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MIDDLE PLEISTOCENE SMALL MAMMAL FAUNAS OF EUROPE: EVOLUTION, BIOSTRATIGRAPHY, CORRELATIONS

ABSTRACT. The paper is concerned with the small mammal fauna evolution in Europe in the Middle Pleistocene. The information on the faunas of the end of the Early Pleistocene has been also taken into consideration. The data available made possible identifying several stages in the small mammal evolution. Not all intervals within the Middle Pleistocene are provided with sufficient information for recognizing individual stages; that is particularly true for the cold periods of the Middle Pleistocene – the Donian and the Okian glaciations (=Elsterian, =Anglian). Based on the studies of small mammal localities, the biostratigraphic scheme has been developed, the principal phylogenetic lineages of Arvicolinae were traced, and maps of the Middle Pleistocene small mammal localities have been compiled

KEY WORDS: Middle Pleistocene, small mammals, Europe, biostratigraphy, evolution, correlations

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INTRODUCTION

Problems of evolution of the Middle Pleistocene small mammals and the synchronization of the principal stages of their evolution with geological and climatic events have been examined in many previous publications (Agadjanian 2009; Alexandrova 1976; Chaline 1972; Cuenca-Bescós et al. 2013; Heinrich 1990; Fejfar and Horaček 1990; Markova 1982, 2005, 2006, 2007, 2014; Markova and Kolfschoten 2012; Markova and Puzachenko 2016; Markova and Vislobokova 2016; Masini and Sala 2011; Maul 2001; Maul and Markova 2007; Maul et al. 2000, 2007; Nadachowski 1990; Rekovets 1994; Schreve 2004 a,b,c; Vislobokova and Tesakov 2013; van der Meulen 1973; van Kolfschoten 2014; von Koenigswald and van Kolfschoten 1996 and many others). In this paper we try to analyze generally the main stages in the evolution of the European small mammal faunas referring to the period from the Jaramillo paleomagnetic event (the end of the Early Pleistocene 1.07 – 0.99 Ma, ~MIS 26-30) till the end of the Middle Pleistocene – the end of Saalian (=Walstonian, =Dnieper) glaciation (MIS 6). The ages of the temporal intervals were given according to oxygen isotope curve (Lisiecki and Raymo 2005). A significant number of global climatic events, glaciations and interglacials, correspond to this period. We tried to recognize the response of the small mammal faunas to the different climatic events during the Middle Pleistocene, to synchronize the faunas of Eastern Europe with those of

Western Europe, to examine the principal evolutional changes in the different phylogenetic lineages of Arvicolinae during the Middle Pleistocene.

PRINCIPAL STAGES OF THE MIDDLE PLEISTOCENE SMALL MAMMAL FAUNAS

The end of the Early Pleistocene – the beginning of the Middle Pleistocene (MIS 31 – 19)

The analysis of small mammal faunal data from Eastern and Western Europe dated to the interval from the Jaramillo paleomagnetic event to the beginning of the early Middle Pleistocene (1.06-0.7 Ma) provided evidence for several phases in the small mammal evolution recognizable within this interval. It is established that the boundary between large mammal fauna stages corresponds to those of Tamanian and Tiraspolian mammal assemblages in Eastern Europe, Early/Late Galerian in Italy, and MNQ 20/MNQ 21 zones. A more detailed picture was revealed in the evolution of small mammal faunas during the regarded interval; the phases are distinguishable by changes in the species composition, first occurrences of new species, and evolutionary changes in a several phylogenetic lineages of Arvicolidae.

On the Russian Plain most of localities are found in great geological sequences studied not only paleontologically, but also by several methods including paleomagnetic stratigraphy. Those supplementary data help to determine the stratigraphic position of mammal faunas. Many localities in the region of the Black Sea coasts include, along with mammals, shells of brackish-water mollusks differing in their evolutionary level. The mollusk assemblages permit to correlate the mammal faunas directly with the Black Sea transgressions and paleogeographic events in the Eastern Mediterranean.

A relatively large part of localities in Western Europe are related to karst caves and fissures. In such localities faunal remains of different age are often found to be mixed, and paleomagnetic analysis data are also not quite reliable. There are, however, a number of multilayered localities (Kärlich, Shöningen, Sima del Elephante, Grand Dolina, Colle Curti, Castagnone, the localities related to the different Themes River terraces, and some others) where multidisciplinary studies (including paleomagnetic analysis and absolute dating) were performed.

Every phase in the evolution of small mammals is identifiable not only by appearance of new taxa, but also by the prevalence of certain morphotypes within a taxon. The main evolutionary transformations within the phylogenetic lineages resulted from anagenesis; several "paleontological" species were identified on the basis of the dominant tooth morphotypes. In the *Prolagurus - Lagurus* lineage, for example, we never found a single tooth morphotype in a certain time interval; there is always a considerable variability recorded. At the level of faunas correlatable with the Jaramillo event there are some steppe lemmings with morphotypes typical of *Prolagurus ternopolitanus (= P. praepannonicus)* against the background of prevailing tooth morphotypes characteristic of *P. pannonicus*. Faunas dated to the very end of the Matuyama reversed polarity epoch (the Karai-Dubina locality) include steppe lemmings with tooth morphotypes of *P. pannonicus, P. posterius, L. transiens*. More than 90% of the teeth feature morphotypes characteristic of *P. pannonicus*, while *L. transiens* is represented by a single specimen displaying the extreme variant of the morphological variability (Markova 1982). Therefore, it is easy to make a mistake in attributing a locality to another evolutionary stage (faunal assemblage) if the species list of the locality is considered formally in the absence of other datable materials. All these phenomena require a careful investigation of fossil materials. Certain difficulties in correlations between West European faunas and those in Eastern Europe arise from different levels of knowledge and different taphonomic features.

Small mammal faunas related to Jaramillo normal polarity event

Small mammal faunas confidently correlated with the Jaramillo normal polarity event contain remains of *Mimomys savini, M. pusillus, Clethrionomys sokolovi,* advanced *Allophaiomys, Borsodia fejervaryi, Prolagurus pannonicus, Lagurodon arankae, Eolagurus argyropuloi* (Masini and Sala 2011; van der Meulen 1973; Siori and Sala 2007; Markova 2007; Maul and Markova 2007). Characteristic for the Iberian faunas is the presence of archaic representatives of the endemic *Iberomys genus (I. huescarensis)*, voles of the *Ungaromys* genus and surprisingly finds of the water vole *Arvicola jacobensis* found together with *Allophaiomys lavocati* (Cuenca-Bescós 2013). It is noteworthy that no voles of *Microtus (Terricola), M. (Pallasiinus), Lasiopodomys (Stenocranius)* genera and subgenera have been recorded in faunas correlatable with the Jaramillo event. In Eastern Europe faunas of that evolutionary level had been earlier identified as **Kairian (=Ostrogozhskian)** small mammal faunas (Markova 1990, 2007; Shik 2014) (Fig. 1).

In Western Europe they have been correlated with West European Biharian faunas, with those of the Colle Curti stage (Colle Curti F.U.) in Italy and the “Allophaiomys lavocati” phase in Spain, etc. (Cuenca-Bescós et al. 2013; Masini and Sala 2011; Siori and Sala 2007) (Fig. 5).

The other opinion exists also that more advanced voles of *Allophaiomys - Microtus* linage (for example, Microtus thenii) also existed during Jaramillo event (Maul et al. 2007) (Fig. 2). For our opinion it is necessary to carry out the additional studies to resolve this problem.

Small mammal faunas related to post-Jaramillo interval. but located before Brunhes - Matuama paleomagnetic boundary

The next step in the small mammal evolution is represented by faunas with the first documented representatives of *Lasiopodomys (Stenocranius) hintoni* and *Microtus (Terricola)* sp. *Mimomys savini, M. pusillus, Allophaiomys pliocaenicus nutiensis, Prolagurus pannonicus* are also present in these faunas.

Those faunas were identified as the **Morozovkian** small mammal assemblage (Alexandrova 1976; Markova 1990) and fall within the Matuyama reversed polarity zone. It is possible that those East European faunas may be correlated with the faunas with *Microtus thenii* from Untermassfeld (Germany) (Maul 2001) (Fig. 1, 2, 5).

More advanced faunas are identified by the first occurrence of *Microtus* ex gr. *oeconomus (= M. protooeconomus, =M. ratticepoides)*. The bulk of the fauna is formed by *Prolagurus pannonicus* and *Eolagurus argyropuloi*; remains of *Mimomys savini* and *Allophaiomys pliocaenicus nutiensis* are present in small number. According to paleomagnetic data, these faunas are correlated to the end of the Matuyama epoch. The faunas at that stage of evolution are recognized as **Petropavlovkian** assemblage of small mammals in Eastern Europe (Alexandrova 1976; Markova 1998) (Fig. 1, 2, 5).

The faunas marked by the first appearance of *Microtus arvalinus* and *Prolagurus posterius* (Shamin locality, Don R. basin) occur in inversely magnetized deposits and are dated to the very end of the Matuyama epoch. The presence of the above named species makes the faunas closer to the **Early Tiraspolian** ones. In the localities pertaining to the beginning of the Brunhes epoch the rooted voles of *Mimomys* genus still persist. Steppe lemmings are represented mostly by *Prolagurus posterius*, though remains displaying the *Prolagurus pannonicus morphotype* were presented long enough (up to the end of the Don glacial epoch). The genus *Microtus* became more diversified at that time (Agadjanian 2009; Markova 1992, 2007).

New species appeared in Western and Eastern Europe more or less simultaneously. The comparison between West European and East European faunas is considerably

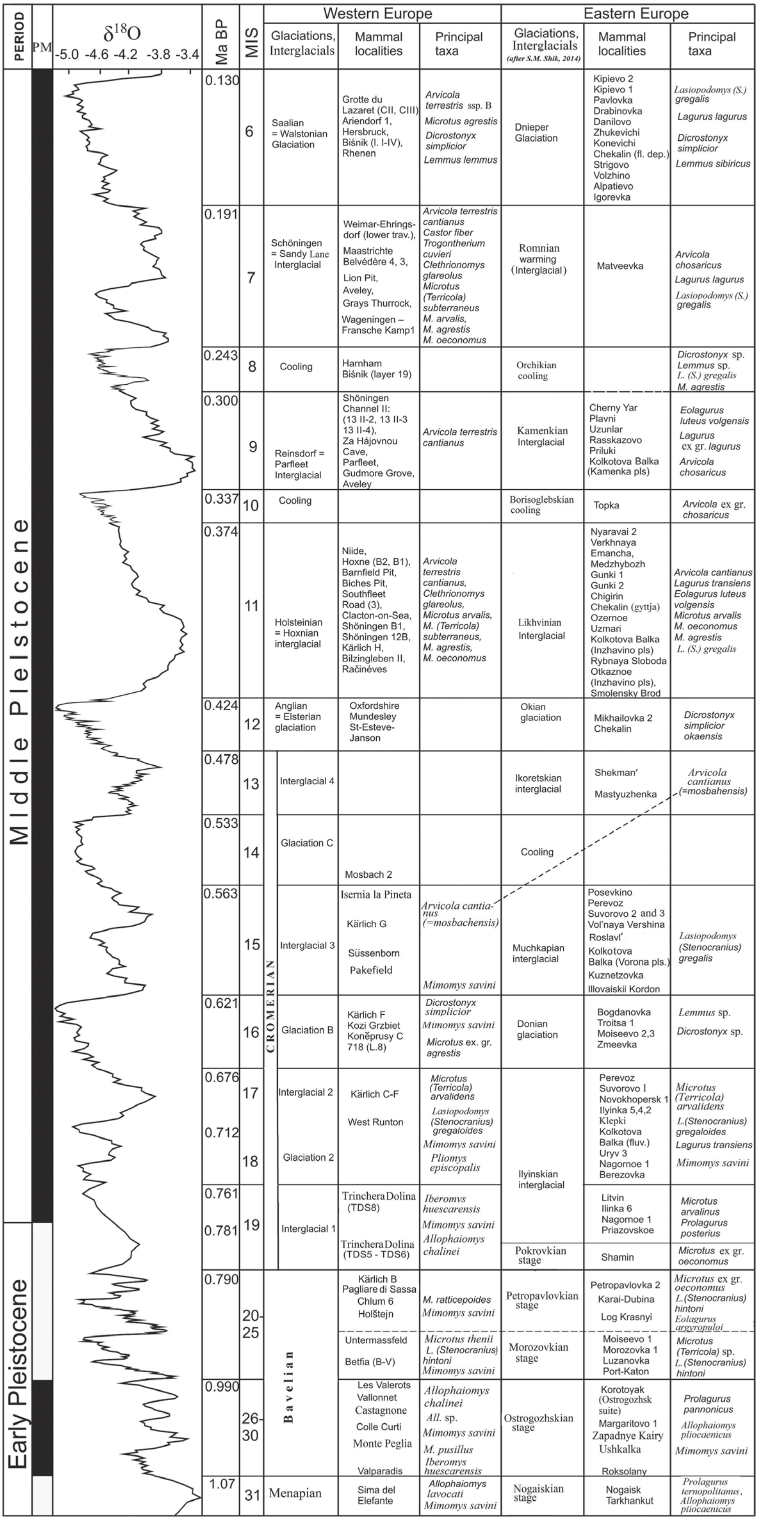


Fig.1. Biostratigraphical scheme of the Middle Pleistocene by small mammal data from Western and Eastern Europe

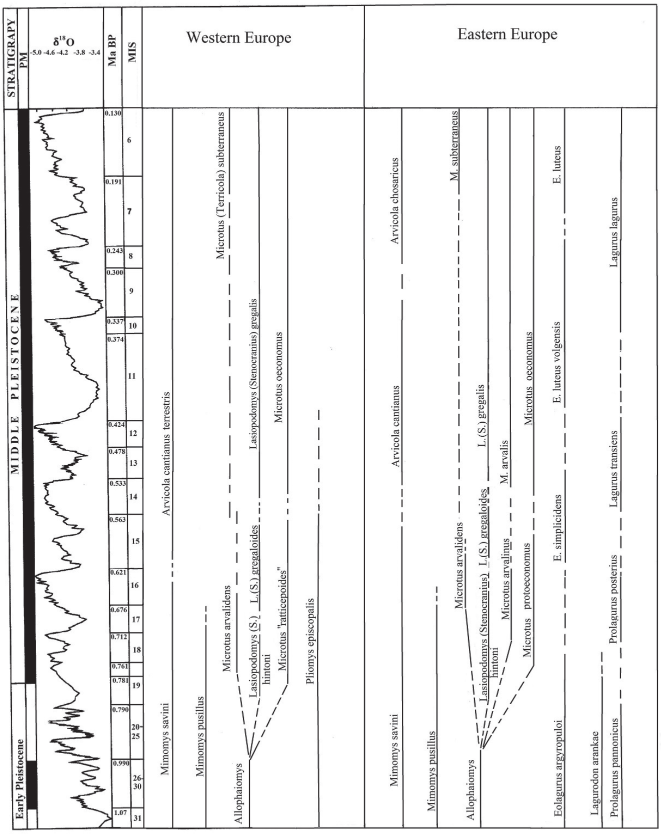


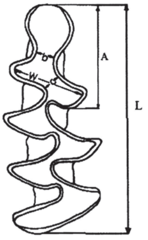
Fig. 2. Arvicolinae phylogenetic lines during the Middle Pleistocene by the materials from European localities

hindered by almost a total absence in Western Europe of steppe lemmings belonging to the *Prolagurus* - *Lagurus* lineage. Those rodents show a highly dynamic evolution through the Pleistocene and are the best diagnostic taxa for the East European faunas. The variability in the morphology of the genus *Allophaiomys* teeth often used by European specialists as a basis for their biostratigraphical conclusions is undoubtedly extremely important. So the indexes of M/1 are used very widely as indicative of the main trends in evolution of this taxon (van der Meulen 1973; Agusti 1992; Maul and Markova 2007, Rekovets 1994) (Fig 3).

It should be noted, however, that correlations are often performed on small collections and on insufficiently representative remains recovered from different localities. In such cases, the comparison may lead to a false conclusion. On the whole, the analysis of small mammal remains dated to Early-Middle Pleistocene (and of Arvicolinae in particular) is a useful tool, as it enables the evolution process to be traced in various phylogenetic lineages, and the sediments from which they originate to be dated. This palaeontological dating is particularly important, as absolute dates are practically lacking for the interval under consideration; as to the paleomagnetic method in itself, unsupported by paleontological materials, it hardly can deliver a conclusive date.

First half of the Middle Pleistocene (MIS 18 – 12)

The main intervals of the first half of the Middle Pleistocene include: Ilyinian complex interglacial (MIS 18 and 17), that apparently corresponds to the glacial A of the Cromerian complex and interglacial Cromer II; the Donian glaciation (MIS16)



Localities	A/L				B/W				C/W			
	N	min	mean	max	N	min	mean	max	N	min	mean	max
Nagornoe 1	5	40,82	44,31	49,02	5	11,67	21,16	31,25	5	15,79	20,83	25,00
Shamin	1		44,16		1		22,58		1		16,66	
Karai-Dubina	7	41,82	43,65	46,00	7	11,76	17,38	37,50	7	11,11	18,92	30,00
Untermassfeld	31	44,02	48,68	52,38	53	2,44	6,65	17,95	53	5,00	21,13	32,43
Morozovka 1	7	46,90	48,6	51,6								
Port-Katon	7	40,00	44,59	47,00	7	13,33	19,56	26,67	7	21,43	25,97	28,57
Castagnone	6	42,10	44,31	44,89	8	5,13	14,67	25,76	10	15,94	27,66	30,00
Monte Peglia (terra rossa)	101	42,00	46,00	51,00	148	<5	13,90	33,00	147	6,00	22,40	37,00
Monte Peglia (breccia)	81	41,00	45,70	49,00	48	13,00	22,80	32,00	40	6,00	19,60	28,00
Vallonnet	8	43,8	45,6	47,7								
Les Valerots (A. nutiensis)			47,21				6,88					
Les Valerots (A. burgundiae)			45,80				14,78					
Ushkalka	7	40,00	45,33	46,00	7	12,50	19,88	22,50	7	11,76	18,62	25,00
Zapadnye Kairy	4	43,40	45,07	46,00	4	16,67	21,68	28,89	4	16,67	21,02	26,32
Korotoyak (ostrogozhsk suite)	6	42,11	44,73	47,56	7	16,13	20,34	26,88	7	12,90	20,83	25,92
Colle Curti	2	41,22	41,57	41,92	2	26,88	28,23	29,41	2	18,18	19,79	22,58
Roksolany	6	37,50	40,48	42,86	6	18,95	23,54	31,25	6	13,68	19,43	25,00
Sima del Elefante	301	43,55	48,74	54,54								

Fig. 3. *Allophaiomys* M_1 quotient by the materials from European localities

= glaciation B of the Cromerian complex; the Muchkapian interglacial complex =Cromer III (MIS 15). The Muchkapian interglacial stage (by the data from Eastern Europe) includes Glazov and Konakhov warm phases and the cool interval (Podrudnyansky) separating them (MIS 15). The Navlinian cooling (MIS 14) and the later Ikoretskian warming (MIS13) follow it. The Navlinian cooling probably corresponds to the cooling (glaciation) C of the Cromerian complex, the Ikoretskian interglacial corresponds to Cromer IV (MIS 13), and the Okian glaciation (=Anglian glaciation = Elsterian glaciation) corresponds to MIS 12 (Shik 2014). Durations of these intervals are given according to Lisiecki and Raymo (2005) (Fig 1, 2, 5). In this paper, when dealing with the materials from Eastern Europe, the authors follow the last stratigraphic scheme, proposed by Shik (2014). The West European stratigraphic subdivisions are given according to Gibbard et al. (2004).

The analysis performed on the European small mammal faunas dated to the first part of the Middle Pleistocene gives ground for distinguishing several stages in their evolutionary development during ~0.76-0.42 Ma BP.

Ilyinian complicated interglacial = glacial A of the Cromerian complex and Cromer II interglacial

The faunas of these intervals correspond to MIS 18 and MIS 17 (~0.780 Ma - 0.676 Ma). They are characterized by the presence of rhizodont voles *Mimomys pusillus, M. savini, Pliomys episcopalis*, steppe lemmings *Prolagurus pannonicus, P. posterius (dominating), Lagurus transiens*, voles *Lasiopodomys (Stenocranius) gregaloides, Microtus (Terricola) arvalidens, M. arvalinus, M.* ex gr. *oeconomus (=M. protooeconomus, = M. ratticepoides)*, and *Microtus hyperboreus*. Insectivores are represented by *Sorex runtonensis* and *S. (Drepanosorex) savini*. Voles of *Allophaiomys* genus are absent from these faunas (Agadjanian 2009; Maul and Parfitt, 2010; Markova 2007 et al) (Fig. 1, 2, 5).

Donian glaciation

The next evolutionary stage of small mammal faunas is correlatable with the Donian glaciation, well expressed in Eastern Europe (MIS 16, ~0.676 - ~0.621 Ma). There are known several localities of this age. These faunas differ from the earlier ones by the presence of cold-adapted species: *Dicrostonyx* ex gr. *simplicior* and *Lemmus* sp. Rhizodont voles of *Mimomys (M. savini)* and *Pliomys* genera are parts of these faunas. The steppe lemmings are represented by *Prolagurus posterius* and *Lagurus transiens*; the narrow-skulled voles – by *Lasiopodomys (Stenocranius) gregaloides. M. (Terricola) arvalidens, M. arvalinus, M. oeconomus (= M. ratticepoides)*, and *M. hyperboreus* also are present in these faunas (Agadjanian 2009, Markova 1982, 1992). According to the material from West European localities, the first documented appearance of *Microtus agrestis* is dated to that time (Nadachowski 1985) (Fig. 1, 2, 5).

Muchkapian interglacial (=Cromer III)

The Eastern European faunas, correlated with the Muchkapian interglacial (MIS 15, Cromer III, ~0.621 = ~0.563 Ma), are characterized by the presence of rhizodont voles *Mimomys savini*, steppe lemmings *Prolagurus posterius* and *Lagurus transiens*, voles *M. (Terricola) arvalidens, M. arvalinus*, and *M. oeconomus*. The narrow skulled voles are represented by *L. (Stenocranius) gregalis*, though the morphotypes of the teeth, typical for L. *(S.) gregaloides*, still are present in small numbers. The first appearance of L. *(S.) gregalis* distinguishes these faunas from the previous ones. In Western Europe at the beginning of this interglacial. The fauna with *Mimomys savini* was described (Pakefield site) (Stuart and Lister, 2001). In the second part of this interglacial. The first *Arvicola* was distinguished (van Kolfschoten and Turner, 1996) (Fig. 1, 2, 5). Thus, there is a significant difference in the first *Arvicola* appearance (FAD) in Eastern and Western Europe.

Ikoretskian Interglacial (=Cromer IV)

In the localities attributed to the Ikoretskian interglacial in Eastern Europe (Cromer IV in Western Europe, MIS 13, 0.533-0.478 Ma), the first appearance of the archaic water voles *Arvicola cantianus* is recorded. **Rhizodont** voles of *Mimomys* genera are not detected in these faunas (Iosifova et al. 2006). In West-European faunas of that age *Sorex runtonensis*, *Drepanosorex savini, Arvicola cantianus, Microtus arvalinus, M. agrestis*, and *M. oeconomus* have been found (Pitts and Roberts 1997 and others) (Fig. 4).

Okian (=Elsterian, = Anglian) glaciation

In the faunas, correlatable with the Okian (= Elsterian, = Anglian) glaciation (MIS 12; ~0.478 - ~0.424 Ma), *Lemmus* sp., *Dicrostonyx simplicior okaensis, Lagurus transiens*, and *L. (Stenocranius) gregalis* have been described in Eastern Europe (Agadjanian 2009). This assemblage of small mammals undoubtedly reflects the glacial conditions of that time. *Spermophilus* sp., *Allocricetus bursae, Lemmus lemmus, Arvicola cantianus,* and *L. (Stenocranius) gregalis* have been described for this period in Western Europe (van Kolfschoten and Turner 1996). In various parts of Europe that glacial stage is represented by glacial till, fluvioglacial sediments and by loesses. The small mammal data reflect the drastic cooling and aridization during this glaciation (Fig. 1, 2, 5).

The second half of the Middle Pleistocene (MIS 11 - MIS 6)

Likhvinian (= Holsteinian, = Hoxnian) interglacial (MIS 11)

Stratigraphy	MIS	Western European localities	SDQ values				Eastern European localities	SDQ values			
			N	min	mean	max		N	min	mean	max
Saalian = Walstonian= Dnieper Glaciation	6	Grotte du Lazaret,									
		CII	47		107,9						
		CIII	8		108,6		Igorevka	15	110	125	135
Schöningen= Sandy Lane =Romny Interglacial	7	Weimar-									
		Ehringsdorf	30	102	112	126	Matveevka	1		102	
		(lower trav.)									
		Maastrichte	4	86	102	113					
		Belvédère 4,									
		Maastrichte	66	94	102	114					
		Belvédère 3		100,65		107,1					
		Biśnik Cave, L.19									
Cooling	8										
Reinsdorf= Parfleet= = Kamenka Interglacial	9	Shöningen-					Cherny Yar	12	98	108	125
		Channel II:									
		13 II-2	61	100	119	150	Uzunlar	1		110	
		13 II-3	117	94	118	160					
		13 II-4	135	99	115	137	Plavni	13	105	112	122
		Aveley	2		120						
		Parfleet	4		130	147					
		Gudmore Grove	48	105	133,3						
Cooling	10										
Holsteinian= Hoxnian= Likhvin Interglacial	11	Niide	58	124	146	169	Medzhybozh				
		Hoxne	8	110	140	162	L.10-11	25	91	107	125
		Swanscombe,	4		140		L. 14-15	17	90	116	155
		Bilzingleben II,	52	121	132	145	Gunki 1,	23	120	125	169
		Barnham	14	120	142	170	Gunki 2,	12	120,5	132	170
							Chigirin,	48	101,7	129	167
							Verkhnaya	33	100	125	170
							Emancha,				
							Osernoe,	36	122	130	145
							Rybnaya	14	112	125	160
							Sloboda,				
							Uzmari,	52	112	130	140
							Smolensky				
							Brod	16		124	
Elsterian= Anglian= Oka Glaciation	12										

Fig. 4. Water vole *Arvicola* enamel thickness quotient SDQ by the materials from the Middle Pleistocene European localities

Middle Pleistocene (or the beginning of the Middle Neopleistocene in Russian stratigraphical schemes) is recognized by a noticeable warming of interglacial order – the Likhvinian (Holsteinian, Hoxnian) interglacial. This interglacial is most close to the Holocene optimum in its climatic characteristics. The deposits attributed to the Likhvinian (Holsteinian, Hoxnian) interglacial overlie those of the preceding glaciation (Elsterian in Western Europe, Anglian in Great Britain, Oka glaciation in Eastern Europe). 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 well enough into the time limits of MIS 11 (Grün and Schwartz 2000). More than ten localities of this age were found in Eastern Europe (Markova 2006). They are distributed from the Upper Volga basin to the northern Black Sea region. Studies of the loess-paleosol series on the Russian Plain permitted to identify a horizon of fossil soil – the Inzhavino paleosol – attributable to the Likhvinian Interglacial (Velichko et al. 1992; Shik 2014).

Several very important localities were found in Western Europe. Among them, there is the famous Barnfield Pit locality in Great Britain (Swanscombe, Kent) in the south of the Thames drainage basin. The bone-bearing layers lie on those dated to the Anglian glacial epoch. The fauna was described by D. Schreve under the name

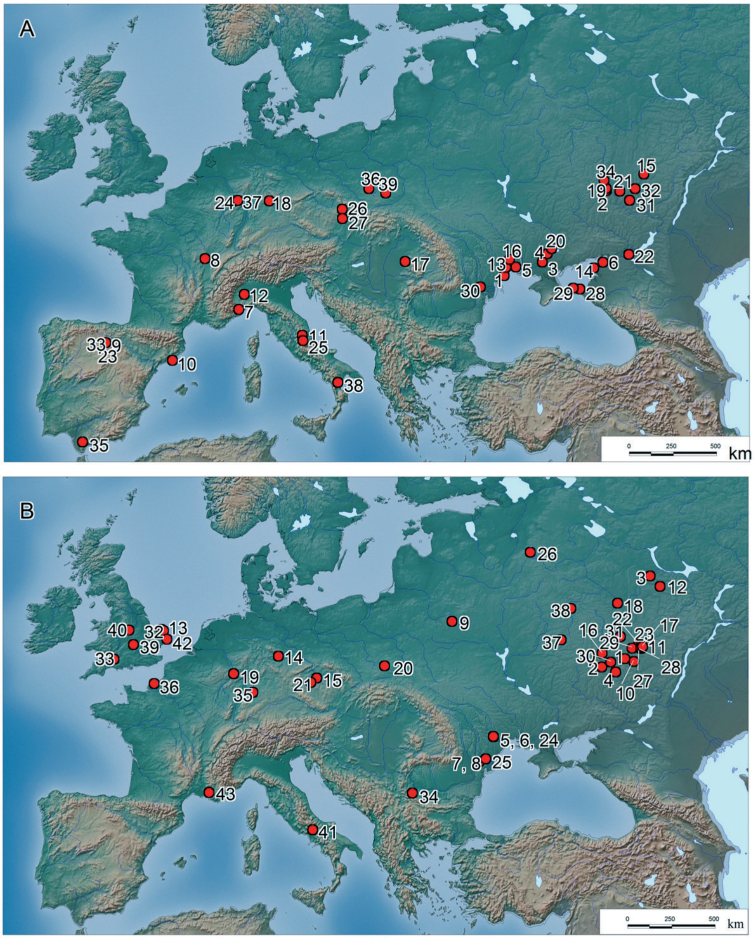


Fig. 5. A – European small mammal localities related to the end of the Early Pleistocene – to the beginning of the Middle Pleistocene (MIS 31 – MIS 19): 1 - Roksolany, 2 - Korotoyak (Ostrogozhsk suite), 3 - Zapadnye Kairy, 4 - Ushkalka, 5 - Limany, 6 - Margaritovo, 7 - Vallonnet, 8 - Les Valerots, 9 - Sima del Elefante, 10 - Vallparadis, 11 - Colle Curti, 12 - Castagnone, 13 - Morozovka 1, 14 - Port-Katon, 15 - Moiseevo 1, 16 - Chirkovo, 17 - Betfia B-V,18 - Untermassfeld, 19 - Petropavlovka 2, 20 - Karai-Dubina, 21 - Log Krasny, 22 - Shamin, 23 - Trinchera Dolina (TD5-TD6), 24 - Kärlich B, 25 - Pagliare di Sassa, 26 - Chlum 6, 27 - Holštejn, 28 - Priazovskoe, 29 - Litvin, 30 - Nagornoe 1, 31 - Ilyinka 6, 32 – Novokhopersk (l.7), 33 - Trinchera Dolina (TD8), 34 - Uryv 3, 35 - El Chaparral. 36 - Zalesiaki IA, 37 - Kärlich C, 38 - Sant'Arcangelo, 39 - Kozi Grzbiet. B – European small mammal localities related to first half of the Middle Pleistocene (MIS 18 - MIS 13): 1-Ilyinka, 2 -Veret'e, 3 - Zaplatino, 4 - Klepki, 5 - Kolkotova Balka (alluv.), 6 - Levada, 7 - Nagornoe I (strip. 4), 8 - Nagornoe II (strip. 2,3,5), 9 - Korchevo, 10 - Novokhopersk 1, 2, 11 - Korostylevo 1, 12 - Berezovka, 13 - West Runton, 14 - Voigtstedt, 15 - Přezletice, 16 - Bogdanovka, 17 - Moiseevo 2,3, 18 - Troitsa 1, 19 - Kärlich F, 20 - Kozi Grzbiet, 21 - Koněprusy -C-718 (L. 8), 22 - Posevkino, 23 - Perevoz, 24 - Kolkotova Balka (Vorona paleosol), 25 – Suvorovo 2, 3, 26 - Roslavl', 27 - Vol'naya Vershina, 28 - Kuznetsovka, 29 - Zherdevka, 30 - Mastyuzhenka, 31 - Shekhman', 32 - Ostend, 33 – Westbury (Unit 15/2 þ 4), 34 - Kozarnika (L.10в), 35 - Mosbach 2, 36 -Boxgrove, 37 - Mikhailovka 2, 38 - Chekalin (Oka glacial deposits), 39 - Oxfordshire, 40 - Mundesley, 41 - Isernia la Pineta, 42 - Pakefield, 43 - St-Esteve-Janson (layers F, G, H).

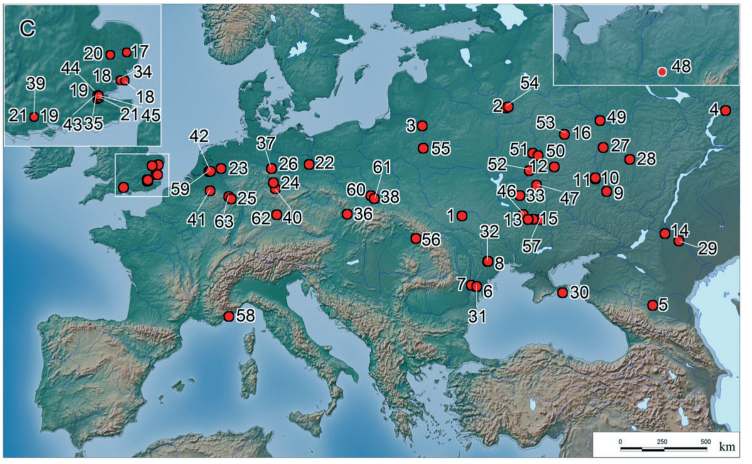


Fig. 5. C – European small mammal localities related to second half of the Middle Pleistocene (MIS 11 – MIS 6): 1 – Medzhibozh, 2 – Smolensky Brod, 3 – Nyaravai-2, 4 – Rybnaya Sloboda, 5 – Okaznoe, 6 – Ozernoe, 7 – Uzmari, 8 – Kolkotova Balka (Inzhavin. paleosol), 9 – Vladimirovka 2, 10 – Strelitsa, 11 – Verkhnaya Emancha, 12 – Mikhailovka 3, 13 – Pivikha, 14 – Raigorod, 15 – Gun'ki 1, 2, 16 – Chekalin (gittja), 17 – Hoxne (layers B2 and B1), 18 – Clacton-on-Sea, 19 – Southfleet Road (L. 3), 20 – Biches Pit, 21 – Barnfield Pit, 22 – Račinéves, 23 – Niide, 24 – Bilsingleben II, 25– Kärlich H, 26 – Shöningen (13 1, 12 B), 27 – Topka, 28 – Rasskazovo, 29 – Cherny Yar, 30 – Uzunlar, 31 – Plavni, 32 – Kolkotova Balka (Kamenk.paleosol), 33 – Priluki, 34 – Gudmor Grouve, 35 – Parfleet, 36 – Za Hájovnou Cave, 37 – Shöningen (L. 13 II-1, II-2, II-3, II-4), 38 – Biśnik (L. 19), 39 –Harnham, 40 – Weimar-Ehringsdorf (lower travert.), 41 – Maastrichte-Belvédère (L. 3,4), 42 – Waginingen Fransche Kamp 1, 43 – Grays Thurrock, 44 – Aveley, 45– Lion Pit, 46– Matveevka, 47 – Igorevka, 48 – Kipievo 1, 2, 49 – Alpatievo, 50 – Pavlovka, 51 – Volzhino, 52 – Strigovo, 53 – Chekalin (fluviogl. deposits), 54 – Konevichi, 55 – Zhukevichi, 56 – Danilovo, 57 – Drabinovka, 58 – Grotte du Lazaret, 59 – Rhenen, 60 – Deszczowa (layers I-IV), 61 – Biśnic (L. 15-14), 62 – Hersbruk, 63 – Ariendorf 1

of Swanscombe Mammalian Zone, MAZ (Schreve 2004a). Of particular interest are remains of primitive *Arvicola terrestris cantianus* with SDQ index equal to ~140 (n=4) (Fig. 1, 2, 4, 5). The Kärlich H locality (Germany) also attributed to this interglacial (van Kolfschoten and Turner 1996).

When studying the faunas dated to that period, much attention is given to evolutionary changes in the phyletic line of *Arvicola* water voles. It should be noted that the earliest stage in this genus evolution is known under different names in different European countries: *Arvicola mosbachensis*, or *A. cantianus* or *A. terrestris cantianus*. When describing particular faunas in the paper, we used the name of the taxon given by the author. An index designating the enamel surface ratio in the *Arvicola* teeth has been widely used in determination of the water vole evolutionary stage and the relative age of enclosing deposits (Markova 1975, 1981; Heinrich 1978) (Fig. 4).

The small mammal faunas of this interglacial are characterized by archaic water voles *Arvicola cantianus (A. mosbachensis, = Arvicola cantianus-terrestris), Lagurus transiens, L. (Stenocranius) gregalis, M. arvalis, M. oeconomus.* The rhizodon voles of *Mimomys* and *Pliomys* genus are absent from these faunas. The SDQ index of *Arvicola* enamel indicates the "mimomys" structure of the teeth (Fig. 4). The intensive evolutionary changes were revealed for the steppe lemming *Prolagurus – Lagurus* phylogenetic linage. *Lagurus transiens* (progressive type) was typical for the localities of Likhvinian in Eastern and Central Europe (= Holsteinian, = Hoxnian) interglacial (Fig. 2).

Borisoglebskian cooling (MIS 10)

The only locality with small mammals, Topka locality (the Don R. drainage basin), was discovered in the deposits overlying those of the Likhvinian Interglacial and in all probability belonging to the cold interval correlatable with the Borisoglebsk loess horizon (MIS 10) (Krasnenkov and Kazantseva, 1993). The locality yielded remains of *Arvicola chosaricus*, but no voles of the *"Terricola= Pitymys"* subgenus typical for Pre-Okian faunas have been found at the Topka (Fig. 1). No small mammal localities of that age are known in Western Europe (Fig. 1, 2, 5).

Kamenkian =Reinsdorf= Parfleet Interglacial (MIS 9)

The well pronounced warming – the Kamenka interglacial (MIS 9, 337–300 ka BP) is represented in Eastern European loess-paleosol sequence by Kamenka paleosol. This paleosol is widely spread over the Russian Plain (Velichko et al. 1992). Several localities of small mammals were described directly in this paleosol (Markova 1982) (Fig. 1, 5). The most characteristic to this interval are *Lagurus* ex gr. *transiens – lagurus (=L. chosaricus), Arvicola chosaricus, L. (Stenocranius) gregalis, Microtus arvalis, Microtus oeconomus.* The above-listed materials possibly are correlatable with the fauna from the Cherny Yar stratotypical section in the Volga drainage basin (Astrakhan Region). The Cherny Yar fauna including *Arvicola chosaricus, Lagurus lagurus pleistocaenicus, Eolagurus volgensis* described by Alexandrova (1976) was recovered from the same layers as the large mammal fauna described by Gromov (1948) and known since then as Khozarian mammal assemblage. The latter includes *Mammuthus trogontherii chosaricus, Camelus knoblochi, Megaloceros euryceros germaniae (= M. giganteus ruffii), Bison priscus longicornis, Equus caballus chosaricus*. The water vole *Arvicola chosaricus* is evolutionary more advanced species as compared with *A. cantianus* and is an indicator species of the Khozarian faunas (Fig. 2, 4). In steppe lemmings of the *Lagurus* genus the 'lagurus' morphotype is dominant in the faunas of the Khozarian type; more archaic 'transiens' morphotypes have been recorded in the steppe lemming remains, but their proportion is rater small (Markova 1982). The new OSL data indicate however more younger age of Khozarian fauna from the Cherny Yar stratotype locality (Zastrozhnov et al. 2017). So, till now the position of the Khozarian faunas is discussed.

The locality of Schöningen 13-II, Layers 13 II-1, II-2, II-3, II-4 includes *Arvicola terrestris cantianus, Microtus (Terricola) subterraneus, M. arvalis, M. agrestis, M. oeconomus, L. (Stenocranius) gregalis, Apodemus sylvaticus* and others. Geological data and the Arvicolinae morphological characteristics gave grounds for dating the fauna to an interglacial younger than Holsteinian – to the **Reinsdorf** one correlatable with MIS 9 (van Kolfschoten 2014) (Fig. 1, 2, 4, 5).

The Purfleet locality (Great Britain) is usually assigned to the second interglacial that followed the Anglian glacial stage and is correlated with MIS 9 (Schreve 2004b). The mammal fauna includes 21 taxa. Among the identified taxa are *Sorex araneus, S. minutus, Arvicola terrestris cantianus, Microtus agrestis, M. arvalis, Apodemus sylvaticus* and others. The water vole teeth are distinct for more advanced morphology than have *Arvicola* from the Barnfield Pit locality with SDQ=130, but more archaic than those described in water vole remains from the localities correlatable with MIS 7 (Fig. 1, 2, 4, 5). Schreve (2001b) described this fauna as belonging to the Purfleet Mammal Assemblage-Zone – MAZ Purfleet. Unfortunately the lagurides are practically absent from Western European faunas.

Orchikian cooling (MIS 8)

The Kamenka (=Purfleet, =Reinsdorf) interglacial was followed by a new cooling (MIS 8, 300-243 ka BP), which was named after the name of loess horizon distributed on the Russian Plain as the Orchikian one (Velichko et al. 1992). The faunas of this age are absent from Eastern Europe. A few localities of this age were found in Western Europe. The Harnham locality was discovered in the south of Great Britain, at the Avon and the Ebble interfluve. 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 mammal bones: *Apodemus* sp., *Clethrionomys* sp. *Microtus oeconomus*, *Microtus* sp. (Fig.1, 2, 5). A unique multilayered cave site with artifacts of the Middle Palaeolithic was discovered in Poland in the south of Częstochowa Upland (Biśnic cave, layer 19) (Fig. 1, 2, 4, 5). The sequence includes several cultural layers spanning time interval from MIS 9 (?) to MIS 2 (Cyrec et al. 2010). Layer 19 correlated by Cyrec and his coauthors with MIS 8-8/7 and with the Odra glaciation yielded remains of mammal fauna, including cold-tolerant, steppe, aquatic, and forest species (Socha 2014). The fauna is dominated by cold-adapted (lemmings, narrow-skulled vole) and eurybiont species. As follows from the enamel index of water vole teeth (SDQ = 100.65-107.12) (Fig.4), the fauna may be dated to the second half of the Middle Pleistocene.

Romnian, = Schöningen, = Sandy Lane interglacial

The fauna found in the Matveevka locality on the Sula R. (the Dnieper R. drainage basin, Cherkassy Region, Ukraine, 49º31´ N, 32º41´ E) may be assigned to the end of the Romnian warming (MIS 7). The sequence includes a layer of sand and gravel with bone remains of small mammals. Upwards it is replaced with loess layer overlain in turn with the Dnieper till; still higher a loess-like loam occurs including a paleosol horizon (Krokhmal and Rekovets 2010; Rekovets, 1994). The fauna composition is as follows: *Lagurus lagurus, Eolagurus* sp., *Arvicola chosaricus, Microtus arvalidens, M. arvalis, M. oeconomus, L. (Stenocranius) gregalis,* et al. (Fig. 1, 2, 4, 5). The Lion Pit locality in the lower reaches of the Thames R. (West Thurrock, Great Britain) yielded mammal fauna including *Apodemus sylvaticus, Vulpes* cf. *vulpes, Ursus arctos, Mammuthus trogontherii, Palaeoloxodon antiquus, Equus ferus, Stephanorhinus kirchbergensis,* et al. The fauna was attributed by Schreve (2004c) to the Sandy Lane Mammal Assemblage Zone (MIS 7) (Fig. 1, 2, 5). The Aveley locality, Great Britain, was exposed in a sand quarry; the fauna includes *Arvicola terrestris cantianus, Microtus agrestis* or *Microtus arvalis, Apodemus sylvaticus*, and others. The enamel index of water voles SDQ=120 (Parfitt 1 998; Schreve 2004c) (Fig. 4).

In Central Europe several faunas were correlated with MIS 7. The small mammal fauna of the Wageningen - Fransche Kamp 1 locality (the Netherlands) includes *Arvicola cantianus, Microtus arvalis/agrestis, Apodemus sylvaticus, A. maastrichensis* and others and undoubtedly corresponds to a warm interval. Van Kolfschoten (2014) correlates the locality with the interglacial preceding the Saale glaciation and with MIS 7 to the **Shöningen Interglacial** (Fig. 1, 2, 5). A fauna closely resembling the above listed was described in the Maastrichte-Belvédère, layers 3-4. In the opinion of van Kolfschoten, it is synchronous to the previous locality and in common with it corresponds to MIS 7 (Fig.1, 2) (van Kolfschoten 2014). A rich locality of Weimar-Ehringsdorf (Lower Travertine) in Thuringia, Central Germany, contains *Clethrionomys glareolus, Arvicola cantianus, Microtus oeconomus, Microtus subterarraneus, Lasiopodomys gregalis* and others [Maul 2000]. Judging by the water vole enamel index (SDQ) equal to 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: >350,000–200,000 yr BP (Blackwell and Schwarcz 1986). Van Kolfschoten agrees with the locality dating to the last Middle Pleistocene interglacial. MIS 7 (van Kolfschoten 2014).

Dnieper, = Saalian, = Walstonian glaciation (MIS 6)

More than ten Eastern European localities are correlated with the Dnieper glaciation (MIS 6). They distributed from 65º N to 49º N on the Russian Plain (Fig. 7) (Agadjanian 2009; Krokhmal and Rekovets 2010; Markova 1992; Motuzko 1985 et al.). The fauna includes cold-tolerant species *(Dicrostonyx cf. simplicior, Lemmus sibiricus, L. (Stenocranius) gregalis)*, several steppe species (*Spermophilus* sp., *Ellobius* sp., *Eolagurus* cf. *luteus, Lagurus lagurus* and others), and also sub-aquatic and meadow-plain animals (*Arvicola* cf. *chosaricus, Microtus oeconomus, Microtus arvalis*). The forest species are practically absent from the localities of this age; only *Microtus agrestis* and *Clethrionomys glareolus* occur occasionally in these faunas (Fig. 1, 2, 4, 5).

Several important localities were found in Western Europe (the Ariendorf 1 and the Hersbruck cave locality, Germany; the Biśnic cave locality, layers 15-14 and the Deszczowa in Poland; the Rhenen locality in the Netherlands; the Grotte du Lazaret in France) (van Kolfschoten 1990; von Koenigswald and Heinrich, 1999; Nadachowski et al. 2009; Krajcarz 2012; Chaline 1972; Socha 2014 and others). Among the small mammals recovered are *Dicrostonyx* cf. *henseli/gulielmi, D. simplicior, Lemmus lemmus, Arvicola cantianus (=terrestris ssp.A), Clethrionomys glareolus, Microtus agrestis, Microtus arvalis, M. oeconomus, L. (S.) gregalis*, and others. In the south of France (Grotte du Lazaret) bones of *Marmota marmota, Eliomys quercinus, Microtus (=Terricola) duodecimcostatus, Pliomys lenki (=coronensis), Apodemus sylvaticus* were also found (Chaline 1972). The dates obtained (by U-Th series and ESR techniques) for the cultural layer of the Grotte du Lazaret permit the site to be attributed to MIS 6 and to the last Middle Pleistocene glacial stage (Fig. 1, 2, 4, 5).

CONCLUSION

The principal trends in the small mammal evolutionary changes during the very end of the Early Pleistocene and the Middle Pleistocene have been revealed, and the East European and West European faunas were compared. An integrated analysis of theriological, geological and geochronological data available from the Middle Pleistocene localities in Europe has shown marked changes in the small mammal fauna through the period under consideration and provided information on the climate and environments at different time intervals. The changes in Arvicolinae phyletic lines made possible a correlation between the West European and East European mammal localities. They are traceable by changes in the species composition, first occurrences of new species, and morphological changes in several phylogenetic lineages.

There are some difficulties in correlation between West European faunas and those in Eastern Europe which arise from different levels of knowledge and different taphonomic features of the localities. On the Russian Plain most of the localities are found in great geological sequences (mostly in the fluvial sequences overlain by the well studied loess-paleosol series). These sequences were investigated not only paleontologically, but also by several geological methods including paleomagnetic analysis. Those supplementary data help to determine the stratigraphic position of mammal faunas. Most of the localities in the region of the Black Sea coasts include, along with mammals, shells of brackish-water mollusks varying in their evolutionary level. The mollusk assemblages permit the mammal faunas to be directly correlated with the Black Sea transgressions and palaeogeographic events in the Eastern Mediterranean (Mikhailesku and Markova 1992). As is known, a significant part of localities in Western Europe are related to karst caves and fissures. In such localities faunal remains of different age are often found to be mixed, and data of palaeomagnetic analysis are also not quite reliable. There are, however, a number of multilayered localities (Kärlich, Shöningen, Sima del Elephante, Grand Dolina, Colle Curti, Castagnone, the localities from the fluvial sequences from the Thames R. terraces and some others) where multidisciplinary studies (including palaeomagnetic analysis and absolute dating) were performed. The correlation between the East European localities and those mentioned above are very realistic.

The relatively long time interval of the Middle Pleistocene is noted for several climatic events of global scale (glaciation – interglacial) that occurred during it. The biostratigraphic scheme of the Middle Pleistocene has been developed and maps of small mammal localities compiled (Fig. 1, 2, 5).

Thus, faunas of small mammals related to the long Middle Pleistocene interval allow assessment of their taxonomy and evolutionary development. These data can also help us to divide the geological deposits by age and permit reconstruction of the palaeogeographic picture of the past. The results obtained may serve as an important component for compiling biostratigraphic schemes of the Middle Pleistocene and of the Pleistocene in general.

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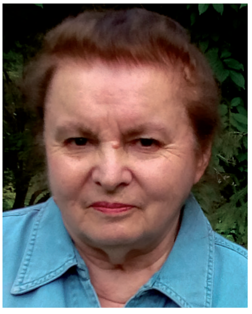

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