* and North American *Paramicrotoscopites* and *Goniodontomys* suggests an intercontinental exchange of Microtoscopini between northern Asia and North America. That is, Microtoscopini must have crossed Beringia at least once between MN 10 and MN 13.

According to Dawson (1999), throughout the Miocene, the Holarctic was essentially a single, huge biogeographic province, with Beringia acting as a filter to faunal exchange. At least in Early Miocene, Beringia was a productive forested area (intermittently with a steppe belt at its margins), but during cool phases faunal elements were obligated to shift their ranges southwards (Dawson 1999).

Qiu and Li (2003) state that the rodent faunal exchange between Asia and Europe was always larger than with North America. In the Early Miocene China and Europe had 8 rodent genera in common, China and North America 3, in the Middle Miocene the ratio is 8/5, in the Late Miocene 24/7, and in the Pliocene 25/4 (Qiu and Li 2003). This pattern shows that the dispersal of rodents between Asia and North America reached its peak during the Late Miocene, and then declined.

Repenning (2001: 28) argued that, based upon the most primitive microtine lineages, nearly all dispersing microtines were of Eurasian origin, but *Microtoscopites* (considered by Repenning as a North American element), dispersed to Eurasia, apparently at the time when the “first Eurasian microtine immigrant, *Promimomys*, entered North America in the Late Miocene, but no records are well dated”. However, the oldest records of Microtoscopini both from Eurasia and North America are much older than the first records of *Promimomys* – thus, coincidence is rather unlikely.

According to (Dawson 1999) the filtering effect of Beringia was especially strong during the Late Miocene for mammals adapted to warm environments. Increased provincialism of mammalian faunas accompanied the increased temperature gradient of the later Cenozoic, as northern areas became colder, and southern areas acquired more distinctively faunas.

Implying from the appearance of the Atlantic-Arctic bivalve mollusc *Astarte* in sediments of the North Pacific Basin, the Bering Strait opened not earlier than the Late Miocene. The minimum age of *Astarte* immigration from the Arctic is 4.8–5.5 Ma based on diatoms of well-established age (Marincovich and Gladenkov 1999, 2001, Sher 1999). The maximum age of the first opening is considered to be at 7.2 Ma (Marincovich and Gladenkov 2001), which is late MN 12. Based on her study of diatoms from North Chukotka, Polyakova (cited in Sher 1999) postulates a much older Arctic-Pacific marine connection: around 16–17 Ma, and periodically again since the end of the Middle Miocene (11–12 Ma). However, the Chukotka record, lacking molluscs, is still open to debate (Sher 1999).

There are indications for several major dispersals of terrestrial mammals from North America to Eurasia: at about 11 Ma hipparionine horses and odocoileine cervids, in the latest Miocene, the first Canidae, the Eucyon dogs and the camelid *Paracamelus* coinciding with interval when essential changes of environment and climate occurred (Dawson 1999, Vishlubokova et al. 2003). Another dispersal wave in the Late Miocene might provide the “Leporid datum” (Flynn et al. 2014). *Allepus* dispersed to northern Asia around 8 Ma (MN 12), since it is in Eurasia nowhere certainly more than ~8 Ma (Flynn et al. 2014). Currently we therefore neither know the time of the expected Eurasian-American dispersal of Microtoscopini nor do we know the factors concerning its beginning and termination (opening of the Bering Strait or climatic change).

It is striking that the distribution of localities of Microtoscopini especially in Eurasia matches with the extant grassland biome in Text-fig. 4. This is obviously not the same vegetation type as it was in the Late Miocene. The development of steppe biomes in Eurasia is linked to increasing aridification during the Late Miocene, which began at about 8–7 Ma in the interior of central Eurasia (Liu
et al. 2016) and is detected in western Eurasia viz Eastern Europe (e.g., Ukraine) only after the Tortonian (Bruch et al. 2011). The drivers of this development are widely discussed: Besides the general cooling trend of the late Neogene, which causes a decrease in water availability in the atmosphere, also palaeogeographic changes including the uplift of the Tibetan Plateau and the retreat of the Paratethys Sea, as well as possible vegetation-climate feedbacks due to the expansion of C4 plants, likely contributed (Miao et al. 2012, Liu et al. 2016) to this process. In North America,
the Late Miocene opening of the landscape in the interior of the continent is accompanied by a sharp increase in C4 vegetation after 7 Ma (Cerling et al. 1997, Strömberg and McInerney 2011), which might have been forced by the opening of the Bering Strait (Marincovich and Gladenkov 2001). However, the detailed temporal and spatial patterns of the aridification process remain unresolved. Because the climate is imprecisely known, it is not possible yet to infer from the distribution points climatic or ecological requirements of the palaeofauna, nor of the reasons of their spread and extinction.

The extinction of Microtoscopini also remains obscure. Theoretically they could have been outcompeted by arvicoline rodents that were better adapted to dry or moist steppe conditions. What do the records say? Goniodontomys coexisted for some time with the early arvicoline rodent Promimomys that invaded from Eurasia to North America during the late Hemphillian (Hh 3) at 6.7 Ma and survived there up to 5.8 Ma (Repennig 1987, Martin 2008: 491, fig. 28.3, Lindsay 2008: 475, fig. 27.3, Tedford et al. 2004). The temporal range of Goniodontomys is 9.0–5.8 Ma, that of Paramicrotoscopites 9.0–6.7 Ma (Lindsay 2008: 475, fig. 27.3). The LAD of Goniodontomys coincides with the LAD of Promimomys and with the FAD of the first endemic North American arvicoline Protoptilophenacomys at 5.8 Ma (Martin 2008: 491, fig. 28.3, Lindsay 2008: 475, fig. 27.3), the temporal range of which ends at 5.0 Ma in the Pliocene (early Blancan: Martin 2008). It is noteworthy that a joint occurrence of Microtoscopini (Microtoscopites) and early arvicoline rodents (Promimomys) is hitherto unknown from the Late Miocene of Eurasia. These differences need further investigation. Competition with arvicolids does not seem to be the main reason, since in several Eurasian sites (Ertemte, Olan Chorea, Harr Obo, Bilutu, Kholu, Sarayskoe, Hyargas-nuur) Microtoscopites co-existed with Microtodon – one of the old vole-like cricetid rodents. However, another factor might be that Microtoscopini were ecologically too specialised and could not cope with changes in climate and landscape.

Conclusion

The present paper is a current outline of the spatial and temporal distribution of Microtoscopini – one of the most fascinating branches of microtoid cricetids, which is considered to be different from but closely related to arvicolines.

Although the fossil record of Microtoscopini is rather sparse, the presented compilation improves our knowledge compared to previous considerations. We were able to compile 33 records of this group, which are confined to the Late Miocene of Central Asia, Eastern Europe and North America. Records are lacking from the more western parts of Europe, the fossil record of which is rather well known (various authors in Rössner and Heissig 1999). Therefore the pattern of records probably reflects their real western distribution boundary on the European continent.

Previously the range of Microtoscopini in Eurasia was considered to be MN 13 – MN 14, and in North America

\footnote{Only during proof reading of the present article we got access to the publication Qiu and Li (2016) “Neogene Rodents from Central Nei Mongol, China”. Therefore we could not consider the species Microtoscopites fahlbuschi sp. nov. Qiu et Li, 2016 described in that paper.}

early Hemphillian (approximately MN 11 – MN 12) (Fejar et al. 2011). The present compilation seems to indicate the overall temporal range is MN 10 or MN 11 – MN 13. The earliest record to date could come from Shala (MN 10 or MN 11) in northern China (Microtoscopes), but this is not yet certain, since the oldest finds (Paramicrotoscopes and Goniodontomys) in North America could be of similar age. The FADs in Eurasia and North America cannot yet be determined with sufficient accuracy.

Moreover, even if the referral to particular ELMAs or NALMAs is correct, it remains unclear whether it is from the beginning or the end of the respective zone, whose age might differ by 0.5 to 1.0 million years. Last but not least, a currently oldest record does not automatically indicate the origin, which would require the knowledge of the direct ancestor among cricetids. So far, no potential forerunner of Microtoscopini is known. Therefore the question, whether the Microtoscopini originated in Eurasia or North America remains a topic for further studies.

The fossil record reveals that the Microtoscopini disappeared in North America during the early late Hemphillian (around the middle of MN 13), whereas they survived in Eurasia until the close of MN 13. Further discoveries must clarify whether these data reflect a real difference or only a knowledge gap.

The presence of Microtoscopini both in Eurasia and North America has been used as evidence for dispersal through Beringia during the Late Miocene. Unfortunately, no remains of Microtoscopini have been recorded that could elucidate this faunal interchange in detail. New results about the opening and closing of Beringia Strait could clarify the timing of the dispersal of Microtoscopini.

One of the remaining crucial questions is the detailed phylogenetic relation of Microtoscopini to the arvicolines. Repenning (1968) discussed this issue on the base of the mandibular musculature. He found that in Goniodontomys, masseteric musculature resembles that of other microtoid cricetids, but temporal muscle structure is as in arvicolines. This pattern was observed also in Paramicrotoscopites (Hibbard 1970). However, it is not clear whether this means that Microtoscopini have a common ancestor with arvicolines. Further information is needed from Eurasian finds of Microtoscopes, which is at the moment not available.

This concerns the general problem that most records of Microtoscopini are isolated molars and few of them have been figured in the literature. Mandible fragments are known and documented only from North American localities: 2 mandible fragments from Rome (Wilson 1937), 3 mandible fragments from Kelley Road (Hibbard 1959, 1970), 1 mandible fragment from Stroud claim (Hibbard 1970). All Eurasian finds figured in publications are isolated teeth: 1 m1 from Ertemte 1, 1 m2 from Olan Chorea (Schaub 1934), 40 isolated molars (of >100 listed) from Ertemte 2 and 5 (of 16 listed) from Harr Obo (Fahlbusch 1987), 20 isolated molars from Sarayskoe (Mats et al. 1982), 10 isolated molars from Petropavlovsk (Savinov 1982, 1988). Several species are inadequately diagnosed, described and figured and have to be revised.

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