



SMALL MAMMAL FAUNA IN EUROPE DURING THE SECOND HALF OF THE MIDDLE PLEISTOCENE

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Abstract: Evolutionary changes in European small mammals during the second half of the Middle Pleistocene, from the Likhvin (Holsteinian, Hoxnian) Interglacial (MIS 11) to the beginning of the Mikulino (Eemian) Interglacial (MIS 5e), that is between 424 ka BP and 130 ka BP were traced. Trends in evolutionary change were documented, and East European and West European faunas were compared. An integrated analysis of available theriological, geological, and geochronological data for the second half of the Middle Pleistocene in Europe has shown marked changes in the small mammal fauna throughout the period under consideration and provided information on the climate and environments at different time intervals. Changes traceable in the Arvicolinae phyletic lines made a correlation between the West European and East European mammal localities possible. The biostratigraphic scheme of the second half of the Middle Pleistocene has been developed and maps of small mammal localities compiled.

Key words: small mammals, second half of the Middle Pleistocene, Europe, taxonomy, evolution, stratigraphy, correlation

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Introduction

The Middle Pleistocene mammalian faunas (corresponding to the Early and Middle Neopleistocene of the Russian stratigraphic scheme) have not been studied in sufficient detail as yet. The European mammal faunas dated to the beginning of the Middle Pleistocene and its first half, before the Likhvin Interglacial (= Holsteinian Interglacial in Western Europe and Hoxnian Interglacial in Great Britain) were discussed in previous publications (Markova 2014, 2016, Markova and Puzachenko 2016, Markova and Vislobokova 2016). Here we would like to concentrate on the mammalian faunas dated to the second half of the Middle Pleistocene, from the Likhvin Interglacial (MIS 11) up to the Mikulino (Eemian) Interglacial (MIS 5e), that is from 424 ka BP to 130 ka BP (Lisiecki and Raymo 2005) (Text-figs 1–3, Tab. 1). This relatively long time interval is known for several climatic events on a global scale and covers at least three climatic cycles (with glacials and interglacials). Those events had a strong ecological influence resulting in drastic changes in the small mammal faunas. In addition, this long time interval was characterized by evolutionary changes recorded in many Arvicolinae lineages; the changes appeared most noticeably in the dental morphology of these taxa. In the present paper, the succession of small mammal

faunas and their evolutionary changes will be discussed. In addition to the data on the Middle Pleistocene small mammal faunas of Western Europe (which have been thoroughly covered in specialist literature), we consider material on the small mammals that inhabited Eastern Europe in the second half of the Middle Pleistocene.

Chronological intervals

The time interval covered in this paper spans about 300,000 years, from the Likhvin Interglacial in Eastern Europe, correlatable with the Holsteinian Interglacial in Western Europe and the Hoxnian Interglacial in the British Isles (MIS 11, 424–374 ka BP), to the beginning of the Mikulino Interglacial (Eemian – Ipswichian in Western Europe and in the British Isles, respectively) – MIS 5e, ~130 ka BP (Lisiecki and Raymo 2005). The climatic conditions changed repeatedly during the interval under consideration (Text-figs 1–3).

The beginning of the second half of Middle Pleistocene (or the beginning of the Middle Neopleistocene) is recognized by a noticeable warming of interglacial order – the Likhvin (Holsteinian, Hoxnian) Interglacial. This interglacial is most close to the Holocene optimum in its

climatic parameters. The deposits attributed to the Likhvin (Holsteinian, Hoxnian) Interglacial overlie those of the preceding glaciation (Elsterian in Western Europe, Anglian in Great Britain, Oka glaciation in Eastern Europe). In various parts of Europe this glacial stage is represented by glacial till, fluvio-glacial sediments and by loesses. The deposits exposed in the Hoxne stratotype in Great Britain (Layer C) have been dated by uranium series and ESR at 404 ± 33/–42 ka BP which fits clearly within the time limits of MIS 11 (Grün and Schwarcz 2000).

Studies of the loess-paleosol series in the Russian Plain allow identification of a horizon of fossil soil – the Inzhavino paleosol – attributable to the Likhvin Interglacial (Velichko et al. 1992, Shik 2014). According to further investigations in Eastern Europe, the Likhvin Interglacial was followed by a colder interval (MIS 10, 374–337 ka BP) (Velichko et al. 1992), which in turn was replaced by a significant warming – the Kamenka Interglacial (MIS 9, 337–300 ka BP); it was at that time that the Kamenka paleosol developed and became widely distributed over the Russian Plain. The Kamenka Interglacial was followed by a further cooling (MIS 8, 300–243 ka BP). As to the subsequent warm interval marked by the Romny fossil soil formation (MIS 7, 243–191 ka BP), it has been interpreted in two different ways – either as an interglacial (Bolikhovskaya 1995, Shik 2014), or as interstadial (Velichko et al. 2009).

Above the Romny soil the Dnieper loess horizon occurs in sections beyond the Pleistocene ice sheets (in the periglacial zone), and the Dnieper till is characterized by a complicated structure – within the limits of the ice sheet (MIS 6, 191–~130 ka BP). This glacial stage is known as the Saalian in Western Europe and as the Walstonian in Great Britain. However it should be noted that the Netherland stratigraphic schemes consider the duration of the Saalian to be much longer (Markova and van Kolfshoten 2012).

In Western Europe the most comprehensive stratigraphy of this interval was based on the materials from Great Britain (Schreve and Bridgland 2002, Schreve 2004a, b, c). The data obtained by the British specialists revealed the complicated character of the interval and are in close agreement with those from Eastern Europe. Similarly complete materials have been obtained by studies of the German multi-layered locality Schöningen (van Kolfshoten 1993, 2014). The presently available materials from Western Europe show a complicated history of climatic fluctuations in the second half of Middle Pleistocene and are relatively correlatable with the East European materials.

When studying the faunas dated to that period, much attention is given to evolutionary changes in the water vole *Arvicola*. It should be noted that the earliest evolutionary stage and species of genus evolution is known under different names in different European countries: such as *Arvicola mosbachensis* or *A. cantianus* or *A. terrestris cantianus*. In this paper, we used the name of the taxon in the way it was originally used by the authors of the faunas in question. A differentiation in enamel thickness was observed by some investigators (Heller 1968). An index (referred to as “k”) designating the enamel thickness ratio in *Arvicola* teeth was first suggested by Markova (1975) and has been since used to detect the evolutionary stage and thus the relative age of surrounding deposits. Somewhat later a similar index

(named “SDQ” which is the reciprocal value of “k”) was introduced independently by Heinrich (1978) and SDQ became extensively used in the European literature. Here we also used this index when comparing the East European and West European *Arvicola* finds. It is noteworthy that studies of the modern water voles revealed a considerable geographical variability in that index. It is much higher in southern regions than in the north (Markova 1981, 1982, Röttger 1987) (Tab. 3). On the whole, the index should be used with caution, and, if possible, together with other stratigraphic information.

Major evolutionary changes were revealed in the lineage of steppe lemmings *Prolagurus-Lagurus* not only in faunas from the Pannonian Basin (Jánossy 1986), but even more frequently in the materials from Eastern Europe (Markova 1974, 1982, Rekovets 1994, Agadjanian 2009). Several stages in steppe lemming evolution were observed in the second half of the Middle Pleistocene and considerably assist dating of the Eastern European faunas: *Lagurus transiens* (progressive type) was typical for the localities of the Likhvin (Holsteinian) interglacial; *L. ex gr. transiens-lagurus* (= *L. chosaricus*) – for the Kamenka and the Romny interglacials; *L. lagurus* – for Dnieper glacial time (Text-figs 4, 5). Unfortunately the lagurine species are almost absent in Western European faunas, except for the south eastern part of Central Europe.

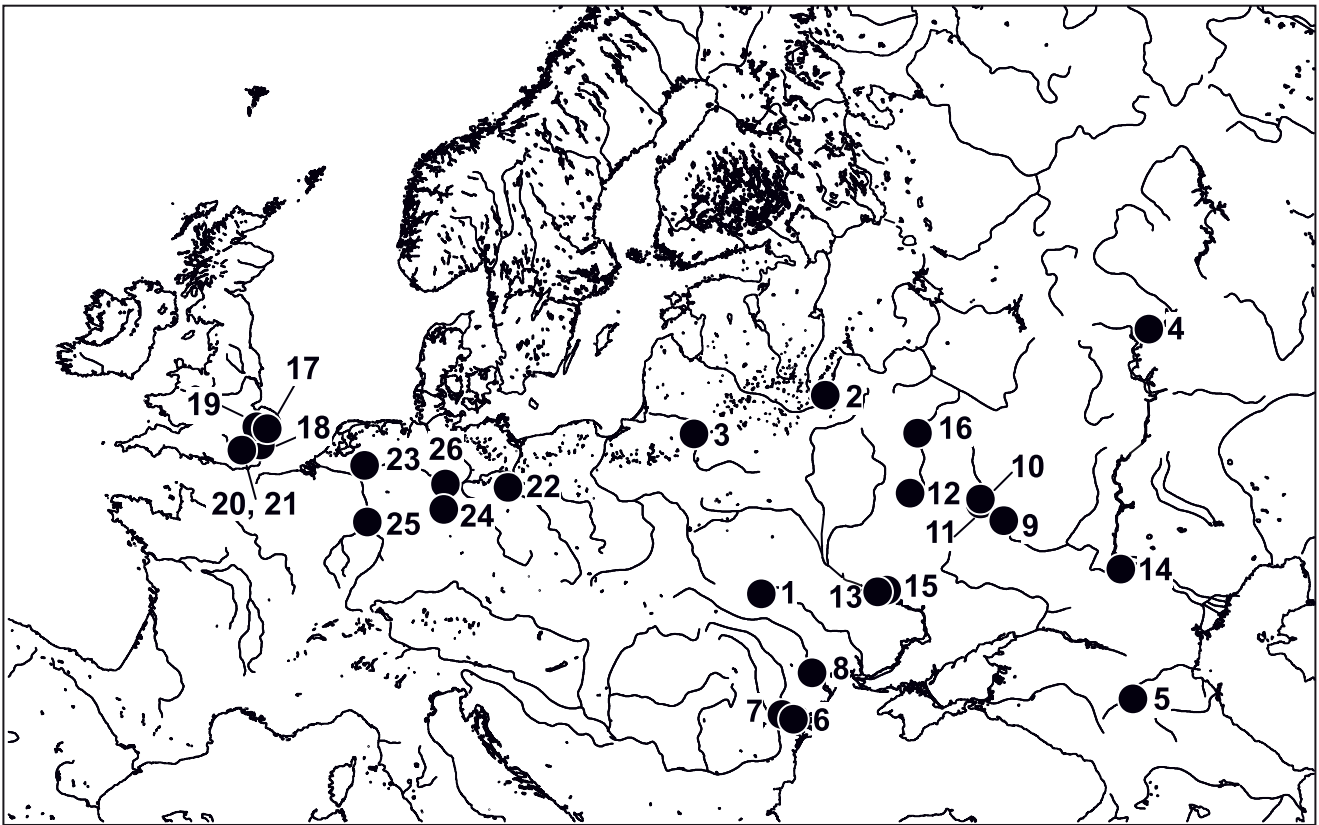
Small mammal faunas of MIS 11

Eastern Europe

In Eastern Europe numerous localities with small mammal remains dated to the Likhvin Interglacial have been discovered and studied over the last decades (Motuzko 1985, Rekovets 1994, Markova 2004a, b, 2005, 2006, 2007, Agadjanian 2009) (Text-fig. 1). 16 Likhvin localities with small mammals can be found on the Russian Plain between 57° N in the north and the Black Sea coasts and the Northern Caucasus in the south. The stratigraphic context of the faunas in the key loess-paleosol series is relatively distinct: they occur above the deposits of the Oka glaciation and below the Kamenka and Romny paleosol horizons separated by loesses and overlain by Dnieper till or Dnieper loess.

Chekalin, Tula Region, Oka River drainage basin, Russia (54° 05′ 39″ N, 36° 14′ 34″ E). According to Agadjanian’s (2009) data, the species composition from the Likhvin stratotype (recovered from the gytja layer) includes *Apodemus cf. sylvaticus*, *Clethrionomys glareolus*, *Microtus* sp. and the small sized water vole *Arvicola mosbachensis* (= *cantianus*) with the tooth enamel differentiation of “*Mimomys*” type (Bolikhovskaya and Sudakova 1996, Agadjanian 2009) (Text-fig. 1, Tab. 1).

Gun’ki, Poltava Region, Kremenchug District, Ukraine, lower reaches of the Psyol River (left tributary of the Dnieper River) (49° 14′ 43″ N, 33° 33′ 43″ E). The fauna was recovered from the alluvial and lacustrine (oxbow lake) sediments on the 4th terrace of the Psyol River. The bone-bearing layers are overlain by a thick loess-paleosol series and glacial deposits of the Dnieper glacial. In this locality the part of the sequence between the Dnieper till and the bone-bearing deposits includes Kamenka and Romny paleosols with a loess horizon between them (Markova 1975, Velichko



Text-fig. 1. Map with European small mammal localities of MIS 11 age: 1 – Medzhybozh, 2 – Smolensky Brod, 3 – Nyaravai-2, 4 – Rybnaya Sloboda, 5 – Otkaznoye, 6 – Ozernoye, 7 – Uzmari, 8 – Kolkotova Balka (Inzhava paleosol), 9 – Vladimirovka, 10 – Strelitsa, 11 – Verkhnyaya Emancha, 12 – Mikhailovka 3, 13 – Chigirin, 14 – Raigorod, 15 – Gun’ki 1 and 2, 16 – Chekalin (Likhvin gittja), 17 – Hoxne (layers B2 and B1), 18 – Clacton-on-Sea, 19 – Southfleet Road (layer 3), 20 – Beeches Pit, 21 – Barnfield Pit, 22 – Račinéves, 23 – Niide, 24 – Bilzingsleben II, 25 – Kärlich H, 26 – Shöningen (13 DB, 13 I).

et al. 1992). The greenish loam (Gun’ki 2) yielded small mammal remains identified as *Sorex praeareaneus*, *Ochotona* sp., *Allactaga major*, *Spermophilus* sp., *Alactagulus pumilio*, *Spalax* sp., *Cricetus cricetus*, *Clethrionomys* sp., *Lagurus transiens*, *L. aff. lagurus*, *Eolagurus luteus* aff. *volgensis*, *Arvicola cantianus*, *Microtus (Stenocranius) gregalis*, *Microtus arvalis*, *M. oecconomus*. The loam is underlain by gytjtja (Gun’ki 1) including numerous remains of *Arvicola cantianus* (230) and *Microtus arvalis* (172). The pollen spectra from the gytjtja are characteristic for the Likhvin Interglacial (Gubonina 1975). The mollusc fauna recovered from the layer was correlated with that found in deposits of the Old Euxinian transgression of the Black Sea (Velichko et al. 1997) (Text-fig. 1, Tabs 1, 2).

The small mammal fauna recovered from the Gun’ki section is much richer than the fauna from the Likhvin deposits exposed in the Chekalin stratotype section and includes about 1,500 identifiable remains (Markova 1982) many of them belonging to *Arvicola cantianus*. Lagurins are represented by some evolutionarily advanced steppe lemmings *Lagurus transiens*, including *L. lagurus* morphotypes. No rhizodont voles of the genera *Mimomys* and *Pliomys*, nor of *Microtus (Terricola) arvalidens* and *Microtus (Stenocranius) gregaloides* have been found. Such a faunal spectrum is typical for the so-called Gun’ki small mammal assemblage (Markova 1990) correlatable with the Singilian large mammal assemblage described by Gromov (1948).

The Singilian stratotype section near the town of **Raigorod**, Volgograd Region, Svetloyarsk district, the Volga River drainage basin, Russia (48° 25’ 40” N, 44° 55’ 17” E) was described by Gromov (1948). He distinguished the Singilian mammal assemblage on the base of the large mammal fauna from Raigorod. This locality also contains a few small mammal remains sampled by Aleksandrova in 1965 (GIN RAS collection, No. 824). The small mammal fauna described in Raigorod includes a transitional form of steppe lemmings *Lagurus transiens-lagurus*, as well as *Eolagurus luteus*, *Microtus (Stenocranius) gregalis*, *Microtus arvalinus*, *Microtus oecconomus*, *Ellobius* sp. and *Spermophilus* sp. (A. S. Tesakov, pers. communication). Unfortunately, no *Arvicola* remains have been found in that fauna. The stratigraphical position of the Raigorod fauna is discussed. Based on the geological data, Zastrozhnov et al. (2015) considered that this locality should be correlated with the early stage of the Khazar mammal assemblage.

Chigirin on the right bank of the Dnieper River valley, in the drainage basin of Tyasmin River (right tributary of the Dnieper), Cherkassy Region, Ukraine (49° 05’ 00” N, 32° 40’ 00” E). The fauna-bearing deposits are exposed in an old quarry. The upper part of the sequence consists of loess-like loams including fossil soil horizons and is underlain by thick till and fluvio-glacial deposits of Dnieper age. The loess-like loams lying under the till include two horizons of paleosols. Underneath the loess-paleosol series, there

Table 1. Biostratigraphical scheme of the second half of the Middle Pleistocene of Europe.

MIS	Glaciations, Interglacials	Western European localities	Principal taxa	Eastern European localities	Principal taxa
6	Saalian = Walstonian = Dnieper Glaciation	Grotte du Lazaret (C II, C III), Ariendorf I, Hersbruck, Bišnik Cave (layers 15–14), Rhenen	<i>Dicrostonyx simplicior</i> , <i>Lemmus lemmus</i> , <i>Arvicola terrestris</i> ssp. B, <i>Microtus agrestis</i>	Kipievo 1, 2, Pavlovka, Drabinovka, Danilovo, Zhukevichi, Konevichi, Chekalin (fluvioglac. depos.), Strigovo, Volzhino, Alpatyevo, Igorevka	<i>Microtus gregalis</i> , <i>Lemmus sibiricus</i> , <i>Lemmus lemmus</i> , <i>Lagurus lagurus</i> , <i>Dicrostonyx simplicior</i>
7	Schöningen = Sandy Lane = Romny warming (Interglacial)	Weimar- Ehringsdorf (lower travertine), Maastrichte Belvédère 4, 3, Lion Pit, Aveley, Grays Thurrock, Wageningen-Fransche Kamp I	<i>Arvicola terrestris cantianus</i> (adv. type), <i>Castor fiber</i> , <i>Trogontherium cuvieri</i> , <i>Clethrionomys glareolus</i> , <i>Microtus (Terricola) subterraneus</i> , <i>Microtus arvalis</i> , <i>Microtus agrestis</i> , <i>Microtus oeconomus</i>	Matveevka	<i>Arvicola chosaricus</i> , <i>Lagurus lagurus</i> , <i>Microtus gregalis</i>
8	Cooling	Harnham, Bišnik Cave (layer 19)	<i>Dicrostonyx</i> sp., <i>Lemmus lemmus</i> , <i>Microtus gregalis</i> , <i>Microtus agrestis</i>		
9	Reinsdorf = Parfleet = Kamenka Interglacial	Schöningen (13 II-1–4; 12 B, 12 II-1–5) Za Hájovnou Cave, Parfleet, Gudmore Grove	<i>Arvicola terrestris cantianus</i>	Cherny Yar, Plavni, Uzunlar, Rasskazovo, Priluki, Kolkotova Balka (Kamenka paleosol)	<i>Eolagurus luteus volgensis</i> , <i>Lagurus</i> ex gr. <i>lagurus</i> , <i>Arvicola chosaricus</i>
10	Cooling			Topka	<i>Arvicola</i> ex gr. <i>chosaricus</i>
11	Holsteinian = Hoxnian = Likhvin Interglacial	Niide, Hoxne (layers B2, B1), Barnfield Pit, Beeches Pit, Southfleet Road (layer 3), Clacton-on-Sea, Schöningen 13 I, Schöningen 13 DB, Kärlich H, Bilzingsleben II, Račiněves	<i>Arvicola terrestris cantianus</i> , <i>Clethrionomys glareolus</i> , <i>Microtus arvalis</i> , <i>Microtus (Terricola) subterraneus</i> , <i>Microtus agrestis</i> , <i>Microtus oeconomus</i>	Nyaravai 2, Verkhnyaya Emancha, Medzhybozh I, Gun'ki 1, 2, Chigirin, Chekalin (gittja), Ozernoye, Uzmari, Kolkotova Balka (Inzhavino paleosol), Rybnaya Sloboda, Otkaznoye, Smolensky Brod	<i>Arvicola cantianus</i> , <i>Lagurus transiens</i> , <i>Eolagurus luteus volgensis</i> , <i>Microtus arvalis</i> , <i>Microtus gregalis</i> , <i>Microtus agrestis</i> , <i>Microtus oeconomus</i>

is a member of cross-stratified alluvial sands with small mammal bone remains (Markova 1982). Among the faunal remains there are: *Desmana* sp. (4), *Sorex* sp. (3), *Ochotona* sp. (11), *Spermophilus* sp. (10), *Allactaga major* (1), *Spalax microphthalmus* (7), *Cricetus cricetus* (3), *Clethrionomys glareolus* (12), *Lagurus transiens* (73), *Eolagurus luteus volgensis* (62), *Arvicola cantianus* (199), *Microtus (Stenocranius) gregalis* (25), *M. oeconomus* (15), *M. ex gr. arvalis* (25) (Markova 1982) (see Text-fig. 1, Tabs 1, 2).

Pivikha, left side of the Dnieper River valley, the Kremenchug reservoir bank, Poltava Region, Ukraine (49° 13' 48" N, 33° 06' 36" E). The small mammal fauna is confined to fluvial deposits of the 4th Dnieper terrace exposed in the lower part of the scarp facing the reservoir; the scarp known as Pivikha Mountain resulted from sediment distortion by the Dnieper ice sheet margin. The fauna includes *Sorex* sp., *Ochotona* sp., *Spermophilus* sp., *Spalax* sp., *Clethrionomys glareolus*, *Mimomys* sp., *Prolagurus posterius*, *Lagurus transiens*, *Lagurus lagurus*, *Eolagurus luteus volgensis*, *Arvicola cantianus*, *Microtus (Terricola) arvalidens*, *M. (Stenocranius) gregalis*, *M. arvalis*, *M. oeconomus*. The lagurini belonging to *L. transiens* and *L. lagurus* are of transitional morphotypes, which is typical for Likhvinian faunas. The records of one *Mimomys* tooth and 4 teeth of *P. posterius* may be redepositions. The principal part of the Pivikha fauna is similar to those of the Gun'ki and Chigirin localities and is also attributed to the Likhvin Interglacial (Markova 1982) (Text-fig. 1, Tabs 1, 2).

Mikhailovka 3 in the Kursk Region, Russia is named after the Mikhailovka quarry (52° 14' 6" N, 35° 22' 12" E). The fauna was found in brown clay loam underlying the Likhvin paleosol. Below the clay loam there are blue-gray clays attributed to the Oka glacial. The fauna includes *Spermophilus* sp., *Clethrionomys cf. glareolus*, *Microtus ex gr. middendorffi-hyperboreus*, *Microtus (Stenocranius) gregalis*, *Ochotona cf. pusilla* (Agadjanian and Glushankova 1986) (Text-fig. 1, Tab. 1).

A few localities with Likhvin faunas have been discovered in the Don drainage basin: **Verkhnyaya Emancha** (51° 33' N, 38° 54' E), **Strelitsa** (51° 36' 29" N, 38° 54' 36" E), **Vladimirovka 2** (50° 49' 54" N, 39° 52' 57" E), all Russia (Agadjanian 1976, 2009, Udartsev 1980, Markova 1981, 1990) (Text-figs 1, 6, 7, Tabs 1, 2). In these sections the faunas occur below the Kamenka and Romny paleosols with a loess horizon between them (Tab. 1). The Dnieper till is absent from the sequence, as the Dnieper ice sheet did not enter the Don basin.

Several localities with a similar species composition of small mammals have been discovered in the southwest of the Russian Plain in the sections of **Kolkotova Balka** in Tiraspol, the Dniester River drainage basin, Moldova (46° 50' 25" N, 29° 38' 35" E), **Uzmari** near the Giurgiulești settlement, Prut River drainage basin, Moldova (45° 29' N, 28° 12' E), **Ozernoje**, on the eastern coast of Lake Yalpug, the Danube River drainage basin, Ukraine (45° 24' 18" N, 28° 40' 41" E) (Mikhaylesku and Markova 1992, Markova 2005) (Text-fig. 1, Tabs 1, 2). In Kolkotova Balka the small mammal remains were recovered directly from crotovines within the Inzhavino paleosol correlatable with the Likhvin Interglacial. The sequence overlying the Inzhavino paleosol includes four paleosols (from the top downwards): Bryansk

interstadial soil, Mezin paleosol complex, Romny and Kamenka paleosols, with loess horizons occurring between the fossil soils. Below the Inzhavino paleosol the sequence is as follows: loess horizon; Vorona paleosol; and an assemblage of alluvial deposits from the 6th Dniester terrace (Markova 1992, 1998, Mikhaylesku and Markova 1992, Dodonov et al. 2006).

The southernmost locality datable to the Likhvin interval – **Otkaznoye** – was discovered in the Northern Caucasus, in the Kuma River drainage basin, near the city of Georgievsk, Russia (44° 19' 44" N, 43° 51' 15" E). The fauna is confined to the Inzhavino paleosol horizon (Text-fig. 1, Tab. 1) and includes mostly species typical of open landscapes: ground squirrels, steppe and yellow lemmings, mole-rats, etc. The facies of the locality (fossil soil) excludes the possibility of finding the remains of water voles there. The locality Otkaznoye has a very complicated structure, the loess-paleosol series being more than 130 m thick. The Inzhavino paleosol is overlain by several fossil soils (Kamenka, Romny, Mezin) intercalated by loess horizons (Bolikhovskaya et al. 2016).

The northernmost localities dated to the Likhvin are from **Rybnaya Sloboda** in the Kama River basin (at the river mouth), Russia (55° 27' 18" N, 50° 09' 14" E) (Text-fig. 1) (Markova 1992, Markova and Udartsev 2004), from **Nyaravai-2** in the Neman drainage basin, in Lithuania (54° 34' 59" N, 23° 58' 30" E) (Text-fig. 1, Tabs 1, 2), and from **Smolenskiy Brod** in the Zapadnaya (= Western) Dvina (= Daugava) drainage basin, in Velizh District, Smolensk Region, Russia (55° 40' 12" N, 31° 24' 00" E) (Text-fig. 1, Tabs 1, 2) (Voznyachuk et al. 1979, 1984). The core of all of these faunas includes *Arvicola cantianus* and abundant *Microtus oeconomus*, *M. ex gr. arvalis* and *M. agrestis* (Text-fig. 1, Tabs 1, 2). According to Motuzko's opinion (1985), the Smolenskiy Brod fauna belongs to the phase preceding the Likhvin Interglacial. The mean values of SDQ index 124, n = 16 (Voznyachuk et al. 1979), as well as the length of the water vole M_1 fall into the range of *Arvicola* characteristics for the Likhvin interglacial.

The Likhvin locality of **Rybnaya Sloboda** at the Kama River mouth, Tatarstan Republic, Russia is at the far east of Eastern Europe, its geographic position being reflected in the composition of the faunal assemblage. The latter includes abundant remains of *Arvicola cantianus*, *Clethrionomys glareolus*, *Lagurus transiens*, *Microtus ex gr. arvalis*, *M. oeconomus*, *M. agrestis* typical for the Likhvin Interglacial, as well as *Clethrionomys rufocanus* remains (this is a very rare find of that species in the Pleistocene deposits of the Russian Plain) (Markova 1992) (Text-fig. 1, Tabs 1, 2).

The multilayered locality **Medzhybozh 1** on the left bank of the Southern Bug River, Khmelnytsky Region, Ukraine (49° 26' 20" N, 27° 24' 18" E) is known for Early Man artifacts attributed to different cultures from the Early Paleolithic (in the two lowermost horizons) and of the Late Palaeolithic (occasional finds in the upper horizons of the sequence (Krokhmal' and Rekovets 2010, Stepanchuk 2014). The lower layers (10 to 15) with mammal fauna and Early Palaeolithic (Acheulean) artifacts are correlated with the Likhvin Interglacial. The small mammal fauna includes *Marmota* sp., *Spermophilus suslicus*, *Spalax* sp., *Trogotherium cuvieri*, *T. minus*, *Castor fiber*, *Micromys* sp., *Arvicola mosbachensis*, *Microtus arvalidens*, *M. arvalinus*,

Table 2. SDQ of *M₁ Arvicola* from the localities related to the second half of the Middle Pleistocene.

Stratigraphy	MIS	Western European localities	N	min.	mean	max.	Eastern European localities	N	min.	mean	max.
Saalian = Walstonian = Dnieper Glaciation	6	Grote du Lazaret: CII CIII	47 8		107.9 108.6		Igorevka	15	110	125	135
Schöningen = Sandy Lane = Romny Interglacial	7	Weimar-Ehringsdorf (Lower Trav.) Maastrichte Belvédère 4 Maastrichte Belvédère 3 Bišnik, layer 19	30 4 66	102 86 94	112 102 102	126 113 114	Matveevka	1		102	
Cooling	8										
Reinsdorf = Parfleet = Kamenka Interglacial	9	Shöningen-Channel II: 13 II-2 13 II-3 13 II-4 Parfleet Gudmore Grove	61 117 135 4 48	100 94 99	119 118 115	150 160 137	Cherny Yar Uzunlar Plavni	12 1 13	100	110 112	102 122
Cooling	10										
Holsteinian = Hoxnian = Likhvin Interglacial	11	Niide Hoxne Swanscombe Bilzingsleben II Barnham	58 8 4 52 14	124 110	146 140	169 162	Medzhybozh L. 10–11 L. 14–15 Gun'ki 1 Gun'ki 2 Chigirin Verkhnyaya Emancha Ozernoye Rybnaya Sloboda Uzmari Smolensky Brod	25 17 23 12 48 33 36 14 52 16	91 90	107 116 125 132 129 125 130 125 130 124	125 155 169 170 167 170 145 160 140

M. gregalis, *M. agrestis*, *M. oeconomus*, *M. ex gr. arvalis* (Text-fig. 1, Tab. 1). There is another Early Palaeolithic horizon (Medzhybozh A), tentatively correlated with the Muchkap Interglacial. The enamel index of the *Arvicola* *M₁* is given in Table 2 (according to Rekovets et al. 2007, Krokmal' and Rekovets 2010).

So, the species composition of the Likhvin faunas includes *Arvicola cantianus*, *Lagurus transiens* (progressive

type), *Microtus (Pallasinus) oeconomus*, *M. (Microtus) ex gr. arvalis*, *M. (Microtus) agrestis*, *M. (Stenocranius) gregalis*. The remains of rhizodont voles *Mimomys*, *Pliomys* and *Microtus (Stenocranius) gregaloides* haven't been recovered from the localities. *Microtus (Terricola) arvalidens* is absent in the absolutely majority of the localities of Likhvin age (Markova 2004a, b, 2006). It was found only in Medzhybozh 1 (Krokmal' and Rekovets 2010).

In conclusion, the small mammal localities correlatable with the Likhvin Interglacial, yield water vole remains with a specific structure. The *Arvicola* teeth are small sized, and occasionally have a *Mimomys*-type fold on M_1 , the mean SDQ = 125–130 (Markova 1975, 1981, 1982, 2006). Average values for this index from several localities are shown in Tab. 2. Unfortunately, values of SDQ index have not yet been published for teeth of water voles recovered from the gyttja in the Likhvin Interglacial stratotype locality at Chekalin.

Western Europe

The multilayered locality of **Schöningen**, Germany (52° 08' 22" N, 10° 57' 57" E) includes several accumulations of mammal bones in different parts of the quarry and at different geological levels. Human-made artifacts are found occasionally. The oldest of the bone accumulations (**Schöningen 13 DB** and **13 I**) contain the following small mammals: *Sorex minutus*, *Sorex (Drepanosorex)* sp., *Desmana* sp., *Castor fiber*, *Trogontherium cuvieri*, *Spermophilus* sp., *Dicrostonyx* sp., *Lemmus lemmus*, *Clethrionomys glareolus*, *Arvicola terrestris cantianus*, *Microtus (Terricola) subterraneus*, *M. arvalis*, *M. agrestis*, *M. oeconomus*, *M. gregalis*, *Apodemus sylvaticus*. From large mammals there are: *Panthera spelaea*, *Ursus spelaeus*, *Ursus thibetanus*, *Palaeoloxodon antiquus*, *Equus mosbachensis*, *Stephanorhinus kirchbergensis*, *Sus scrofa*, *Cervus elaphus*, *Megaloceros giganteus*, *Capreolus capreolus*, *Bos primigenius*, *Bos/Bison*. The localities are attributed to the Holsteinian Interglacial (MIS 11) and are correlated with Likhvin localities in Eastern Europe (Markova and van Kolfschoten 2012, van Kolfschoten 2014) (Text-fig. 1, Tabs 1, 2).

Kärlich H in Germany (50° 24' 28" N, 7° 29' 23" E) is found in the Neuwied drainage basin. The rather scanty mammal fauna (*Talpa* sp., Sciuridae gen. sp., *Microtus arvalis/Microtus agrestis*, *Microtus* sp., *Apodemus* sp., *Mammuthus trogontherii* (van Kolfschoten and Turner 1996) is correlated with the Holsteinian (Text-fig. 1, Tab. 1).

Bilzingsleben II, Thuringia, Germany (51° 19' 36" N, 11° 7' 30" E). The mammal fauna of the locality includes *Trogontherium cuvieri*, *Arvicola cantianus* (= *mosbachensis*), *Microtus (Terricola) subterraneus*, *Elephas antiquus*, *Stephanorhinus kirchbergensis*, *Ursus deningeri*, *Sus scrofa*, *Capreolus*. In addition, remains of *Macaca sylvanus* and *Homo* sp. have been found there (von Koenigswald 2007). The fossiliferous deposits (including the fauna of Bilzingsleben II) were dated by U-Th and ESR at $\leq 414 \pm 45$ ka BP (Schwarcz et al. 1988), so they belong to the Holsteinian Interglacial (MIS 11). The SDQ of *Arvicola* equals ~133 (Heinrich 1990) (Text-fig. 1, Tabs 1, 2).

Neede, the Netherlands (52° 08' 6" N, 6° 36' 37" E). The fauna recovered from clayey sediments (Neede Clay) was described by van Kolfschoten (1990a, b). Among small mammals there are *Sorex* cf. *araneus*, *Trogontherium cuvieri*, *Apodemus* sp., *Clethrionomys* cf. *glareolus*, *Arvicola terrestris cantianus*, *Microtini* indet. Large mammals include *Equus* sp., *Dicerorhinus mercki*, *Cervus elaphus*. The pollen assemblage allows the Neede Clay to be dated to the Holsteinian Interglacial (MIS 11) (Text-fig. 1, Tab. 1).

Račíněves locality, the Czech Republic, Vltava River drainage basin (50° 22' 30" N, 14° 13' 12" E), yielded remains

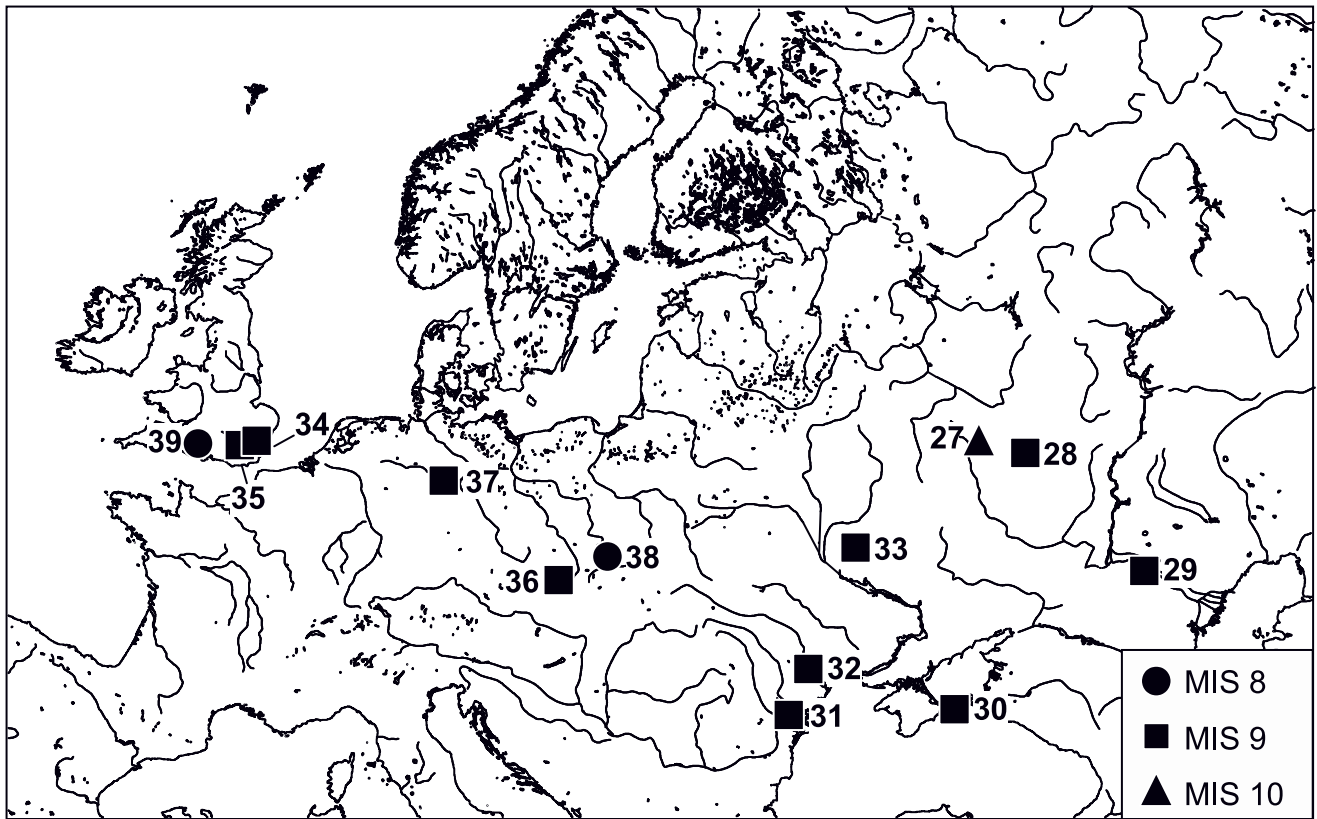
of *Microtus* sp., *Arvicola terrestris cantianus*, *Mammuthus trogontherii*, *Mammuthus primigenius* and others. It was also placed in the Holsteinian Interglacial on the basis of the Holsteinian paleosol overlying fossiliferous alluvial deposits (Tyráček et al. 2004). The species composition of the fauna supports this decision (Text-fig. 1, Tab. 1).

Barnfield Pit in Swanscombe, Kent, Great Britain (~51° 25' N, ~0° 15' E) is located in the south of the Thames drainage basin, 5 km east of Dartford (Schreve 2004a) and is famous for the skull of an ancient man plus some artifacts attributed to Clactonian and Acheulean cultures. The bone-bearing layers lie over deposits dated to the Anglian glacial epoch. The fauna was described by D. Schreve under the name of Swanscombe Mammalian Assemblage Zone (MAZ) (Schreve 2004a). The mammal fauna was recovered from several layers and included a number of large and small mammals: *Talpa minor*, *Macaca sylvanus*, *Oryctolagus cuniculus*, *Trogontherium cuvieri*, *Arvicola terrestris cantianus*, *Microtus (Terricola) subterraneus*, *M. arvalis*, *M. agrestis*, *M. oeconomus*, *Ursus spelaeus*, *Dama dama clactoniana*, *Stephanorhinus kirchbergensis*, *S. hemitoechus*, *Megaloceros giganteus*, *Bos primigenius*, *Equus hydruntinus*, etc. (Parfitt 1998). Of particular interest are remains of primitive *Arvicola terrestris cantianus* with an SDQ index equal to ~140 (n = 4) (Text-fig. 1, Tabs 1, 2). Some *Lemmus lemmus* remains were found in the upper layer.

Beeches Pit, West Stow, Suffolk, U.K. (52° 18' 15" N, 0° 40' 24" E) is correlated with the optimum of the Hoxnian (Holsteinian) Interglacial. The fauna found in the locality includes *Sorex minutus*, *Neomys* sp., *Talpa minor*, *Lepus* sp., *Sciurus* sp., *Trogontherium cuvieri*, *Clethrionomys glareolus*, *Arvicola terrestris cantiana*, *Microtus (Terricola)* cf. *subterraneus*, *Microtus agrestis*, *Apodemus sylvaticus*, *Apodemus maastrichtiensis*, *Eliomys quercinus*, *Ursus* sp., *Mustela nivalis*, *Equus ferus*, *Stephanorhinus hemitoechus*, *Dama dama*, *Cervus elaphus*, *Bos primigenius* (Preece et al. 2000). The dating results permit the locality to be attributed to MIS 11: its age, according to the uranium series, is 390–400 ka BP. Thermoluminescent analysis however gave a date of 471 ± 51 ka BP (Preece et al. 2000, Candy et al. 2014).

Southfleet Road locality, Ebbsfleet, NW Kent, U.K. (51° 26' 16.64" N, 0° 18' 57.40" E). **Unit 3** (tufa and grey clay) in the sequence contains remains of *Neomys* sp., *Talpa minor*, *Sorex minutus*, *Castor fiber*, *Clethrionomys glareolus*, *Apodemus sylvaticus*, *Arvicola terrestris cantiana*, *Microtus (Terricola)* cf. *subterraneus*, *Microtus agrestis*, *Microtus* sp. Of large mammals there were found *Palaeoloxodon antiquus*, *Stephanorhinus hemitoechus*, *Sus scrofa*, *Cervus elaphus*, *Capreolus capreolus* (Wenban-Smith et al. 2006). Some Clactonian tools were also found in the section. The locality was dated to MIS 11 (Hoxnian Interglacial) (Text-fig. 1, Tab. 1).

Similar fauna has also been found in the **Clacton-on-Sea** locality, U.K. (51° 47' 6" N, 1° 84' 2" E) where it occurs together with Palaeolithic Clactonian tools (Bridgland 1994, Wenban-Smith et al. 2006). Rich pollen assemblages recovered from the bone-bearing layers permitted it to be confidently attributed to the Hoxnian (Turner and Kerney 1971). Fauna similar to the above was described in the Hoxnian Interglacial stratotype, U.K. (**Hoxne**, layers **B2**, **B1**, 52° 21' 32" N, 1° 12' 6" E). It included *Castor fiber*,



Text-fig. 2. Map with European small mammal localities of MIS 8, MIS 9, and MIS 10 age: 27 – Topka, 28 – Rasskazovo, 29 – Cherny Yar, 30 – Uzunlar, 31 – Plavni, 32 – Kolkotova Balka (Kamenka paleosol), 33 – Priluki, 34 – Gudmor Groupe, 35 – Parfleet, 36 – Za Hájovnou Cave, 37 – Shöninggen (13 II-1-4, 12 B, 12 II-1-5), 38 – Bišnik (layer 19), 39 – Harnham.

Trogontherium cuvieri, *Talpa minor*, *Microtus (Terricola)* cf. *subterraneus*, *Lemmus lemmus*, and some species of large mammals: *Ursus* sp., *Panthera leo*, *Lutra lutra*, *Stephanorhinus* sp., *Equus ferus*, *Cervus elaphus*, *Capreolus capreolus*, *Dama dama*, *Macaca sylvanus* (Schreve 2000, 2001a, Ashton et al. 2008) (Text-fig. 1, Tab. 1).

Small mammal faunas of MIS 10

The only locality with small mammals was discovered in the deposits overlying those of the Likhvin Interglacial (**Topka** locality, the Don River drainage basin, 53° 20' 21" N, 39° 35' 10" E) and in all probability belongs to the cold interval correlatable with the Borisoglebsk loess horizon (Krasnenkov and Kazantseva 1993). The locality yielded remains of *Arvicola* cf. *chosaricus*, but no voles of the “*Terricola* = *Pitymys*” subgenus, typical for pre-Oka faunas, have been found at Topka (Text-fig. 2, Tab. 1).

Small mammal faunas synchronous to MIS 9

Eastern Europe

At present there are three localities with a small mammal fauna datable to the Kamenka Interglacial of Eastern Europe. The small mammal remains were found in the mole burrows within the Kamenka fossil soil at **Priluki**, the Dnieper drainage basin, Ukraine (50° 35' 42" N, 32° 23' 24" E), and **Rasskazovo**, Oka-Don Plain, Russia (52° 40' 20" N, 41° 54' E) (Markova 1982).

Kolkotova Balka locality, **Kamenka paleosol**, near the city of Tiraspol, the Dniester drainage basin, Moldova (46°

50' N, 29° 36' 36" E) (Text-fig. 2, Tabs 1, 2). The scarce fauna of small mammals recovered from crotonines within the Kamenka paleosol includes steppe lemming (*Lagurus lagurus*) remains (Mikhaylesku and Markova 1992).

Another locality which seemingly belongs to the same interval is **Plavni**, Odessa Region, Ukraine (45° 24' 18" N, 28° 35' 24" E), discovered in the liman-fluvial series on the 3rd terrace of the Danube River. Another supposedly of the same age is **Uzunlar**, Crimea Peninsula, Russia (45° 03' N, 36° 05' E), surrounded by the liman-marine sediments of the Uzunlarian transgression of the Black Sea. It is vaguely possible, however, that the deposits might correspond to MIS 7 stage. All the above faunas contain several species of microtines (*Microtus arvalis*, *Microtus gregalis*, *M. oeconomus*). Steppe lemmings of the *Lagurus* genus are similar in tooth morphotypes to *L. lagurus*, though morphotypes typical of *L. transiens* are found occasionally (Chepalyga et al. 1986, Markova 1990, Mikhaylesku and Markova 1992) (Text-fig. 2, Tabs 1, 2).

The above-listed materials are correlatable with the fauna from the **Cherny Yar** stratotypical section in the Volga drainage basin, Astrakhan Region, Russia (48° 03' 18" N, 46° 07' 12" E). The Cherny Yar fauna including *Arvicola chosaricus* (with a SDQ of 100–102), *Lagurus lagurus pleistocaenicus*, and *Eolagurus volgensis*, described by Aleksandrova (1976) and Kirillova and Tesakov (2004), was recovered from the same layers as the large mammal fauna described by Gromov and known since then as the Khozarian mammal assemblage (Gromov 1948). The latter

includes *Mammuthus trogontherii chosaricus*, *Camelus knoblochi*, *Megaloceros euryceros germaniae*, *Bison priscus longicornis*, *Equus caballus chosaricus*.

The water vole *Arvicola chosaricus* is an evolutionarily more advanced species when compared with *A. cantianus* and is an indicative of Khozarian faunas (Text-fig. 2, Tabs 1, 2). Among steppe lemmings of the genus *Lagurus* the 'lagurus' morphotype is dominant in faunas of the Khozarian type, whereas archaic 'transiens' morphotype occurs in small numbers (Markova 1982). Recently it was suggested that the Cherny Yar fauna may be younger than considered by Gromov and might even be attributable to the Mikulino Interglacial. This conjecture, however, has not been substantiated by detailed studies of the small mammals. The composition of large mammals recovered from Cherny Yar allows neither attributing it to the Mikulino Interglacial or the Shkurlatovo large mammal assemblage. It might be synchronous, however, with the last warm stage of the Middle Pleistocene – Romny Interglacial. Undoubtedly, the geological context and accompanying paleontological material prevent the small mammal faunas recovered directly from the Kamenka fossil soil from being attributed to a younger stratigraphic unit (Priluki, Rasskazovo, Kolkotova Balka, the Kamenka paleosol). Unfortunately, taphonomic characteristics of those sites rule out the presence of water vole remains being there.

Faunas from alluvial and liman-marine sediments (Cherny Yar, Plavni, Uzunlar) display a geological context which may suggest a younger age and in which case the faunas could be correlated with MIS 7.

Western Europe

The locality of **Schöningen 13 II-1-4, 12 B, 12 II-1-5**, Germany (52° 08' 22" N, 10° 57' 57" E) is situated approximately 1 km south of Schöningen 13 I. Unique archeological objects (artifacts) have been found there, including wooden arrows. A rich mammal fauna includes *Sorex minutus*, *Sorex* sp., *Neomys newtoni*, *Desmana* sp., *Castor fiber*, *Trogontherium cuvieri*, *Lemmus lemmus*, *Clethrionomys glareolus*, *Arvicola terrestris cantianus*, *Microtus (Terricola) subterraneus*, *M. arvalis*, *M. agrestis*, *M. oeconomus*, *M. (Stenocranius) gregalis*, *Apodemus sylvaticus*, *Canis lupus* (in Schöningen 13 II-4 only), *Vulpes vulpes*, *Ursus thibetanus*, *Mustela erminea*, *M. nivalis*, *Mustela* sp., *Martes* sp., Elephantidae gen. et sp. indet. (in Schöningen 13 II-4 only), *Equus mosbachensis*, *E. hydruntinus*, *Stephanorhinus kirchbergensis*, *S. hemitoechus*, *Megaloceros giganteus*, *Capreolus capreolus*, *Bos primigenius* (in Schöningen 13 II-4 only), *Bison priscus* (in Schöningen 13 II-4 only), *Bos/Bison*. Geological data and the dental morphology of Arvicolinae gave grounds for dating the fauna to an interglacial younger than the Holsteinian – to the Reinsdorf, correlatable with MIS 9 (Turner 1998, van Kolfschoten 2014) (Text-fig. 2, Tabs 1, 2).

The locality **Za Hájovnou Cave**, Moravia, Czech Republic (~49° 40' N, 16° 55' E) is in the Javoříčko Karst region. The locality consists of several bone-bearing layers. The richest material has been recovered from layers 3b–2a (the main bone bed) and includes a great number of *Ursus deningeri* bones together with remains of *Panthera* cf. *fossils*, *Canis* sp., *Bos/Bison* sp., *Sus scrofa*, *Rupicapra*

Capra sp. The fauna is attributed to the Holsteinian Interglacial, although it is not inconceivable that it could be dated to the Reinsdorf Interglacial. The dates available suggest correlating the fauna with MIS 9 (Lundberg et al. 2014). The small mammal fauna from layers 2a, b includes *Clethrionomys glareolus*, *Microtus (Stenocranius) gregalis* and *M. oeconomus*. According to Ivanov and Vörös (2014) these were layers deposited during MIS 9 under an open woodland environment.

Purfleet, U.K. (51° 29' 6" N, 0° 15' E) is usually assigned to the second interglacial that followed the Anglian glacial stage and is correlated with MIS 9 (Bridgland 1994, Schreve et al. 2002, Schreve 2004b). The mammal fauna includes 21 taxa. Among the identified taxa are *Myotis* cf. *bechsteini*, *Sorex araneus*, *S. minutus*, *Neomys* sp., *Crociodura* sp., *Macaca sylvanus*, *Castor fiber*, *Clethrionomys glareolus*, *Arvicola terrestris cantiana*, *Microtus agrestis*, *M. arvalis*, *Apodemus sylvaticus*, *Crocota crocuta*, *Felis* cf. *silvestris*, *Palaeoloxodon antiquus*, *Equus ferus*, *Dama dama dama*, *Cervus elaphus*, *Capreolus capreolus*, Cervidae sp., Bovidae indet. (*Bos* or *Bison*). The water vole teeth are distinct in having more advanced morphology than *Arvicola* from the Barnfield Pit locality, with a SDQ = 130, but more archaic than described in water voles from the localities correlatable with MIS 7 (Text-fig. 2, Tabs 1, 2). Schreve (2001a) described this fauna as belonging to the Purfleet MAZ.

Gudmore Grove locality, Marsea Island, Essex, U.K. (51° 47' 40.15" N, 0° 59' 59" E), has been thoroughly studied as regards its geology and paleontology (Roe et al. 2009). The multidisciplinary studies carried out there indicate unambiguously that it belongs to the interglacial correlatable with MIS 9. The faunal assemblage includes *Sorex* cf. *araneus*, *Sorex* cf. *minutus*, *Neomys* cf. *brouni*, *Crociodura* cf. *leucodon*, *Macaca sylvanus*, *Sciurus vulgaris*, *Castor fiber*, *Clethrionomys glareolus*, *Arvicola terrestris cantianus*, *Microtus agrestis*, *M. agrestis* or *M. arvalis*, *Apodemus* cf. *sylvaticus*, *Canis lupus*, *Ursus arctos*, *Meles meles*, *Mustela* cf. *putorius*, *Equus ferus*, *Capreolus capreolus*. The *Arvicola* SDQ index equals 133.36 (n = 48, range 105–147), which indicates an age younger than Hoxnian, as the average SDQ of the latter equals 140 (Text-fig. 2, Tabs 1, 2). The presence of *Macaca sylvanus* suggests the fauna is not older than MIS 9 (Roe et al. 2009). Other data also point to the second interglacial after the Anglian Glaciation.

Small mammal faunas of MIS 8

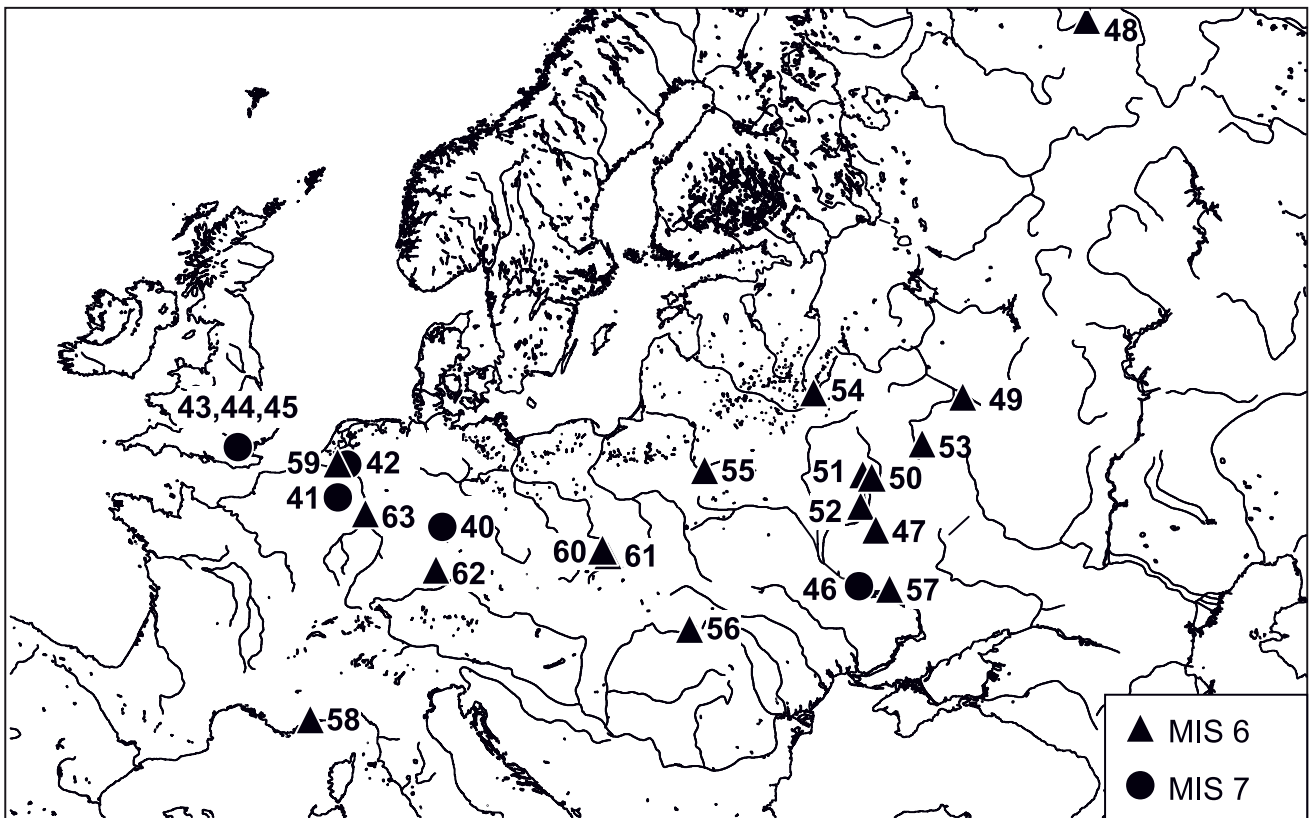
Eastern Europe

No faunas attributable to the MIS 8 cold interval have been found as yet.

Western Europe

The **Harnham** locality is found in the south of Great Britain, at the confluence of the Avon and Ebbles (51° 03' 48" N, 1° 48' 40" W). It was dated by OSL to approximately 250 ka BP and attributed to the end of MIS 8 (Bates et al. 2014). The locality yielded some Acheulean artifacts and mammal bones (*Apodemus* sp., *Clethrionomys* sp., *Microtus oeconomus*, and *Microtus* sp.) confined to the cultural layer (Text-fig. 2, Tab. 1).

A unique multilayered cave site with artifacts of the Middle Palaeolithic was discovered in Poland in the south



Text-fig. 3. Map with small mammal European localities of MIS 6 and MIS 7 age: 40 – Weimar-Ehringsdorf (Lower Travertine), 41 – Maastrichte-Belvédère (layers 3, 4), 42 – Wageningen-Fransche Kamp 1, 43 – Grays Thurrock, 44 – Aveley, 45 – Lion Pit, 46 – Matveevka, 47 – Igorevka, 48 – Kipievo 1 and 2, 49 – Alpatievo, 50 – Pavlovka, 51 – Volzhino, 52 – Strigovo, 53 – Chekalin (fluvioglac. deposits), 54 – Konevichi, 55 – Zhukevichi, 56 – Danilovo, 57 – Drabinovka, 58 – Grotte de Lazaret, 59 – Rhenen, 60 – Deszczowa (layers I–IV), 61 – Biśnik (layers 15–14), 62 – Hersbruck, 63 – Ariendorf I.

of Cześćochowa Upland – **Biśnik Cave** (50° 25' 35" N, 19° 49' 54" E) (Text-fig. 2, Tabs 1, 2). The sequence includes several cultural layers spanning a time interval from MIS 9 (?) to MIS 2 (Cyrec et al. 2010). **Layer 19**, correlated by Cyrec et al. (2010) with MIS 8–8/7 and with the Odra glaciation, yielded remains of mammal fauna, including cold-tolerant, steppe, aquatic, and forest species: *Ochotona pusilla*, *Neomys fodiens*, *Sciurus vulgaris*, *Glis glis*, *Sicista betulina*, *Apodemus flavicollis/sylvaticus*, *Cricetus cricetus*, *Cricetulus migratorius*, *Clethrionomys glareolus*, *Arvicola amphibious* (= *terrestris*), *Dicrostonyx* cf. *henselii/guilielmi* (dominant), *Lemmus lemmus* (dominant), *Microtus subterraneus*, *Microtus arvalis* (dominant), *Microtus gregalis* (dominant), *Microtus agrestis*, *Microtus oeconomus* (dominant). From large mammals there are *Martes martes*, *Ursus spelaeus*, *Equus caballus*, *Capra ibex/caucasica*, *Alces alces*, *Capreolus capreolus* (Cyrec et al. 2010, Socha 2014). The fauna is dominated by cold-tolerant (lemmings, narrow-skulled vole) and eurybiont species, such as field vole, or root vole (*Microtus oeconomus*). According to the enamel index of water vole teeth (SDQ = 100.65–107.12), the fauna may be dated to the second half of the Middle Pleistocene. As noted by P. Socha, collared lemmings in layers 19–14 feature a “simplicior” morphotype dominant in M¹ and M² (up to 73% in the sample). That also suggests the 2nd half of Middle Pleistocene as the age of the fauna. In all probability, it corresponds to a cold stage – MIS 8. In our

opinion, it would be incorrect to correlate it with MIS 7 – the warm interval within the Middle Pleistocene.

Layer 18 lying above layer 19 is considered by Socha (2014) to be correlatable with MIS 7–7/6. Judging from the cited list of rodents (also dominated by two lemming genera, narrow-skulled vole and root vole), that fauna is cold-tolerant and may be correlated with a cold stage of the Middle Pleistocene. Conceivably, it could be attributed to MIS 8 (Tab. 1).

Small mammal faunas of MIS 7

Eastern Europe

The fauna found in **Matveevka** locality on the Sula River, the Dnieper River drainage basin, Cherkassy Region, Ukraine (49° 31' N, 32° 41' E) may be assigned to the end of the Romny warming. The sequence includes a layer of sand and gravel with bone remains of small mammals. Upwards it is replaced with a loess layer overlain in turn with the Dnieper till, higher still a loess-like loam occurs including a paleosol horizon (Rekovets 1994, Krokmal' and Rekovets 2010). The fauna composition is as follows: *Sorex* sp., *Ochotona* sp., *Spermophilus suslicus*, *Spalax* sp., *Cricetus* sp., *Ellobius* sp., *Clethrionomys* sp., *Lagurus lagurus*, *Eolagurus* sp., *Arvicola chosaricus*, *M. arvalis*, *Microtus* (*Stenocranius*) *gregalis*, *M. oeconomus* (Text-fig. 3, Tab. 1).

Western Europe

Lion Pit in the lower reaches of the Thames, West Thurrock, U.K. (51° 29' 8.9" N, 0° 18' 7.2" E) yielded mammal fauna including *Apodemus sylvaticus*, *Vulpes* cf. *vulpes*, *Ursus arctos*, *Mammuthus trogontherii*, *Palaeoloxodon antiquus*, *Equus ferus*, *Stephanorhinus kirchbergensis*, *Cervus elaphus*, *Bos primigenius*, *Bison priscus*. The fauna was attributed by Schreve (2004c) to the **Sandy Lane MAZ** (Text-fig. 3, Tab. 1).

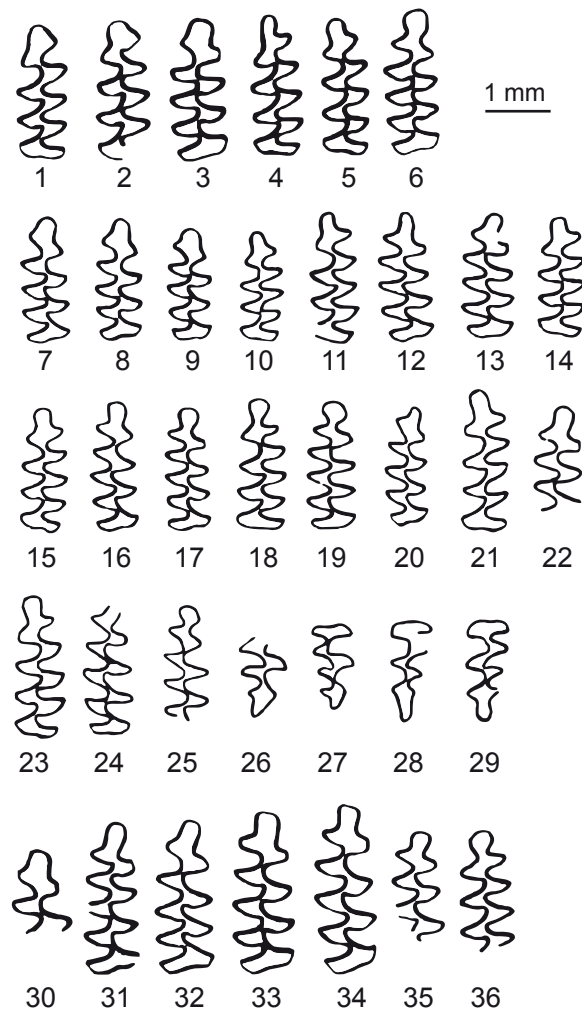
The locality **Aveley**, U.K. (51° 30' 06" N, 0° 15' 12" W) was exposed in a sand quarry, the fauna includes *Crocidura* sp., *Sorex minutus*, *Barbastella barbastellus*, *Castor fiber*, *Clethrionomys glareolus*, *Arvicola terrestris cantianus*, *Microtus agrestis* or *Microtus arvalis*, *Apodemus sylvaticus*, *Canis lupus*, *Ursus arctos*, *Felis chaus*, *Panthera leo*, *Mammuthus trogontherii*, *Palaeoloxodon antiquus*, *Equus ferus*, *Stephanorhinus hemitoechus*, *Megaloceros giganteus*, *Cervus elaphus*, *Bos primigenius*, *Bison priscus*. In common with the above, it is attributed to **Sandy Lane MAZ** and correlated with MIS 7. The enamel index of water voles SDQ = 120 (Parfitt 1998, Schreve 2004c) (Text-fig. 3).

The **Grays Thurrock** fauna, U.K. (51° 28' 30" N, 0° 18' 36" E) includes water voles similar in structure to the above mentioned (Parfitt 1998, Schreve 2004c) (Text-fig. 3, Tabs 1, 2).

The small mammal fauna of **Wageningen-Fransche Kamp 1**, the Netherlands (51° 59' N, 05° 42' E) includes *Sorex araneus*, *Crocidura* sp., *Eliomys quercinus*, *Clethrionomys glareolus*, *Arvicola cantianus*, *Microtus arvalis/agrestis*, *Apodemus sylvaticus*, *A. maastrichtiensis* and undoubtedly corresponds to a warm interval. Van Kolfschoten (2014) correlated the locality with the interglacial preceding the Saale glaciation and with MIS 7, also to the Shöningen Interglacial (Text-fig. 3, Tabs 1, 2).

A fauna closely resembling that listed above was described in **Maastrichte-Belvédère**, layers 3–4, the Netherlands (50° 52' 18" N, 5° 40' 38" E). According to van Kolfschoten's opinion, it is synchronous with the previous locality and therefore corresponds to MIS 7 (Text-fig. 3, Tabs 1, 2) (van Kolfschoten and Roebroeks 1985, van Kolfschoten et al. 1993, van Kolfschoten 2014).

The rich locality of **Weimar-Ehringsdorf** in Thuringia, Central Germany (50° 58' 60" N, 11° 19' 0" E) is multilayered. The **Lower Travertine** horizon contains *Talpa europea*, *Sorex minutus*, *S. ex gr. araneus*, *Ochotona pusilla*, *Spermophilus citelloides*, *Cricetus cricetus*, *Allocricetus bursae*, *Apodemus maastrichtiensis*, *Apodemus sylvaticus*, *Clethrionomys glareolus*, *Arvicola cantianus*, *Microtus oeconomus*, *Microtus subterraneus*, *Microtus gregalis*, *Elephas antiquus*, *Stephanorhinus kirchbergensis*, *Dama dama*, *Sus scrofa*, a.o. (Maul 2000). Morphological characteristics of the bone remains (of water voles and rhinoceros, in particular) permitted some authors to attribute the series to a warming within the Saale glacial stage (Schäfer et al. 2007). Judging by the water vole enamel index (SDQ) of 113.5 (Heinrich 1990), it corresponds to MIS 7 (7e/7c). The U-series dates confirm the validity of the deposits attribution to MIS 7 (> 350–200 ka BP) (Blackwell and Schwarcz 1986). Van Kolfschoten (2014) also supports dating the locality to the last Middle Pleistocene interglacial, MIS 7 (Text-fig. 3, Tabs 1, 2).



Text-fig. 4. 1–25: M_1 of *Lagurus transiens* from localities of the Likhvin Interglacial of Eastern Europe (Gun'ki, Chigirin, Pivikha, Verkhnaya Emancha, Ozernoye, Rybnaya Sloboda etc.); 26–29: M^3 of *Lagurus transiens* from the Likhvin localities; 30–36: M_1 of *Lagurus ex gr. transiens-lagurus* from Priluki locality (Kamenka Interglacial).

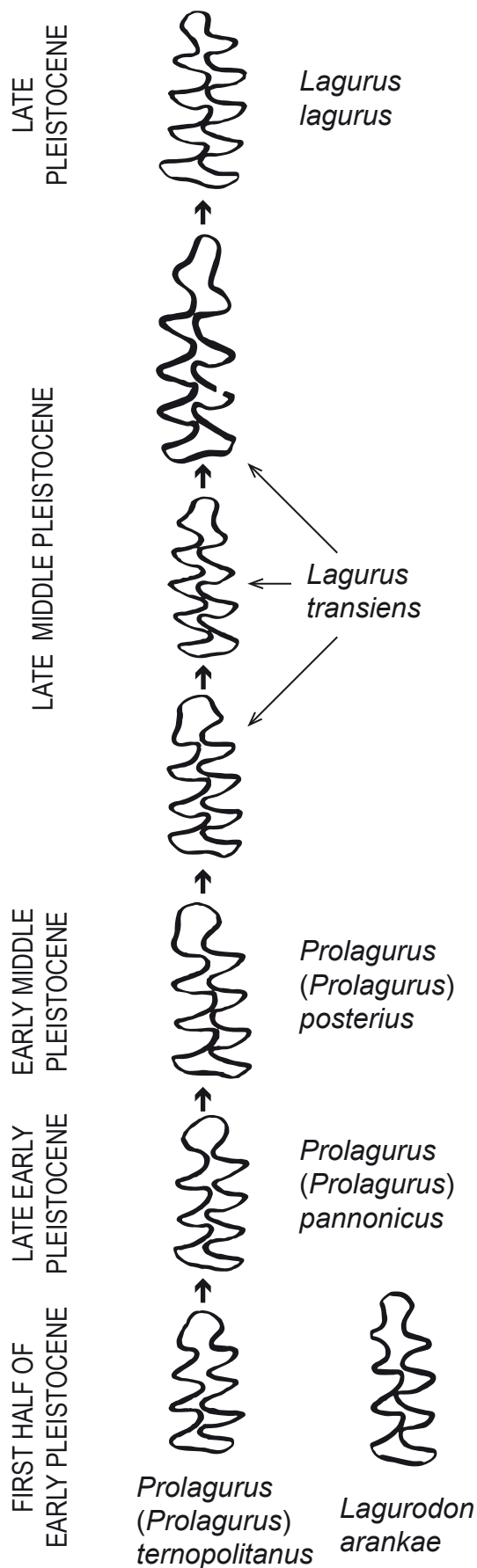
Small mammal faunas of MIS 6

Eastern Europe

Drabinovka, Poltava Region, Ukraine (49° 14' N, 34° 09' E) was described by Rekovets (1994). The mammal fauna was recovered from nonsorted sands dated to the Dnieper cold stage and includes occasional remains of *Spermophilus* sp., *Ellobius* sp., *Lagurus lagurus*, *Arvicola* cf. *chosaricus*, *Microtus (Stenocranius) gregalis* (Text-fig. 3, Tab. 1).

Danilovo, Transcarpathian Region, Ukraine (48° 09' N, 23° 26' E). The fauna recovered from the 4th terrace sediments on the Tereblya River (the Danube drainage basin) may be correlated with the Dnieper glacial stage (Krokhmal' and Rekovets 2010). The fauna includes *Spermophilus* sp., *Eolagurus* cf. *luteus*, *Lagurus* cf. *lagurus*, *Microtus ex gr. arvalis-agrestis*, *Microtus gregalis*. We have no direct evidence of the fauna being of the Dnieper age (Text-fig. 3, Tab. 1).

The only locality known from Belarus – **Zhukevichi**, Neman drainage basin, Grodno Region, Belarus (53° 17'



Text-fig. 5. *Prolagurus-Lagurus* and *Lagurodon* phyletic lineages during the Pleistocene based on data from Eastern Europe (after Markova 1974, 1982).

55° N, 24° 03' 18" E) – has a similar fauna composition to **Konevichi**, Smolensk Region, Russia (55° 36' N, 31° 12' E). Both are confined to the layers overlying the Dnieper till and are overlain with deposits dated to the Mikulino Interglacial, therefore they can be attributed to the very end of the Dnieper glacial epoch. They contain cold-tolerant small mammal fauna including two genera of lemmings (*Dicrostonyx* cf. *simplicior*, *Lemmus sibiricus*), as well as *Microtus gregalis*, *Clethrionomys* aff. *glareolus*, *Arvicola* cf. *chosaricus*. The morphology of the water vole remains indicate its attribution to the Middle Pleistocene form, *Arvicola* cf. *chosaricus* (Motuzko 1985) (Text-fig. 3, Tabs 1, 2).

The **Chekalin** locality, Tula Region, the Oka drainage basin, Russia (54° 05' 42" N, 36° 14' 42" E). Small mammal fauna recovered from fluvioglacial deposits of Dnieper age include *Lemmus sibiricus*, *Dicrostonyx simplicior*, *Microtus oeconomus*, *M. (Stenocranius) gregalis*. The fauna is dominated by lemmings (two genera) indicative of an extremely severe climate (Agadjanian 1976) (Text-fig. 3, Tab. 1).

Small mammal fauna from **Strigovo** near the town of Pochep, Bryansk Region, Russia (52° 50' 6" N, 33° 12' 18" E) occurs in the cross-bedded sands underlying the till. The fauna includes *Ochotona* ex gr. *pusilla* (2), *Arvicola* sp. (1), *Lagurus* sp. (1), *Dicrostonyx simplicior* (53), *Lemmus* cf. *sibiricus* (11), *Microtus oeconomus* (4), *M. (Stenocranius) gregalis* (3), *Microtus* sp. (9) (Agadjanian 2009). The fauna strongly suggests a severe cooling and is most probably correlatable with the onset of the Dnieper cooling (Text-fig. 3, Tab. 1).

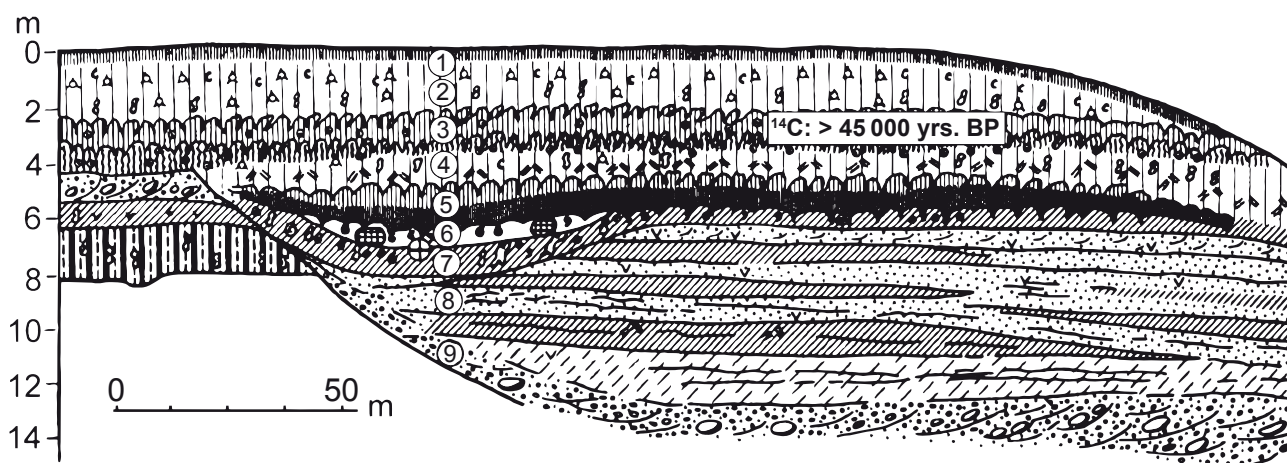
Volzhino, left bank of the Usa River, Bryansk Region, Russia (53° 02' 6.72" N, 33° 30' 54" E) contains remains of *Dicrostonyx* sp. (4), *Microtus oeconomus* (1), *M. (Stenocranius) gregalis* (2), *Microtus* sp. (13). The fauna is attributable to the beginning of the Dnieper glacial stage (Agadjanian 2009) (Text-fig. 3, Tab. 1).

Pavlovka locality is on the right slope of the Desna River valley, the Bryansk Region, Russia (52° 53' 2.4" N, 33° 58' 30" E). The fauna is represented by *Lagurus* cf. *lagurus* (7), *Dicrostonyx* cf. *henseli* (19), *Lemmus* sp (2), *Microtus (Stenocranius) gregalis* (13), *Mammuthus* sp. (1), *Rangifer tarandus* (1). Agadjanian (2009) attributed the locality to the end of the Dnieper glacial (Text-fig. 3, Tab. 1).

Alpatyev in the Oka drainage basin, Russia (54° 53.8' 16" N, 39° 19' 22" E), is confined to periglacial alluvial sediments lying on the Dnieper till and overlain with a loess-paleosol series including the Mezin and Bryansk fossil soils. The fauna includes *Ochotona* sp., *Dicrostonyx* ex gr. *simplicior*, *Lemmus sibiricus*, *Lagurus lagurus*, *Microtus (Stenocranius) gregalis*, *Microtus oeconomus* (Markova 1992). The fauna belongs to the final phase of the Dnieper glacial epoch (Text-fig. 3, Tab. 1).

The fauna found in **Kipievo 1** in the Pechora River drainage basin, Komi Republic, Russia (65° 42' N, 54° 45' E) (Agadjanian 1992) closely resembles that from Alpatyev, with *Dicrostonyx* cf. *simplicior* a.o.

Kipievo 2 locality, also in the Pechora River Basin, Komi Republic, Russia (65° 42' N, 54° 45' E) (Agadjanian 1992), is confined to beds overlying the till of the Moscow stage. The fauna may be dated to the end of the Dnieper ice age and



Text-fig. 6. Verkhnyaya Emancha section (Don basin) (after Udartsev 1980). 1 – modern soil, 2 – pale-yellow clay, 3 – Romny paleosol, 4 – pale-yellow clay, 5 – Kamenka paleosol, 6 – loamy marl with bones of small mammals, 7 – blue-grayish clay with bones of small mammals and shells of freshwater mollusks, 8 – pale-grayish sandy clay with shells of freshwater mollusks, 9 – pale-grayish sands, 10 – sands with gravel and boulders (outwash Don till).

includes remains of collared lemming (*Dicrostonyx gulielmi*) most typical for the late Pleistocene (Text-fig. 3, Tab. 1).

Igorevka on the right bank of the Seim River valley, near Buryń, Sumy Region, Ukraine (51° 11' 18.24" N, 33° 50' 6" E) is contained within an ice-detached outlier dated to the Dnieper age. Its deposits include remains of *Dicrostonyx simplicior*, *Arvicola* ex gr. *cantianus*, *Lagurus lagurus*. The collared lemmings found in the Igorevka locality resemble the lemmings dated to the first half of the Dnieper glaciation. Water voles, however, have rather archaic tooth morphology similar to that of *A. cantianus* (Markova 1992) (Text-fig. 3, Tabs 1, 2).

Western Europe

The fauna of **Ariendorf 1**, Germany (50° 32' N, 07° 17' E) includes *Talpa* sp., *Sorex minutus*, *Spermophilus* cf. *undulatus*, *Cricetus cricetus* cf. *praeglacialis*, *Dicrostonyx* sp., *Lemmus lemmus*, *Arvicola cantianus* (= *terrestris* ssp. A sensu van Kolfschoten 1990), *Microtus arvalis/agrestis*, *M. gregalis*, *M.oeconomus*, *Mammuthus* sp., *Coelodonta antiquitatis*, *Cervus elaphus*, *Bison* vel *Bos*. The species composition suggests a severe cooling and may be correlated with the first half of the Saale glaciation (van Kolfschoten 1990a, b, von Koenigswald and Heinrich 1999) (Text-fig. 3, Tab. 1).

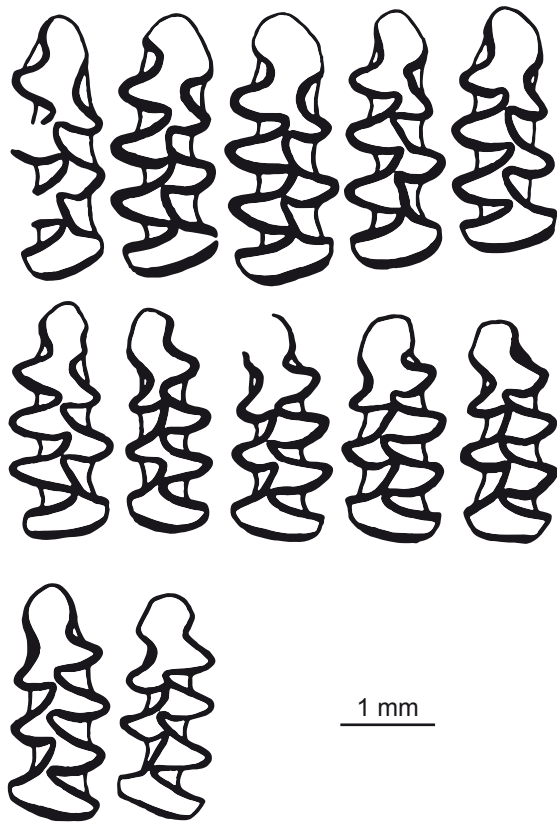
The **Hersbruck** cave locality in the Fränkischer Jura, Germany (49° 30' 26" N, 11° 25' 30" E) yielded a small mammal fauna as follows: *Arvicola cantiana terrestris*, *A. greeni*, *A. praeceptor*, *Clethrionomys glareolus* group, *Dicrostonyx intermedius*, *Lemmus lemmus*, *Microtus arvalinus-arvalis-agrestis* group, *Microtus delusorius*, *M. nivalinus-nivalis* group, *M. oeconomus*, *M. gregaloides*, *Pitymys subterraneus* a.o. (von Koenigswald and Tobien 1990). Some researches are of the opinion that the fauna should be revised and correlated with the Saale glaciation (Heller 1983). The presence of *Microtus gregaloides* may indicate this locality is of an earlier age. It is not improbable that mixing of different-aged remains took place here which is common in cave localities (Text-fig. 3, Tabs 1, 2).

Biśnik Cave, layers 15–14, southern Częstochowa Upland, Poland (50° 25' 35" N, 19° 49' 54" E). According to the data by Socha (2014), the fauna of layers 15–14 may be correlated with MIS 6–6/5e and with the Saale glacial stage, or with the transition from Saale to Eemian. The fauna is dominated by voles belonging to three species: *Microtus arvalis*, *M.gregalis*, *M. oeconomus*. Other rodents are *Dicrostonyx* cf. *henseli/gulielmi*, *Lemmus lemmus*, *Arvicola amphibius*, *Microtus agrestis* are present but in a limited number (Socha 2014). Remains of the porcupine *Hystrix brachyura* were occasionally found; such finds were quite unexpected, as the animal differs considerably from the above-listed species in its environmental preferences. It seems probable that a certain mixing of rodent remains from different layers could have occurred (Text-fig. 3, Tab. 1).

The Palaeolithic cave **Deszczowa** also on the Częstochowa Upland, Poland (50° 35' 15" N, 19° 32' 34" E). **Layers I–IV** contains remains of *Dicrostonyx simplicior*, *Vulpes praeglacialis*, *Gulo schlosseri*, *Panthera spelaea fossils*, *Microtus oeconomus malei*. These layers were attributed to the Saale glaciation (Nadachowski et al. 2009, Krajcarz 2012) (Text-fig. 3, Tab. 1).

Rhenen in the Netherlands (51° 57' 54" N, 5° 34' 12" E) is located on a morainic ridge dated to the Saale glacial age. It yielded small mammal fauna as follows: *Neomys* sp., *Talpa europaea*, *Desmana moschata*, *Clethrionomys glareolus*, *Arvicola terrestris* ssp. B sensu van Kolfschoten (1990), *Microtus agrestis/arvalis*, *Apodemus sylvaticus*, attributable to the 2nd (the last) warm phase (interstadial) within the Saale glaciation (van Kolfschoten 1990a, b) (Text-fig. 3, Tab. 1).

The famous **Grotte du Lazaret site**, Alpes-Maritimes, France (43° 41' 27.50" N, 7° 17' 41.25" E) is widely known for the *Homo heidelbergensis* remains discovered there together with Late Acheulean artifacts. Remnants of an ancient dwelling (hut) were also found. The mammal bones recovered from the site include *Marmota marmota*, *Eliomys quercinus*, *Cricetus cricetus*, *Microtus arvalis*, *Pitymys* (= *Terricola*) *duodecimcostatus*, *Arvicola terrestris*,



Text-fig. 7. *M₁* of *Arvicola* from the Verkhnyaya Emancha Likhvin deposits (from layers 6 and 7).

Clethrionomys glareolus, *Pliomys lenki*, *Apodemus sylvaticus* (Text-fig. 3, Tab. 2). Chaline (1972) attributed the locality to the end of the Middle Pleistocene. This suggestion has been corroborated by the enamel index recorded in studies of *Arvicola* (Tab. 2). Bones of *Canis lupus*, *Vulpes vulpes*, *Panthera spelaea*, *Panthera pardus*, *Lynx spelaea*, *Felis* sp., *Ursus spelaeus*, *U. arctos*, *Meles meles*, *Cervus elaphus*, *Dama dama*, *Rangifer tarandus*, *Capreolus capreolus*, *Megaloceros giganteus*, *Capra ibex*, *Bos primigenius*, *Bison priscus*, *Rupicarpa rupicarpa*, *Stephanorhinus kirchbergensis*, *Coelodonta antiquitatis*, *Equus caballus*, *Elephas antiquus* were found in abundance. The presence of reindeer, as well as marmot and hamster bones at that latitude is surprising and could be considered as indicative of cooling (glaciation). The dates obtained (by U-Th series and ESR techniques) permit the site to be attributed to MIS 6 and to the last Middle Pleistocene glacial stage (Text-fig. 3, Tabs 1, 2).

Conclusion

In summary, the material available from the second half of the Middle Pleistocene reveal the very complex geological and climatic history of the Middle Pleistocene interval between the Oka (Elsterian) and Dnieper (Saale) glaciations. The analysis carried out enabled us to specify the species composition of the small mammal faunas at the time of the Likhvin (Holsteinian – Hoxnian), Kamenka

Table 3. SDQ for *M₁* of modern *Arvicola terrestris*.

Region	N	min.	mean	max.
Krasnodar Krai, Russia	18	100	125	200
Poltava Region, Ukraine	11	59	76	100
Sula River mouth, Ukraine	50	40	66	83
Novosibirsk Region, Russia	20	35	63	75
Arkhangelsk Region, Russia	20	20	74	100
Cheshskaya Bay (Barents Sea)	20	40	76	100
Yamal Peninsula, Russia	5	66	72	80

(Reinsdorf – Purfleet), and Romny (Schöningen – Sandy Lane) interglacials in Europe, as well as during the cold stages between them. At least three paleosols developed in Eastern Europe during the warm periods within that time interval. For most of those layers, data on small mammals with different evolutionary levels have been obtained (Markova 1982, 2005, 2006, Rekovets 1994, Agadjanian 2009).

The numerous Western European localities with small mammals dated to the second half of the Middle Pleistocene also display a complicated history of landscapes and climates (Chaline 1972, van Kolfschoten and Roebroeks 1985, Heinrich 1990, Parfitt 1998, Maul 2000, Schreve 2001a, 2004a, b, c, Socha 2014). The data suggest at least 3 significant warmings of an interglacial order (MIS 11, MIS 9, MIS 7) with cold intervals between them. In addition in Western Europe most of the intervals are characterized by specific faunal assemblages. Holsteinian and Hoxnian localities include Neede, Hoxne, Barnfield Pit, Beeches Pit, Bilzingsleben II, Schöningen 13 DB and 13 I, Kärlich H plus some others (Heinrich 1990, van Kolfschoten 1990b, 2014, von Koenigswald and van Kolfschoten 1996, von Koenigswald and Hienrich 1999, Schreve 2004a). All the above listed localities proved to contain remains of *Arvicola cantianus* (*A. terrestris cantianus*, according to van Kolfschoten), *Sorex* cf. *araneus*, *Microtus agrestis*, and *M. arvalis*. It is noteworthy that species *Sorex* (*Drepanosorex*) *savini*, *Pliomys episcopalis*, *Microtus* (*Stenocranius*) *gregaloides*, *M. (Terricola) arvalidens* are not typical for that interglacial (Tab. 1). The species composition of the Holsteinian and Hoxnian faunas in Western Europe enabled us to confidently correlate them with Likhvin faunas of Eastern Europe.

Data from the colder interval subsequent to the Likhvin (MIS 10) are extremely scarce as yet. The only small mammal locality attributable to it – Topka, in the Don River drainage basin (Krasnenkov and Kazantseva 1993) is noted for the presence of *Arvicola chosaricus* remains, while no *Terricola* voles have been found to date.

A younger interglacial correlatable with MIS 9 has been identified on the Russian Plain and is known as the Kamenka Interglacial; it was studied at the localities Priluki, Rasskazovo, Uzunlar, a.o. An analogue is known under the name of Reinsdorf in Western Europe (van Kolfschoten 2014), and Purfleet in Great Britain (Schreve 2004b). Also the faunas described from Grays Thurrock and Kärlich H have been attributed to this interglacial. The assemblages are distinct due to the presence of a more advanced form of *Arvicola* than those typical of the Likhvin (Holsteinian)

Interglacial. In Eastern Europe this interval is correlatable with faunas containing *Arvicola chosaricus* and *Lagurus* aff. *lagurus* (Text-fig. 2, Tabs 1, 2).

The next cooling (MIS 8) is not well documented. The Harnham locality in Great Britain yielded *Apodemus* sp., *Clethrionomys* sp., *Microtus oeconomus*, and *Microtus* sp.; however no remains of the most diagnostic taxa, such as *Arvicola*, *Microtus (Stenocranius)*, *Lagurus* have been found. The OSL dating, however, gave grounds for its attribution to MIS 8 (Bates et al. 2014).

The latest warming in the second half of Late Pleistocene is known as the Romny warming in Eastern Europe, Sandy Lane in Great Britain and Schöningen in Central Europe. It was marked by further evolutionary modifications in phyletic lines of water voles and is manifested in the tooth enamel index (Schreve 2004c). In Eastern Europe the fauna from the Matveevka locality (Dnieper River drainage basin) including *Lagurus lagurus* and *Arvicola chosaricus* may be attributed to that warming (Rekovets 1994). In Eastern Europe this interglacial is identifiable also by its palynological data (Bolikhovskaya 1995). In Western Europe a number of faunal localities are of this age – Lion Pit, Aveley, Wageningen-Fransche Kamp 1, Maastricht-Belvédère, Weimar-Ehringsdorf (Lower Travertine), etc. (Text-fig. 3, Tabs 1, 2).

The end of the Middle Pleistocene was marked by the Dnieper (Saale – Walstonian) glacial (MIS 6). There is abundant information on the small mammals dated to that interval. The faunas include cold-tolerant species, such as *Dicrostonyx simplicior*, *Lemmus sibiricus*, and *L. lemmus*. Also narrow-skulled voles *Microtus (Stenocranius)* were widespread at the time (Text-fig. 3, Tabs 1, 2).

Thus, integrated analysis of the theriological and geological information on the second half of the Middle Pleistocene in Europe convincingly demonstrated essential changes in the small mammal faunas during that interval and clarified variations in climate and environment. The traceable modifications in Arvicolinae phyletic lines make a correlation between the West European and East European localities possible. The small mammal data provide the basis for development of biostratigraphic schemes for the Middle Pleistocene and also for the entire Pleistocene.

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