



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 Microtoscoptini, comprising the genera *Microtoscopes* from Eurasia and *Paramicrotoscopes* 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 Microtoscoptini is still unknown. The currently oldest records are those of *Microtoscopes* 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 *Paramicrotoscopes* and *Goniodontomys* are from the early Hemphillian beginning at 9.0 Ma (approximately MN 10 – MN 11 transition). Whether *Microtoscopes* from Shala actually indicates the origin of Microtoscoptini in Asia and subsequent dispersal to North America is still unclear. The presence of Microtoscoptini in both Central Asia and North America during the Late Miocene does suggest dispersal through Beringia. The Microtoscoptini inhabited probably open grasslands locally differentiated by shrubs, tree patches and water bodies. It is far from clear why the Microtoscoptini became extinct even though they had developed an efficient arvicoline-like cheek-tooth pattern.

Key words: *Microtoscopes*, *Paramicrotoscopes*, *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 Microtoscoptini, 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 Microtoscoptini-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 Microtoscoptini and those of arvicolines (voles) owing to similar adaptations (for a summary, see Fejfar et al. 2011). Also the molars of the Microtoscoptini 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 Microtoscoptini that is not seen in true arvicolids or other branches of microtoid cricetids.

Microtoscopes, confined to Eurasia and the first described genus of Microtoscoptini, 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 and Polyakov 1977, Zazhigin in Pevzner et al. 1982, Savinov 1982, Zazhigin and Zykina 1984). *Goniodontomys* and *Paramicroscoptes* were exclusively distributed in North America during the Late Miocene (Hemphillian) (e.g., Wilson 1937, Hibbard 1970, Repenning 1987, Repenning et al. 1990).

Because *Microscoptes* SCHAUB, 1934, *Goniodontomys* WILSON, 1937, and *Paramicroscoptes* 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 Microscoptinae (Kretzoi 1955), then as a family Microscoptidae (Kretzoi 1969), and later as tribe Microscoptini (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 (*Microscoptes praetermissus* SCHAUB, 1934, *M. tjuvanensis* ZAZHIGIN in GROMOV et POLYAKOV, 1977, *M. pristinus* SAVINOV, 1982, *M. sibiricus* ZAZHIGIN et ZYKINA, 1984, *M. mongolicus* ZAZHIGIN in PEVZNER et al., 1982, *Goniodontomys disjunctus* WILSON, 1937 and *Paramicroscoptes hibbardi* MARTIN, 1975), the fossil record of the Microscoptini is far from being satisfactorily investigated, nor even sufficiently documented. Some of these species mentioned have not yet been adequately described and illustrated. Therefore, many aspects of the phylogeny, biostratigraphy and palaeobiogeography of these microtoid cricetids have been remained obscure until today.

For a long time the Microscoptini were to many European paleontologists strange small mammals from the Far East. This view changed in the early 1970s, when a single tooth of *Microscoptes* was unearthed from Late Miocene deposits exposed at the Ukrainian site Cherevychna 3 (Topachevskiy 1971), which showed for the first time that Microscoptini were distributed also in Eastern Europe. Since then further sites have been discovered in the Ukraine that yielded numerous finds of *Microscoptes* 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 Microscoptini (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 Microscoptini known so far. It is complementary to the studies on new material of *Microscoptes* from the Ukraine, the description of which is in preparation. The present paper is devoted to Oldřich 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), Bl – Blancan, Cl – 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 Microscoptini

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 *Microscoptes* 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).

Fauna: Ertemte 1 (Schaub 1934, Fahlbusch et al. 1983a, Qiu and Li 2016): *Microscoptes praetermissus*, associated with Erinaceomorpha: Erinaceidae: *Erinaceus mongolicus*, Soricomorpha: Talpidae: *Yanshuella primaeva*, Soricidae: “*Crocidura*” *kormosi*, Lagomorpha: Leporidae: *Alilepus annectens*, Rodentia: Aplodontidae: *Pseudaplodon asiaticus*, Cricetidae: *Nannocricetus mongolicus*, *Sinocricetus zdanskyi*, *Anatolomys teilhardi*, *Microtodon atavus*, Dipodidae: *Lophocricetus pusillus*, *Lophocricetus grabau*, *Paralactaga anderssoni*, *Brachyscirtites wimani*, *Dipus fraudator*, Spalacidae: Myospalacinae: *Prosiphneus eriksoni*, Muridae: *Karnimatooides hipparionus*, *Hansdebruijnina pusillus*, *Apodemus orientalis*.

Ertemte 2 (Qiu Zhuding et al. 2013, Qiu and Li 2016): *Microscoptes praetermissus*, associated with Erinaceomorpha: Erinaceidae: *Erinaceus mongolicus*, Soricomorpha: Talpidae: *Quyania chowi*, *Yanshuella primaeva*, Soricidae: *Sorex minutoides*, *Sorex ertemteensis*, *Sorex pseudoalpinus*, *Zelceina kormosi*, *Alloblarinella sinica*, *Paenepetenya zhudingi*, *Cokia kowalskiae*, *Paranourosorex inexpectatus*, Lagomorpha: Ochotonidae: *Ochotona lagreli*, *Ochotona minor*, Leporidae: *Alilepus annectens*, Rodentia: Aplodontidae: *Pseudaplodon asiaticus*, Sciuridae: *Eutamias ertemtensis*, *Sciurus* sp., *Prospermophilus orientalis*, *Sinotamias gravis*, *Petinomys auctor*, *Pliopetaurista rugosa*, Castoridae: *Castor anderssoni*, *Dipoides majori*, Gliridae: *Myomimus sinensis*, Eomyidae: *Leptodontomys gansus*, Cricetidae: *Sinocricetus zdanskyi*, *Nannocricetus mongolicus*, *Kowalskia similis*,

Kowalskia neimengensis, *Anatolomys teilhardi*, *Microtodon atavus*, Dipodidae: *Paralactaga suni*, *Brachyscirtetes wimani*, *Dipus fraudator*, *Lophocricetus grabau*, *Paralophocricetus pusillus*, *Sicista* sp., *Eozapus similis*, Spalacidae: Myospalacinae: *Prosiphneus eriksoni*, Muridae: *Orientalomys* cf. *similis*, *Hansdebruijnina pusilla*, *Apodemus orientalis*, *Karnimatooides hipparionus*, *Micromys chalceus*, Gerbillinae: *Pseudomeriones abbreviatus*.

Age: Ertemte 1 and 2 are referred to MN 13 (late Baodean, NMU 11 – Storch and Qiu 1983, Fahlbusch 1987, Qiu 1987, Wu 1991, Qiu and Qiu 1995, Flynn et al. 1997, Qiu et al. 1999, Qiu and Wang 1999, Qiu and Li 2003, Qiu et al. 2003, Qiu and Storch 2005). The dating of Ertemte 1 and 2 into MN 13 is in accordance with the range of *Ochotona lagreli* (MN 9 – MN 14) (Erbaeva et al. 2015, Wu and Flynn 2017a), the FAD of *Castor* in MN 9 (Hugueney 1999), the FAD of *Pliopetaurista* in MN 10, that 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).

Remarks: Ertemte is the type locality of the species *M. praetermissus* SCHAUB, 1934, the type species of the genus *Microscoptes*. Fahlbusch (1987) provided a detailed history of the views on *Microscoptes 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 (Fahlbusch et al. 1983b, Qiu and Li 2016).

Fauna: ¹(Schlosser 1924), ²(Schaub 1934), ³(Čermák et al. 2015), ⁴(Qiu and Li 2016): ***Microscoptes praetermissus***², associated with: Soricomorpha: Talpidae: *Yanshuella primaeva*^{1,4}, Lagomorpha: Ochotonidae: *Ochotona lagreli*¹, Leporidae: *Alilepus annectens*^{1,2,3}, Rodentia: Aplodontidae: *Pseudaplodon asiaticus*¹, Castoridae: *Castor anderssoni*^{1,4}, *Dipoides* cf. *majori*¹, Dipodidae: *Brachyscirtetes wimani*^{1,2}, *Dipus fraudator*^{1,2}, *Lophocricetus grabau*¹, *Paralactaga anderssoni*², Cricetidae: *Microtodon atavus*^{1,2}, Muridae: Muridae indet.¹, Spalacidae: Myospalacinae: *Prosiphneus eriksoni*^{1,2}.

Age: Olan Chorea belongs (as Ertemte) to the Baodean Zone (NMU 11), correlated with the Late Turolian, MN 13 (Qiu et al. 1999, Vislobokova and Lavrov 2009). The range of *Ochotona lagreli* (MN 9 – MN 14) (Erbaeva et al. 2015, Wu and Flynn 2017a), the occurrence of *Dipoides* (FAD MN 11) and of *Alilepus* (FAD MN 12) (Mein 1999) is in agreement with the dating to MN 13.

Remark: The molar of *Microscoptes praetermissus* described from Olan Chorea (Schaub 1934) is an m2 not an M1.

Harr Obo 2 (loc. nr. 3)

Location of the site: Northern China, Inner Mongolia (= Nei Mongol) Autonomous Region, Huade county, east of the town of Huade, 300 m north of the village of Gongweizi (Storch and Zazhigin 1996).

Fauna: According to Qiu Zhuding et al. (2013), the fauna contains ***Microscoptes praetermissus***, associated with Soricomorpha: Talpidae: *Quyania chowi*,

Yanshuella primaeva, Soricidae: *Sorex minutoides*, *Sorex ertemteensis*, *Sorex pseudoalpinus*, *Zelceina kormosi*, *Paenepetenya zhudingi*, *Cokia kowalskae*, *Paranourosorex inexpectatus*, Lagomorpha: Ochotonidae: *Ochotona lagreli*, *Ochotona minor*, Leporidae: *Alilepus annectens*, *Trischizolagus* sp., Rodentia: Aplodontidae: *Pseudaplodon asiaticus*, Sciuridae: *Eutamias ertemtensis*, *Sciurus* sp., *Prospermophilus orientalis*, *Sinotamias gravis*, *Petinomys auctor*, *Pliopetaurista rugosa*, Castoridae: *Dipoides majori*, Gliridae: *Myomimus sinensis*, Eomyidae: *Leptodontomys gansus*, Dipodidae: *Eozapus similis*, *Paralactaga suni*, *Brachyscirtetes wimani*, *Dipus fraudator*, *Lophocricetus grabau*, *Paralophocricetus pusillus*, *Sicista* sp., Cricetidae: *Sinocricetus zdanskyi*, *Nannocricetus mongolicus*, *Kowalskia similis*, *Kowalskia neimengensis*, *Anatolomys teilhardi*, *Microtodon atavus*, Spalacidae: Myospalacinae: *Prosiphneus eriksoni*, Muridae: *Apodemus orientalis*, *Orientalomys* cf. *similis*, *Hansdebruijnina pusilla*, *Karnimata?* *hipparionum*, *Micromys chalceus*, *Rhagapodemus* sp., Gerbillinae: *Pseudomeriones abbreviatus*.

Age: Previously Harr Obo was referred to MN 14 (early Ganzhuangian, Early Ruscinian – Qiu and Qiu 1995, Qiu and Li 2003, Qiu et al. 2003, Fahlbusch 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 2 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 *Pseudomeriones* in MN 12, and of *Sorex*, *Rhagapodemus* 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.

Fauna: According to Qiu Zhuding et al. (2013), the Shala fauna contains: ***Microscoptes* sp.** and **cf. *Microscoptes* sp.**, associated with Erinaceomorpha: Erinaceidae: *Erinaceidae* indet., Soricomorpha: Talpidae: *Yanshuella primaeva*, cf. *Asthenoscapter* sp., Soricidae: *Paranourosorex* sp., *Sorex* cf. *ertemteensis*, Soricinae indet., Lagomorpha: Ochotonidae: *Ochotona* cf. *lagreli*, Rodentia: Aplodontidae: *Ansomys* sp., Sciuridae: *Eutamias* cf. *ertemtensis*, *Prospermophilus* cf. *orientalis*, *Sinotamias* sp., *Pliopetaurista* sp., Gliridae: cf. *Prodryomys* sp., *Miodyromys* sp., *Microdryomys* sp. 1, *Microdryomys* sp. 2, Eomyidae: *Leptodontomys* sp., *Pentabuneomys* sp., Dipodidae: *Paralactaga* sp. 1, *Paralactaga* sp. 2, *Dipus* sp., *Cardiocranium* sp., *Lophocricetus* cf. *gansus*, *Sicista* sp., *Sinozapus* sp., Cricetidae: *Kowalskia* sp., *Sinocricetus* sp., cf. *Sinocricetus* sp., *Anatolomys* sp., Cricetidae indet., Spalacidae: Myospalacinae: *Prosiphneus* sp.

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

than the Early Baodean Amuwusu local fauna, which is referred to MN 9 (Qiu Zhanxiang et al. 2013: 62, Qiu Zhuding et al. 2013: 165). Shala is older than Baogeda Ula fauna (roughly correlated with MN 12), although both sites share *Lophocricetus*, *Paralactaga*, *Dipus*, *Kowalskia*, *Sinocricetus*, *Prosiphneus*, and *Ochotona* (Qiu Zhuding et al. 2013: 161). Previously *Sorex* was recorded in China since MN 11 (Storch et al. 1998). Thus the record from Shala either might extend the range of the genus in this area or it indicates an MN 11 age. The referral of Shala to MN 10 or MN 11 would be in agreement with the FAD of *Pliopetaurista* in MN 10, and with the LADs of *Miodiromys* and *Microdyromys* in MN 11 (Mein 1999).

Baogeda Ula (loc. nr: 5)

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

Other name: Baogedawula.

Fauna: Qiu Zhuding et al. (2013) listed in their compilation for Baogeda Ula the following taxa: ***Microscoptes* sp.**, associated with Erinaceomorpha: Erinaceidae: Erinaceidae indet. 1, Erinaceidae indet. 2, Soricomorpha: Soricidae: *Parasoriculus* sp., Lagomorpha: Ochotonidae: *Ochotona* cf. *lagreli*, Leporidae: *Alilepus* sp., Rodentia: Castoridae: *Dipoides* sp., Gliridae: Gliridae indet., Dipodidae: *Paralactaga* sp. 1, *Paralactaga* sp. 2, *Dipus* sp., *Lophocricetus* cf. *gansus*, Cricetidae: *Kowalskia* sp., *Nannocricetus* sp., *Sinocricetus* sp., cf. *Sinocricetus* sp., *Anatolomys* sp., *Rhinocerosodon* sp., Spalacidae: Myospalacinae: *Prosiphneus* sp., Muridae: *Abudhabia* sp., *Hansdebruijnina perpusilla*, familia incerta sedis (?Spalacidae: Rhizomyinae): *Pararhizomys hipparionum*.

Age: Early Baodean, equivalent of MN 12 (Wang et al. 2009, Qiu Zhuding et al. 2013), because *Dipoides*, *Hansdebruijnina*, *Alilepus* made their first appearance during the Baodean, and *Democricetodon*, *Prosiphneus*, *Leptodontomys*, *Microdyromys*, and *Miodiromys* had their last appearance there (Qiu Zhanxiang et al. 2013: 65).

Bilutu (loc. nr: 6)

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

Fauna: (Qiu Zhuding et al. 2013) (* = after Qiu Zhuding et al. 2013 these taxa are probably reworked from an older assemblage): ***Microscoptes* sp.**, associated with Erinaceomorpha: Erinaceidae: **Mioechinus* cf. *gobiensis*, *Erinaceus* sp., Soricomorpha: Talpidae: **Proscapanus* sp., *Quyania* sp., *Yanshuella* sp., Soricidae: **Heterosoricinae* indet., Soricinae indet., Lagomorpha: Ochotonidae: **Desmatolagus?* sp., **Alloptox?* sp., **Bellatona* sp., *Ochotona* cf. *lagreli*, Rodentia: Aplodontidae: **Ansomys* sp. 2, Sciuridae: *Eutamias* cf. *ertemtensis*, *Eutamias* sp., *Sciurus* sp., *Atlantoxerus* sp., *Prospermophilus* sp., *Sciuridae* indet. 2, Gliridae: *Miodiromys* sp., *Microdyromys* sp., *Myomimus sinensis*, Eomyidae: *Keramidomys* sp. 1, *Keramidomys* sp. 2, **Pentabuneomys* sp., *Leptodontomys* sp., Dipodidae: **Protalactaga grabau*, *Paralactaga suni*, *Paralactaga* cf. *anderssoni*, *Dipus fraudator*, **Heterosminthus* cf. *orientalis*, *Sicista* sp., *Lophocricetus grabau*, *Lophocricetus* sp., Cricetidae: **Eucricetodon?*

sp. 2, **Cricetodon* sp. 2, **Democricetodon lindsayi*, **Megacricetodon sinensis*, *Plesiodipus leei*, **Plesiodipus* aff. *progressus*, **Plesiodipus* sp., **Gobicricetodon* cf. *robustus*, *Kowalskia* sp., *Sinocricetus* sp., *Nannocricetus* sp., *Microtodon* sp., *Anatolomys* sp., *Rhinocerosodon* sp., Cricetidae indet. (2 spp.), Spalacidae: Myospalacinae: *Prosiphneus* sp., Muridae: *Hansdebruijnina pusilla*, *Micromys chaldeus*, *Karnimatoides hipparionus*, Gerbillinae: *Pseudomeriones* sp.

Age: The Bilutu bed (top of Aoerban profile) (Qiu Zhuding et al. 2013: 161) is considered to be of Early Baodean age, an equivalent of MN 12 (Wang et al. 2009, Qiu Zhuding et al. 2013). In China, *Pseudomeriones* occurs since MN 12, *Micromys* since MN 13, and *Miodiromys* and *Microdyromys* have their LAD in MN 13 (Qiu Zhanxiang et al. 2013). An open contradiction is that *Keramidomys* has its LAD in MN 10, and *Micromys* its FAD in MN 13 (Qiu Zhanxiang et al. 2013).

Russia

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).

Fauna: Devyatkin et al. (1968) reported from outcrop Kholu, bed 5: ***Microscoptes* sp.** (“large form, a new species, close to *M. disjunctus*, and different from small form of Pavlodar”), associated with: “Insectivora” indet., Lagomorpha: Ochotonidae: *Ochotonoides* sp., Rodentia: Castoridae: *Dipoides* sp. (small), Dipodidae: *Lophocricetus* sp., Cricetidae: *Cricetodon* sp., *Microtodon* cf. *atavus* (small), Muridae: Muridae indet. Later Zazhigin (in Gromov and Polyakov 1977) erected the species ***Microscoptes tjuvanensis***, and Zazhigin et al. (2002) recorded *Lophocricetus pusillus*.

Age: Devyatkin et al. (1968) compared *Microtodon* cf. *atavus* (small) from bed 5 of Kholu with *Microtodon* 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 pusillus* 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 *Microscoptes tjuvanensis* ZAZHIGIN in GROMOV et POLYAKOV, 1977, also named by some authors (Mats et al. 1982) *M. touvaenensis*. 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 Zykin (1984), and one in the lower part: Saray member = member A in Mats et al. (1982) = Olkhon 1 in Zazhigin and Zykin (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): *MicrotoscOPTES praetermissus*¹, *MicrotoscOPTES cf. tjuvanensis*², associated with Soricomorpha: Soricidae: *Sorex* sp.¹, Lagomorpha: Ochotonidae: *Prolagus* sp.^{1,2}, *Proochotona* sp.^{1,2}, *Ochotona* sp.^{1,2}, Leporidae: *Hypolagus* sp.^{1,2}, *Alilepus* sp.^{1,2}, Dipodidae: *Paralophocricetus progressus*² (= *Lophocricetus* sp. ²), *Lophocricetus orientalis*², Rodentia: Cricetidae: *Microtodon* ex gr. *atavus*^{1,2}, Arvicolinae: *Pliomys?* sp. ¹, *Stachomys* ex gr. *trilophodon*¹, *Mimomys* ex gr. *stehlini*¹, Spalacidae: Myospalacinae: *Prosiphneus* ex gr. *eriksoni*^{1,2}.

Saray member (Saray Faunistic complex, section 1, horizon 3 – Erbaeva and Alexeeva 1997): *MicrotoscOPTES cf. tjuvanensis*¹, Soricomorpha: Soricidae: *Sorex* sp.^{1,2}, Lagomorpha: Ochotonidae: *Proochotona* sp.^{1,2}, *Ochotona* sp.^{1,2}, Leporidae: Leporidae indet.^{1,2}, Rodentia: Castoridae: *Monosaulax* sp.^{1,2}, Dipodidae: *Paralophocricetus saraicus*² (= *Lophocricetus* sp. ¹), Cricetidae: *Baranomys* cf. *longidens*¹, Spalacidae: Myospalacinae: *Prosiphneus licenti*² (= *Prosiphneus* sp.¹).

Age: For the Saray member, Mats et al. (1982) gave an age of 6.5–6.3 Ma and for the Odonim member an age of 6.3–5.2 Ma (in that paper still referred to the Pliocene) which corresponds to the late Turolian (MN 13). Erbaeva and Alexeeva (1997) assigned both the Saray Faunistic complex and the Odonim Faunistic complex to MN 13. However, we follow Zazhigin et al. (2002), who correlated the older fauna (Olkhon 1) with Pavlodar 1A (MN 12), based on large mammals, and the younger fauna (Olkhon 2) with Cherklak 1A (MN 14), based on rodents.

Remarks: In Mats et al. (1982), *MicrotoscOPTES praetermissus* and *M. cf. tjuvanensis* had been reported from different beds (see above), but in later papers (Erbaeva and Alexeeva 1997, Daxner-Höck et al. 2013) these index taxa were referred only to the upper horizon (5). This concerns also *Stachomys*, which was originally described from the Odonim faunal complex, but is now referred to the Pliocene Olkhonian fauna (MN 14).

Mongolia

Hyargas-nuur 2 (loc. nr. 9)

Location of the site: Western Mongolia, Uvs province, Hyargas (or Khyargas) 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):

older fauna Hyargas-nuur 2 (18–22 m): *MicrotoscOPTES mongolicus*, associated with Castoridae: *Dipoides* sp., Dipodidae: *Lophocricetus* cf. *vinogradovi*, *Scirtodipus* cf. *kazakhstanica*, Muridae: *Occitanomys* cf. *adroveri*, Gerbillinae: *Pseudmeriones abbreviatus*;

younger fauna Hyargas-nuur 2 (24 m): *MicrotoscOPTES tjuvanensis*, associated with Castoridae: *Dipoides* sp., Dipodidae: *Lophocricetus grabau*, and *Scirtodipus* sp.

Age: Hyargas-nuur 2 is entirely correlated with Ertemte (MN 13) (Vangengeim et al. 2005, Zelenkov 2013, Delinschi 2014) because of the occurrence of *Dipoides* sp., *Lophocricetus* cf. *grabau*, *Scirtodipus* sp. (Pevzner et al. 1982, 1983). *Scirtodipus*, *Lophocricetus*, and *MicrotoscOPTES* are more highly evolved in the younger, upper (24 m) assemblage than in the older lower layers (18–22 m) (Pevzner et al. 1983).

Remark: *MicrotoscOPTES mongolicus* ZAZHIGIN in PEVZNER 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 *MicrotoscOPTES* is named Petropavlovsk 1A by Zazhigin et al. (2002).

Fauna: ¹(Savinov 1977), ²(Savinov 1982), ³(Savinov 1988), ⁴(Zazhigin et al. 2002): *MicrotoscOPTES pristinus*^{2,3}, associated with Soricomorpha: Talpidae: Desmaninae indet. (2 spp.)³, Soricidae: Soricidae indet.³, Lagomorpha: Ochotonidae: *Desmatolagus?* sp.³, Lagomyinae indet.³, Rodentia: Castoridae: *Trogontherium minutum* (= *Monosaulax savinovi*³), Dipodidae: *Lophocricetus minusculus*^{1,3}, Cricetidae: *Ischymomys quadriradicatus*^{2,3,4}, Cricetidae indet.³, Muridae: Muridae indet.³.

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 (Fejfar 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 Cherevychna (the latter with *L. maeoticus*, considered as a synonym of *L. minusculus*). However, the age of Cherevychna 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 *MicrotoscOPTES 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 Zykin 1984). The Pavlodar material collected by Savinov in 1970 (here the fauna 'Pavlodar') contains small mammals (Savinov 1970), but *MicrotoscOPTES* had

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 Irtysh River, in the outskirts of the city (= Gusinnyj Perelet) (Storch and Zazhigin 1996, Zazhigin and Lopatin 2000, Zazhigin 2006).

Fauna: ¹(Savinov 1970), ²(Gromov and Polyakov 1977), ³(Zazhigin and Zykin 1984), ⁴(Savinov 1988), ⁵(Zazhigin et al. 2002), ⁶(Zazhigin 2003), ⁷(Zazhigin 2006), ⁸(Bayshashov 2008):

Pavlodar: *MicrotoscOPTES praetermissus*², *MicrotoscOPTES sibiricus*^{3,4}, associated with Erinaceomorpha: Erinaceidae: *Erinaceus* sp.^{1,3,4}, Soricomorpha: Soricidae: *Similiosorex orlovi*^{1,3,4}, *Crociodura pavlodarica*^{1,3,4}, Chiroptera: Chiroptera indet.¹, Lagomorpha: Ochotonidae: *Ochotona* cf. *eximia*^{1,3,4}, Rodentia: Sciuridae: *Eutamias* sp.^{1,3} (unclear if identical with the record of *Tamias* sp.⁴), Gliridae: Gliridae indet.^{1,3,4}, Dipodidae: *Proalactaga* sp.¹, *Sicista bagajevi*^{1,3,4}, *Lophocricetus vinogradovi*^{1,3,4,5}, *Brachyscirtetes robustus*^{1,3}, *Scirotodipus kazakhstanica*^{1,3,4}, *Paralactaga varians*⁴, Cricetidae: Cricetidae indet. (5 spp.)¹, *Kowalskia* aff. *magna*^{3,4}, *Kowalskia* sp.⁴, Ruscinyminae indet.^{3,4}, *Rhinocerosodon* n. g. (nomen nudum⁴, but later re-erected⁶).

Pavlodar 1A (Gusinnyj Perelet): *MicrotoscOPTES* sp.⁷, associated with Erinaceomorpha: Erinaceidae: *Hemiechinus* sp.⁷, Soricomorpha: Soricidae: *Paranourosorex* sp.⁷, *Petenya* sp.⁷, *Paenelimnoecus* sp.⁷, Lagomorpha: Ochotonidae: *Proochotona* sp.⁷, Rodentia: Sciuridae: *Sciurotamias* sp.⁷, Gliridae: *Myomimus* sp.⁷, Dipodidae: *Lophocricetus vinogradovi*⁷, *Sicista bagajevi*⁷, *Scirotodipus kazakhstanica*⁷, *Brachyscirtetes robustus*⁷, *Allactaga varians*⁷, Cricetidae: *Rhinocerosodon pauli*^{6,7}, *Pseudocricetus* ex gr. *antiquus*⁷, *Pseudocricetus* sp.⁷, Cardiocraniinae indet.⁸.

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, Shpanskiy and Ivantsov 2005, Tyutkova 2005, Zazhigin 2006, Nicoara 2013, Delinschi 2014), or to late MN 12 or early MN 13 (Bayshashov 2008). The dating is in agreement with the range of *Pseudocricetus* (MN 12 – MN 13) (Mein 1999).

Remarks: Gromov and Polyakov (1977) first mentioned *MicrotoscOPTES* from Pavlodar, and referred it to *M. praetermissus*. Savinov (1988) mentioned the occurrence of a new species of *MicrotoscOPTES*, which was named then *M. sibiricus* by Zazhigin and Zykin (1984). However this name is a nomen nudum (Daxner-Höck et al. 2013), since it was not described, figured, or diagnosed, nor was a type specimen designated.

Akshauli (loc. nr. 12)

Location of the site: Northern Kazakhstan, Qostanaï region, west of Karasu River, west of village Akshauli (until 1977: Znamenka, until 1994: Aksaule).

Fauna: (Savinov 1988): *MicrotoscOPTES* sp., associated with Lagomorpha: Ochotonidae: *Proochotona* sp., Rodentia: Dipodidae: *Brachyscirtetes* sp., *Scirotodipus kazakhstanica*.

Age: Pontian (Savinov 1988) (= late MN 13).

Selety 1A (loc. nr. 13)

Location of the site: Northern Kazakhstan, Akmolinsk region, Akkol'sk district, left bank of Selety River, 4–5 km upstream from village Il'inka. Small mammals were found everywhere, mostly in the upper part (Selety 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): *MicrotoscOPTES* sp.^{1,4}, associated with Erinaceomorpha: Erinaceidae: *Hemiechinus* sp.^{1,4}, Soricomorpha: Talpidae: *Desmana* sp.^{1,4}, Soricidae: *Paranourosorex seletiensis*^{1,4}, *Petenya* sp.^{1,4}, *Sorex* sp.^{1,4}, *Paenelimnoecus* sp.^{1,4}, Lagomorpha: Ochotonidae: *Ochotona* sp.^{1,4}, Leporidae: *Veterilepus* sp.^{1,4}, Rodentia: Sciuridae: *Sciurotamias* sp.^{1,4}, Castoridae: *Castoridae* indet.^{1,4}, Dipodidae: *Lophocricetus vinogradovi*^{1,4}, *Lophocricetus minusculus* (= *maeoticus*)², *Sicista* sp.^{1,4}, *Plioscirotopoda antiqua*^{1,4}, *Jaculus sibiricus*^{1,4}, *Brachyscirtetes* sp.^{1,4}, *Allactaga varians*⁴, *Allactaga* sp.⁴, Muridae: *Hansdebruijnina* cf. *neutrum*^{1,4}, Cricetidae: *Pseudocricetus* sp.^{1,4}, *Stylocricetus meoticus*^{1,4}, *Kowalskia* sp.^{1,4}, *Anatolomys* sp.⁴, *Rhinocerosodon seletyensis*³, *Epimeriones* sp.⁴.

Age: The association of *Lophocricetus vinogradovi* with *Paranourosorex seletiensis* 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 *Veterilepus* (MN 11) and the range of *Pseudocricetus* (MN 12 – MN 13) (Mein 1999).

Kedey 1A (loc. nr. 14)

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

Fauna: (Zazhigin 2006): upper part of the outcrop: *MicrotoscOPTES* sp., associated with Soricomorpha: Soricidae: *Sorex* sp., Lagomorpha: Ochotonidae: *Ochotona* sp., Leporidae: *Veterilepus* sp., Rodentia: Dipodidae: *Sibirosmithus seletyensis*, Cricetidae: *Pseudocricetus* sp.; lower part of the outcrop: *MicrotoscOPTES* sp., associated with Lagomorpha: Ochotonidae: *Ochotona* sp., Rodentia: Cricetidae: *Stylocricetus* sp., Muridae: Gerbillinae: *Epimeriones* sp.

Age: Zazhigin's (2006) assignment to MN 13 is in agreement with the FAD of *Veterilepus* (MN 11) and the range of *Pseudocricetus* (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): *MicrotoscOPTES praetermissus*¹, associated with Erinaceomorpha: Erinaceidae: *Erinaceus* sp.¹, Soricomorpha: Soricidae: Soricidae indet.¹, *Beremendia* sp.¹, Lagomorpha: Ochotonidae: *Ochotona* ex gr. *eximia*¹, *Ochotona* ex gr. *eximia-gigas*¹, *Ochotonoides* sp.¹, Rodentia: Sciuridae: *Tamias* sp.¹, Gliridae: *Dryomys* sp.¹, Dipodidae: *Lophocricetus afanasievi*^{1,2}, *Paralactaga* sp.¹, *Scirotodipus kalbica*¹, Cricetidae: *Cricetodon* sp.¹, Cricetinae

indet.¹, *Ischymomys kalbica*¹, Spalacidae: Myospalacinae: *Prosiphneus* sp.¹, 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 (Čermák 2010). Problematic is the record of *Ochotonoides*, which appears according to Wu and Flynn (2017a) only in the Pliocene.

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

Ukraine

Cherevychne 3 (loc. nr. 16)

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

Other names/spellings: Cherevychnij, Cherevychnoe/nizhnij sloj, Cherevichnoe/nizhnij kostenosnyj sloj, Cherevichnoe 3, Cherevychnoe 3, Avgustovka.

Fauna: ¹(Topachevskiy 1971), ²(Gromov and Polyakov 1977), ³(Topachevskiy et al. 1984), ⁴(Nesin and Storch 2004), ⁵(Nesin 2013), ⁶(Čermák and Rekovets 2010), ⁷(Rzebik-Kowalska and Rekovets 2015), ⁸(Sinita 2015), ⁹(Rzebik-Kowalska and Rekovets 2016): ***Microscoptes* sp.¹**, ***Microscoptes tjuvanensis*²**, associated with Erinaceomorpha: Erinaceidae: *Schizogalerix* sp.^{5,7,9}, *Amphechinus* sp.^{5,7,9}, Soricomorpha: Talpidae: *Archaeodesmana pontica*^{5,7,9}, Soricidae: *Miosorex* sp.^{5,7,9}, *Sulimskia* sp.^{5,7,9}, *Paenelimnoecus* sp.^{5,7,9}, *Amblycoptus* sp.^{5,7,9}, Chiroptera: Chiroptera indet.⁵, Lagomorpha: Ochotonidae: *Prolagus* sp.⁵, *Ochotona* cf. *eximia*⁶, Leporidae: *Alilepus* sp.⁶, Rodentia: Sciuridae: *Sciurotamias gromovi*⁵, *Sciurotamias turolensis*⁵, Castoridae: *Trogontherium minutum rhenanum* (= *Monosaulax* sp.⁵), Gliridae: *Muscardinus* sp.⁵, *Glirulus* sp.⁵, *Vasseuromys pannonicus*⁸, Dipodidae: *Eozapus* sp.⁵, *Lophocricetus maeoticus*³ (= *L. minusculus*), Cricetidae: *Byzantinia* aff. *pikermiensis*⁵, *Pseudocricetus antiquus*⁵, *Stylocricetus meoticus*⁵, *Stylocricetus* sp.⁸, *Kowalskia* sp.⁸, Muridae: *Castromys nadachowski*^{4,5}, *Apodemus barbarae*^{4,5}, *Apodemus alae*^{4,5}, *Apodemus lugdunensis*⁸.

Age: Meotian (Topachevskiy 1971), Belkian faunistic complex¹ (because of the occurrence of *Pseudocricetus*, *Lophocricetus*), (Topachevskiy et al. 1997), Belkian complex, Novoelzavetovkian 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 *Amblycoptus* (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 nadachowski* and *Apodemus barbarae* (Nesin and Storch 2004, Nesin 2013). In the opinion of Zazhigin et al. (2002), *Lophocricetus minusculus* is confined to MN 10 – MN 11,

which would indicate an older age of Cherevychne, 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.

Fauna: ¹(Sinita 2015), ²(Sinita in litt. 2015): ***Microscoptes* sp.²**, associated with: Rodentia: Gliridae: *Vasseuromys pannonicus*¹, *Myomimus maritsensis*¹, Cricetidae: *Stylocricetus* sp.¹, *Pseudocricetus orient-europaeus*¹, Muridae: *Apodemus lugdunensis*¹, *Apodemus schaubi*¹.

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, Sinita in litt. 2015).

Verkhnya Krynytsa (loc. nr. 18)

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

Fauna: ¹(Rekovets and Pashkov 2009), ²(Rzebik-Kowalska and Rekovets 2015), ³(Rzebik-Kowalska and Rekovets 2016): ***Microscoptes* cf. *pristinus*¹**, associated with Erinaceomorpha: Erinaceidae: Erinaceidae indet.^{1,2,3}, Soricomorpha: Talpidae: *Archaeodesmana* cf. *verestchagini*^{1,2}, *Archaeodesmana* sp.^{2,3}, cf. *Mygalinia hungarica*^{2,3}, cf. *Desmana* sp.^{2,3}, Soricidae: Soricidae cf. *Miosorex* sp.^{2,3}, *Crusafontina* cf. *kormosi*^{2,3}, *Petenya dubia*^{2,3}, *Neomysorex alpinoides*^{2,3}, cf. *Asoriculus* sp.^{2,3}, *Zelceina* sp.^{2,3}, Soricidae indet.^{2,3}, Soricidae indet. (large form)^{1,2,3}, Soricidae indet. (small form)^{1,2,3}, Lagomorpha: Ochotonidae: *Ochotona* sp. (*Lagotona* type)¹, Rodentia: Castoridae: Castoridae indet.¹, Dipodidae: *Lophocricetus* ex gr. *maeoticus/complicidens*¹, Cricetidae: *Kowalskia* cf. *progressa*¹.

Age: Meotian, Belkian faunistic complex, MN 12 (Topachevskiy et al. 1997, Nesin and Topachevskiy 1999, Rekovets et al. 2014).

Vasylivka 1 (loc. nr. 19)

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

Fauna: Only ***Microscoptes* 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.

Fauna: ¹(Rekovets and Pashkov 2009), ²(Rzebik-Kowalska and Rekovets 2015): ***Microscoptes* sp.¹**, associated with Soricomorpha: Soricidae: *Petenya dubia*², Lagomorpha: Ochotonidae: *Ochotona eximia*¹, Rodentia: Castoridae: *Trogontherium minutum*¹.

¹ Cherevychne 3 is not included in the so-called "Cherevychanskiy theriokomplex" (type locality Novoukrainka 1), which is defined for large mammals by Korotkevich (1988).

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

Fauna: (Wilson 1937): ***Goniodontomys disjunctus***, associated taxa Soricomorpha: Talpidae: ?*Scapanus* sp., Soricidae: *Paracryptotis rex*, Lagomorpha: Leporidae: *Hypolagus* sp., *Hypolagus vetus*, Rodentia: Cricetidae: *Basirepomys romensis*, Zapodidae: *Pliozapus solus*, Castoridae: *Dipoides stirtoni*, Mylagaulidae: *Hesperogaulus wilsoni*.

Age: Early Hemphillian (Repenning 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 Loc 2517 (PBDB op. cit.).

Fauna: (Shotwell 1970, PBDB, op. cit.): ***Goniodontomys disjunctus***, associated with Soricomorpha: Talpidae: *Scapanus* sp., *Scalopoides* sp., Soricidae: Soricidae indet., Lagomorpha: Leporidae: Archaeolaginae indet., Rodentia: Aplodontidae: *Tardontia* sp., Sciuridae: *Spermophilus* sp., *Spermophilus* cf. *wilsoni*, *Eutamias* sp., Castoridae: *Dipoides stirtoni*, Eomyidae: *Leptodontomys* sp., Zapodidae: *Macrognomys* cf. *nanus*, Heteromyidae: "*Pliosaccomyx magnus*" = *Cupidininus magnus*, *Diprionomys* cf. *parvus*, *Dipodomys* sp., Cricetidae: Cricetidae indet., *Copemys* cf. *esmeraldensis*, *Antecalomys valensis*, *Peromyscus antiquus*, *P. valensis*, *Oryzomys* sp.

Age: Early Hemphillian (Repenning 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 (Repenning 1987).

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

² http://fossilworks.org/bridge.pl?a=collectionSearch&taxon_no=41779&max_interval=Miocene&country=United States&state=Oregon&is_real_user=1&basic=yes&type=view&match_subgenera=1

³ http://fossilworks.org/bridge.pl?a=collectionSearch&collection_no=18807

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 2239 (= CIT 107), 2339, 2355, 2356, 2357, 2358 (PBDB op. cit.).

Fauna: (Shotwell 1970, PBDB, op. cit.): ***Goniodontomys disjunctus***, associated taxa Soricomorpha: Talpidae: *Scapanus* cf. *proceridens*, Lagomorpha: Leporidae: Archaeolaginae indet., Rodentia: Aplodontidae: *Liodontia furlongi*, Castoridae: *Hystricops browni*, *Dipoides stirtoni*, Mylagaulidae: *Hesperogaulus wilsoni*.

Age: Late early Hemphillian (Hh 2) (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).

Fauna: (Shotwell 1970, PBDB, op. cit.): ***Goniodontomys disjunctus***, associated taxa Lagomorpha: Leporidae: *Hypolagus vetus*, Rodentia: Cricetidae: Sciuridae: *Spermophilus* cf. *wilsoni*, Castoridae: *Dipoides stirtoni*.

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

Little Valley (loc. nr. 25)

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

Fauna: (Shotwell 1970): ***Goniodontomys disjunctus***, ***Goniodontomys disjunctus***, associated with Soricomorpha: Talpidae: *Scapanus proceridens*, Soricidae: Soricidae indet., Chiroptera: Vespertilionidae: ?Vespertilionidae indet., Lagomorpha: Leporidae: *Hypolagus vetus*, Archaeolaginae indet., Rodentia: Cricetidae: "*Peromyscus* cf. *pliocenicus*" = *Basirepomys pliocenicus*, *Copemys* cf. *esmeraldensis*, *Antecalomys valensis*, *Peromyscus antiquus*, Sciuridae: *Spermophilus* sp., Heteromyidae: "*Pliosaccomyx* cf. *magnus*" = *Cupidininus magnus*, *Diprionomys parvus*, Castoridae: *Dipoides vallicula*.

Age: Hemphillian (PBDB op. cit.).

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).

⁴ http://fossilworks.org/bridge.pl?a=collectionSearch&collection_no=18806

⁵ http://fossilworks.org/bridge.pl?a=collectionSearch&collection_no=18935

⁶ http://fossilworks.org/bridge.pl?a=collectionSearch&collection_no=18944

⁷ http://fossilworks.org/bridge.pl?a=collectionSearch&taxon_no=41833&max_interval=Hemphillian&country=United States&state=Idaho&is_real_user=1&basic=yes&type=view&match_subgenera=1

Fauna: (Hibbard 1970, Repenning 1987): *Paramicroscoptes hibbardi*, associated with Castoridae: *Dipoides stirtoni*.

Age: Early Hemphillian (Repenning 1987), early – late early 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 Kelly Road fauna by Hibbard (1970).

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

Fauna: (Hibbard 1959, 1970): *Goniodontomys disjunctus*, associated with Castoridae: *Dipoides stirtoni*.

Age: Early Hemphillian (Repenning 1987), early Hemphillian (Hh 1) (Lindsay 2008); a K-Ar date of 9.2 Ma (Evernden et al. 1964) is stratigraphically below the fossils (Repenning 1987).

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 tuffs. “These strata yield the diagnostic Late Miocene mammals *Plionictis ogygia*, *Copemys pisinnus*, *Phelosacomys hibbardi*, *Pronotolagus 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.).

Fauna: (Leite 1990): *Paramicroscoptes hibbardi*, associated with Soricomorpha: Talpidae: Talpinae indet., *Achlyoscapter* sp., *Lemoynea biradicularis*, Plesiosoricidae:

Plesiosorex sp., Soricidae: *Sorex* sp., *Sorex edwardsi*, *Sorex yatkolai*, *Crusafontina magna*, cf. *Limnoecus* sp., *Alluvisorex* cf. *arcadentes*, Lagomorpha: Ochotonidae: Ochotonidae indet., Leporidae: *Hypolagus vetus*, *Pronotolagus apachensis*, Rodentia: Sciuridae: *Spermophilus* sp., Eomyidae: *Kansasimys* sp., Geomyidae: *Pliosaccomys* sp., Heteromyidae: Heteromyinae indet., Castoridae: *Dipoides* sp., Mylagaulidae: Mylagaulidae indet.

Age: Early Hemphillian (Repenning 1987).

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

Feltz Ranch (loc. nr. 30)

Location of the site: U.S. State of Nebraska, Keith County (PBDB¹⁰).

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.).

Fauna: (Voorhies 1990): *Paramicroscoptes hibbardi*, associated with Soricomorpha: Talpidae: *Lemoynea* sp., Rodentia: Castoridae: *Dipoides* sp., Mylagaulidae: Mylagaulidae indet.

Cambridge (loc. nr. 31)

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

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

Fauna: (Voorhies 1990): *Goniodontomys disjunctus*, *Paramicroscoptes* cf. *hibbardi*, associated with Soricomorpha: Talpidae: *Lemoynea* cf. *biradicularis*, Plesiosoricidae: *Plesiosorex* sp., Soricidae: *Sorex* cf. *edwardsi*, *Crusafontina magna*, Lagomorpha: Leporidae: Archaeolaginae indet., Rodentia: Cricetidae: *Copemys* sp., Sciuridae: *Spermophilus* sp., Geomyidae: *Pliosaccomys* sp., Castoridae: *Dipoides williamsi*, *Dipoides stirtoni*, Mylagaulidae: “*Pterogaulus cambridgensis*” = *Mylagaulus cambridgensis*.

Age: Hemphillian.

Rick Irwin Site (loc. nr. 32)

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

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

Fauna: (Tucker 2003): *Goniodontomys disjunctus*, associated with Rodentia: Cricetidae: *Prosomys mimus*.

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

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&type=view&match_subgenera=1

⁹ http://fossilworks.org/bridge.pl?a=collectionSearch&collection_no=18225

¹⁰ http://fossilworks.org/bridge.pl?a=collectionSearch&collection_no=18158

¹¹ http://fossilworks.org/bridge.pl?a=collectionSearch&collection_no=18086

¹² http://fossilworks.org/bridge.pl?a=collectionSearch&collection_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).

Other names: US Vertebrate loc. M1254, UC loc. V73117 (Repenning 1987), Rabbit hole, Loc. V73117 (Lindsay 2008, NB30).

Fauna: (Repenning 1987): *Paramicroscoptes hibbardi*, associated with *Dipoides stirtoni*.

Age: Early Hemphillian (Repenning 1987).

Discussion

Late Cenozoic deposits with remains of Microscoptini 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). Microscoptini 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 *Microscoptes*, 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 *Microscoptes*. In the Ukraine two *Microscoptes*-bearing sites occur in the surroundings of Odessa, but others of

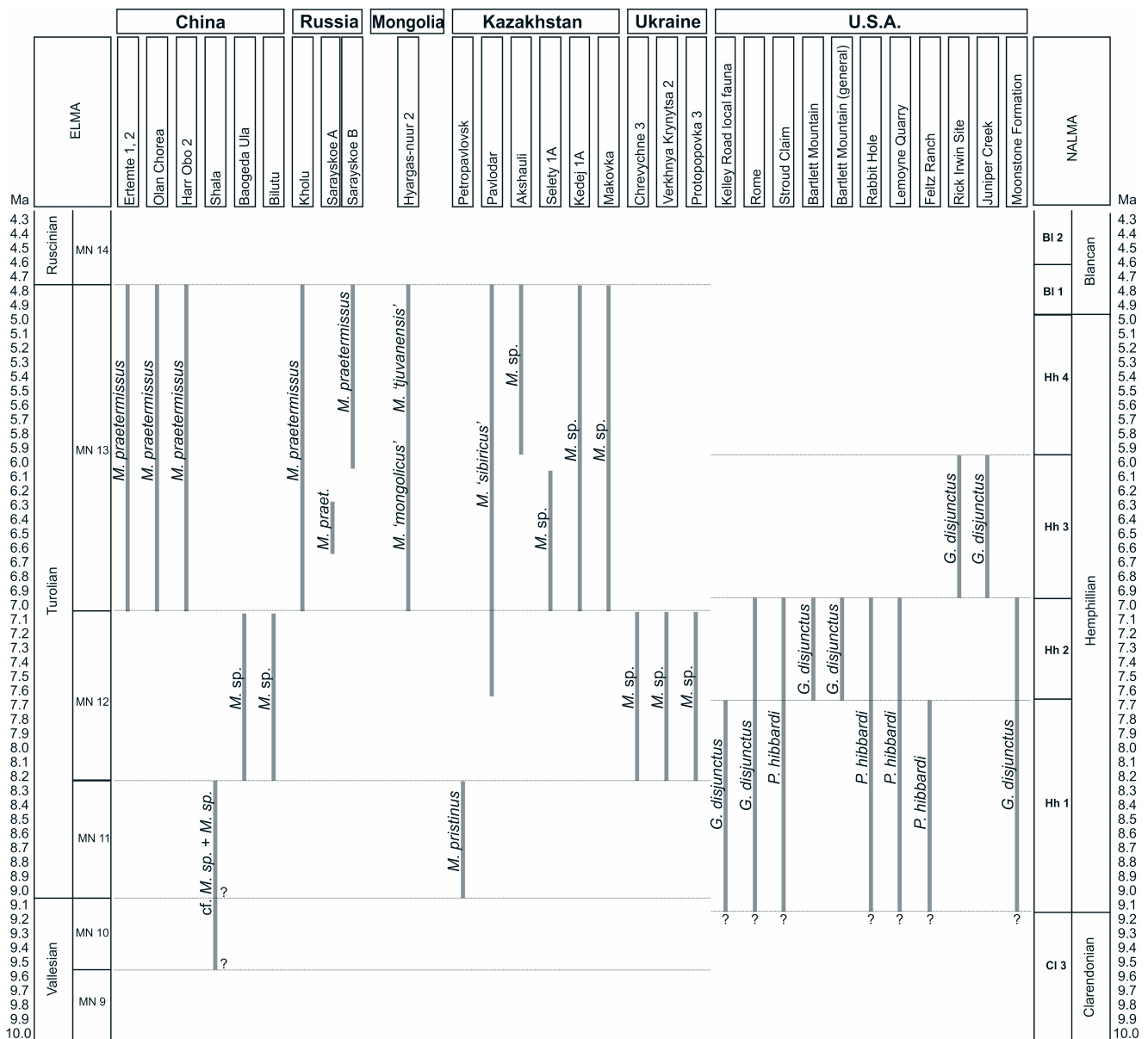
similar age and in close vicinity to these localities lack this taxon (Nesin 2013). Three other sites with *Microscoptes* are situated on the banks of the Kakhovka reservoir of the Dnieper River where no other faunas of this age were found. This distribution pattern could mean that the occurrence of *Microscoptes* is linked to particular geographic areas, as well as to special ecological conditions.

Hibbard (1970) recognised that all North American Microscoptini 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 *Microscoptes* to aquatic habitats. Considering the variety of *Microscoptes*-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 Microscoptini indeed required rather moist habitats and proximate water bodies.

Stratigraphically (Text-fig. 2), known Asian records of Microscoptini are all Late Miocene in age (MN 11, possibly MN 10, to MN 13). The range of *Microscoptes* 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 *Microscoptes* records seem to be correlated with MN 12, but for some sites (Vasylivka 1 and Lobkove) a younger age cannot be excluded.



Text-fig. 1. Known geographic distribution of Microscoptini. 1 – Ertemte 1 and 2; 2 – Olan Chorea; 3 – Harr Obo 2; 4 – Shala; 5 – Baogeda Ula; 6 – Bilutu; 7 – Kholu (Southern Tuva); 8 – Sarayskoe (Olkhon Island); 9 – Hyargas-nuur; 10 – Petropavlovsk; 11 – Pavlodar; 12 – Akshauli; 13 – Selety 1A; 14 – Kedej 1A; 15 – Makovka; 16 – Cherevychnye 3; 17 – Protopopovka 3; 18 – Verkhnya Krynytsa 2; 19 – Vasylivka 1; 20 – Lobkove; 21 – Rome; 22 – Bartlett Mountain; 23 – Bartlett Mountain (General); 24 – Juniper Creek; 25 – Little Valley; 26 – Stroud Claim; 27 – Kelley Road; 28 – Moonstone Formation; 29 – Lemoyne Quarry; 30 – Feltz Ranch; 31 – Cambridge; 32 – Rick Irwin Site; 33 – Rabbit Hole.



Text-fig. 2. Stratigraphic ranges of Microscoptini-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.

Microscoptes 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 *Paramicroscoptes* and *Goniodontomys* (Repenning 1987, Repenning et al. 1990) are also all dated to the Late Miocene, more specifically the Hemphillian. Records of *Paramicroscoptes* 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 *Microscoptes* sp. (Shotwell 1970) is likely a heteromyid (Repenning

1987). According to Lindsay (2008: 475, fig. 27.3), *Paramicroscoptes* and its close relative *Goniodontomys* appeared at the beginning of the early Hemphillian (Hh 1) for the first time. *Paramicroscoptes* 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 *Paramicroscoptes*, the desmanine *Lemoynea*, the nectogaline shrew *Crusafontia*, the rabbit *Hypolagus vetus*, the beaver *Dipoides*, the eomyid *Kansasimys*, the cricetodontine *Pliotomodon*, the geomyid *Pliosaccomys*, and the sigmodontine *Paronychomys*. The late early Hemphillian (Hh 2) is defined in Tedford et al.

(2004) by the FADs of *Goniodontomys* and *Dipoides stirtoni* and the LADs of *Hystricops* and *Leptodontomys*.

It is not yet clear, on which continent Microscoptini originated. No cricetid is known as the potential ancestor of *Microscoptes* – neither in Eurasia nor in North America. Fahlbusch (1987) considered *Microscoptes praetermissus* 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 Microscoptini and found that in *Paramicroscoptes* this structure is more primitive. In addition, only *Paramicroscoptes* retains enamel islets (Martin 1975), which also indicate its primitive state. This would imply an evolutionary trend in Microscoptini towards length reduction of m3/M3.

It is difficult to discern the oldest representative of Microscoptini. 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 Microscoptini 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 Lemoyne 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 Microscoptini 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 Microscoptini is 9.0–4.9 Ma.

Regardless of the question about the oldest finds of Microscoptini, the very similar morphology of Eurasian *Microscoptes* and North American *Paramicroscoptes* and *Goniodontomys* suggests an intercontinental exchange of Microscoptini between northern Asia and North America. That is, Microscoptini 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 *Microscoptes* (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 Microscoptini both from Eurasia and North America are much older than the first records of *Promimomys* – thus, coincidence is rather unlikely.

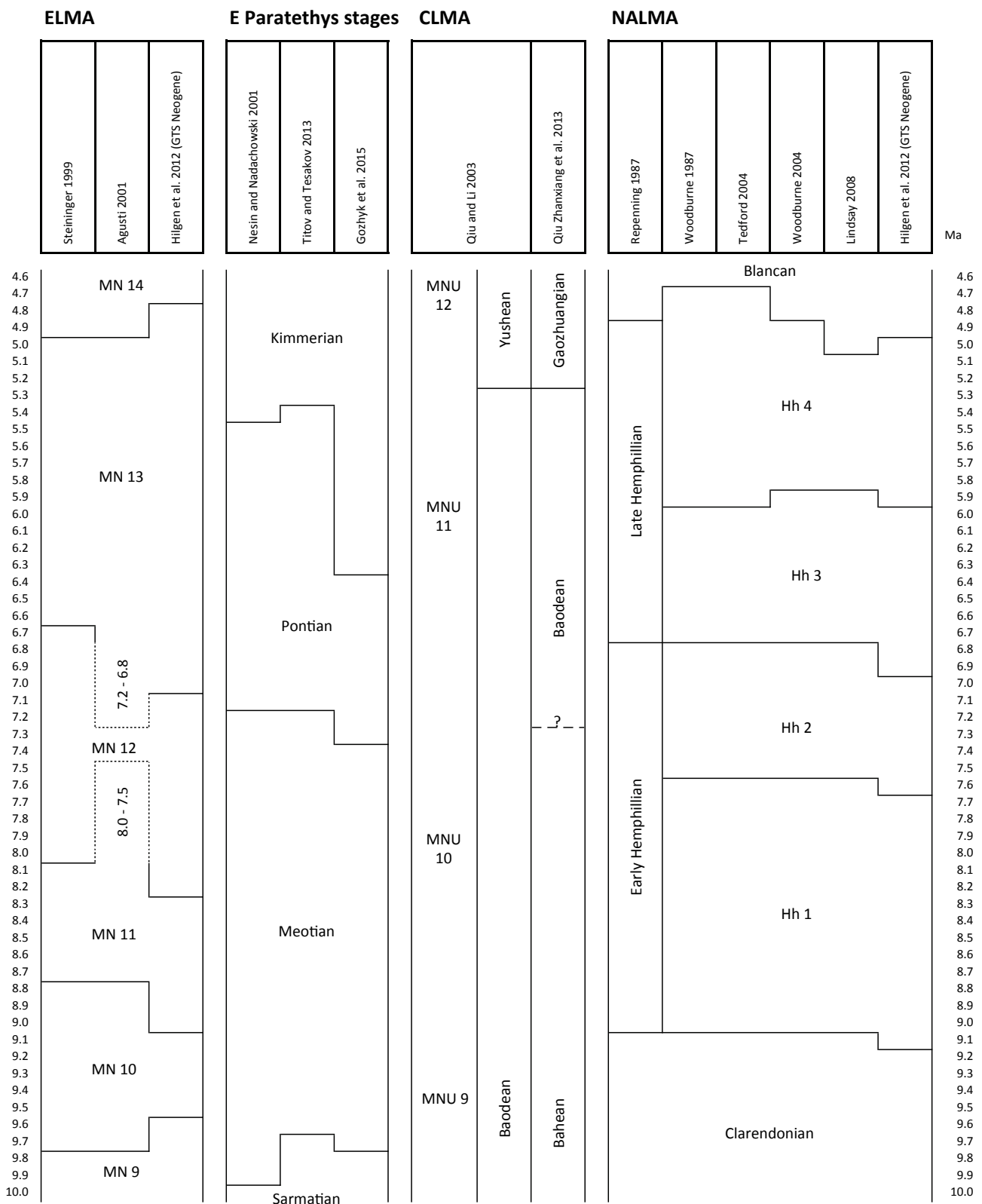
According to (Dawson 1999) the filtering effect of Beringia was especially strong during the Late Miocene for mammals adapted to warm environments. Increased provincialism of mammalian faunas accompanied the increased temperature gradient of the later Cenozoic, as northern areas became colder, and southern 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, Vislobokova et al. 2003). Another dispersal wave in the Late Miocene might provide the “Leporid datum” (Flynn et al. 2014). *Alilepus* 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 Microscoptini nor do we know the factors concerning its beginning and termination (opening of the Bering Strait or climatic change).

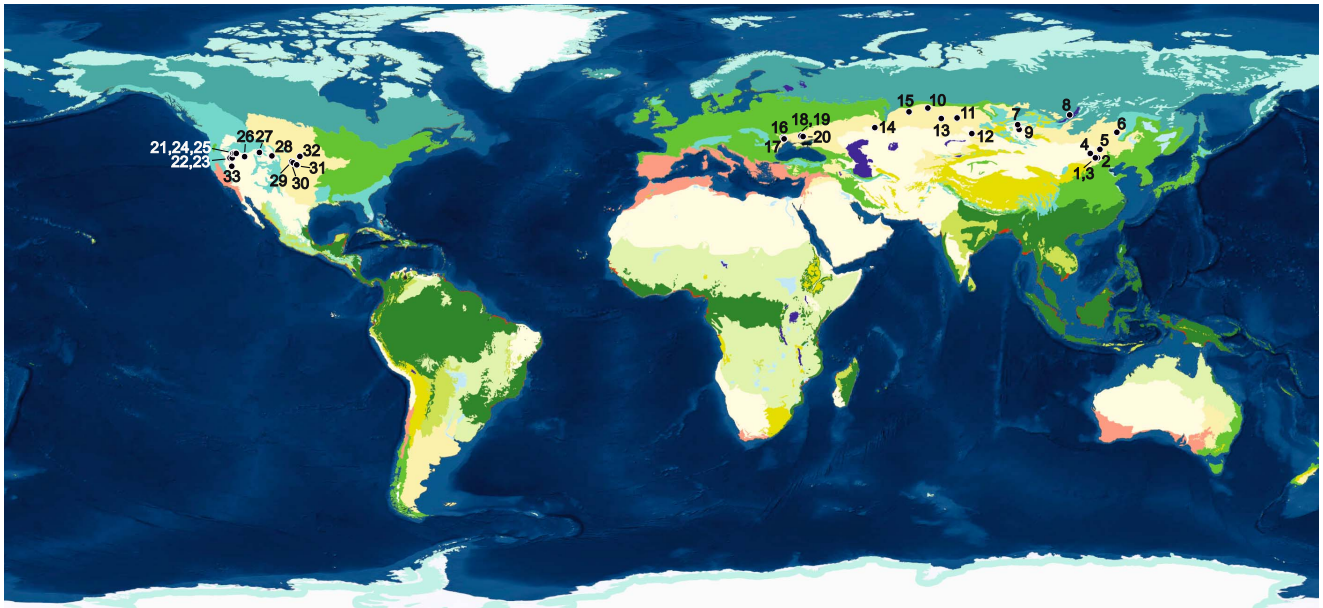
It is striking that the distribution of localities of Microscoptini especially in Eurasia matches with the extant grassland biome in Text-fig. 4. This is obviously not the same vegetation type as it was in the Late Miocene. The development of steppe biomes in Eurasia is linked to increasing aridification during the Late Miocene, which began at about 8–7 Ma in the interior of central Eurasia (Liu



Text-fig. 3 Comparison of various stratigraphic subdivisions: European (ELMA), North American (NALMA) (Hilgen et al. 2012) and Chinese (CLMA) (Qiu Zhanxiang et al. 2013, Qiu Zhuding et al. 2013) Land Mammal Ages and Eastern Paratethys stages.

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,



Text-fig. 4. Known geographic distribution of *MicrotoscOPTINI* on a modern-day biome map (Arc-GIS feature TNC terrestrial ecoregions). 1 – Ertemte 1 and 2; 2 – Olan Chorea; 3 – Harr Obo 2; 4 – Shala; 5 – Baogeda Ula; 6 – Bilutu; 7 – Kholu (Southern Tuva); 8 – Sarayskoe (Olkhon Island); 9 – Hyargas-nuur; 10 – Petropavlovsk; 11 – Pavlodar; 12 – Akshauli; 13 – Selety 1A; 14 – Kedej 1A; 15 – Makovka; 16 – Cherevychnye 3; 17 – Protopopovka 3; 18 – Verkhnya Krynytsa 2; 19 – Vasylyvka 1; 20 – Lobkove; 21 – Rome; 22 – Bartlett Mountain; 23 – Bartlett Mountain (General); 24 – Juniper Creek; 25 – Little Valley; 26 – Stroud Claim; 27 – Kelley Road; 28 – Moonstone Formation; 29 – Lemoyne Quarry; 30 – Feltz Ranch; 31 – Cambridge; 32 – Rick Irwin Site; 33 – Rabbit Hole. 1–20, 30–32 – Steppe biomes, 21–29, 33 – xeric shrubland biomes.

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 *MicrotoscOPTINI* 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 (Repenning 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 *ParamicrotoscOPTINI* 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 *Protopliophenacomys* 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 *MicrotoscOPTINI* (*MicrotoscOPTINI*) 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) *MicrotoscOPTINI* co-existed with *Microtodon* – one of the old vole-like cricetid rodents. However, another factor might be that *MicrotoscOPTINI* were ecologically too specialised and could not cope with changes in climate and landscape.

Conclusion¹³

The present paper is a current outline of the spatial and temporal distribution of *MicrotoscOPTINI* – 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 *MicrotoscOPTINI* 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 *MicrotoscOPTINI* in Eurasia was considered to be MN 13 – MN 14, and in North America

¹³ 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 *MicrotoscOPTINI fahlbuschi* sp. nov. QIU et LI, 2016 described in that paper.

early Hemphillian (approximately MN 11 – MN 12) (Fejfar 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 (*Microscoptes*), but this is not yet certain, since the oldest finds (*Paramicroscoptes* 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 *Microscoptini* is known. Therefore the question, whether the *Microscoptini* originated in Eurasia or North America remains a topic for further studies.

The fossil record reveals that the *Microscoptini* 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 *Microscoptini* both in Eurasia and North America has been used as evidence for dispersal through Beringia during the Late Miocene. Unfortunately, no remains of *Microscoptini* 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 *Microscoptini*.

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

This concerns the general problem that most records of *Microscoptini* 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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