

The Mikulino (= Eemian) mammal faunas of the Russian Plain and Crimea

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Abstract

During the last decades a considerable amount of data on mammals from Mikulino (=Eemian) deposits of the central and southern parts of the Russian Plain has been produced. *Mammuthus primigenius* (the early type), *Palaeoloxodon antiquus* (the advanced form), *Arvicola ex gr. terrestris*, *Eolagurus cf. luteus* and *Lagurus cf. lagurus* characterize this period. The so-called 'Shkurlatian mammal assemblage' was distinguished on the basis of a number of Eemian faunas.

The age of the mammal localities was established by using various geological and palaeontological evidence, together with the results of palaeomagnetic studies and absolute dating. The evolutionary level of the diagnostic species allows correlations between localities from different parts of the Russian Plain that have varying taphonomical conditions. The mammal- and malacofauna of the Mikulino Interglacial can also be used as a basis for correlations between the Karangat marine strata of the Black Sea and the continental deposits (alluvial sediments of the second terrace of the Sudost' River and the Salyn phase of the Mezin fossil pedocomplex (see Dodonov et al., this volume). Forest, forest-steppe and steppe zone landscapes have been reconstructed for the central and southern parts of the Russian Plain on the basis of the Eemian faunas.

Keywords: Crimea, Eemian, mammals, Mikulino, Russian Plain

Introduction

Mammal faunas of the last interglacial have been studied in Eastern Europe for about thirty years (see, among others, David & Lungu, 1972; Markova, 1975, 1986; Alexeeva, 1980; Agadjanian & Erbaeva, 1983; Kalinovski, 1983; Motuzko, 1985; Agadjanian & Glushankova, 1986; Markova & Milkhailesku, 1990; Dodonov et al., 1998). Mammal-bearing sites dating from the Mikulino (= Eemian, Muravino or Merkine) are rather scarce on the Russian Plain; only three localities with large mammal remains and twelve sites with small mammal bones have been found so far. Large mammal records were discovered in the Shkurlat locality (Don River basin), the Karagash locality (the North-western coast of the Black Sea), and the Zaskal'naia IX Palaeolithic site (lower layer in the Crimea). The mammal localities are located between

58° NL and 45° NL (Fig. 1). The so-called 'Shkurlatian mammal assemblage' was described on the basis of the Shkurlat mammal fauna Alexeeva, 1980; Markova, 1986).

Geographical position, geological context, taphonomy and dating of the localities

Mammal bones have been found in alluvial, marshy and marl deposits, in tufa, in cultural layers of Palaeolithic sites and also in so-called crotoivines (burrows) in buried soils. The ages of these finds have been obtained primarily by using geological and palaeontological (theriological, palynological, carpological and malacological) methods. In a few cases, absolute dates have been obtained by using radiometric (U-Th), OSL (optically stimulated luminescence) and ESR (electron spin resonance) methods.

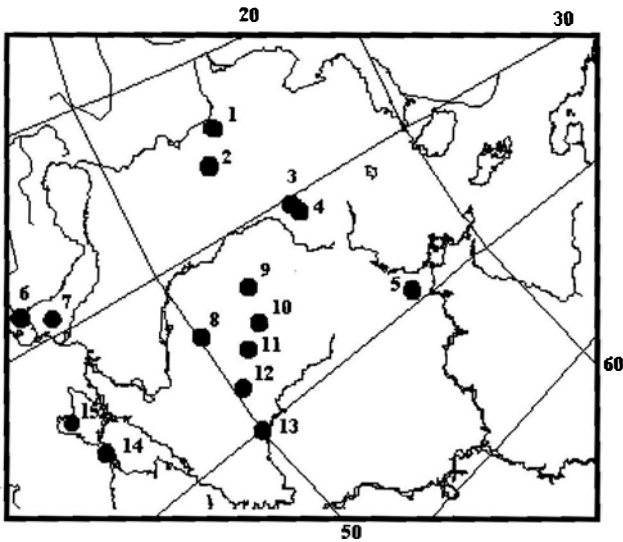


Fig. 1. Mammal localities of the Mikulino interglacial. 1 = Netiesos; 2 = Timoshkovichi; 3 = Borisova Gora; 4 = Konevich; 5 = Cheremoshnik; 6 = Novonekrasovka; 7 = Karagash; 8 = Gadiach; 9 = Posudichi; 10 = Mikhailovka; 11 = Malutino; 12 = Chernianka; 13 = Shkurlat; 14 = El'tigen; 15 = Zaskal'naya IX (lower layer).

Localities in alluvial deposits

The Shkurlat locality (in the middle basin of the Don river) is the stratotype of the Mikulino interglacial mammal fauna. The geology of the complex Shkurlat section was studied by Shevyrev et al. (1987). Geologically, the mammal locality is associated with the alluvial deposits of a tributary of the Don. Shevyrev et al. correlate these deposits with the third terrace of the Don, but the sequence in this section has been complicated by tectonic interference. The Shkurlat alluvial deposits have yielded the typical Mikulino (= Eemian) interglacial flora that was described by Spiridonova, who recognised five palynological zones (Shevyrev et al., 1987). Alexeeva (1980) identified the large mammals of 'the Shkurlatian faunal complex', which include *Mammuthus primigenius* (early type), *Palaeoloxodon antiquus* (advanced type), *Coelodonta antiquitatis* and others (Table 1). The morphology of the *Palaeoloxodon antiquus* remains closely resembles that of *P. antiquus germanicus* from Weimar-Ehringsdorf and Taubach (Germany), correlated with the first part of the Eemian (Kahlke, 1975). The Shkurlat locality yielded ten different small mammal species (Table 2) (Markova, 1986).

Other faunal localities in fluvial deposits are Karagash (Dniester basin), Chernianka (Oskol river basin), Malutino (Seim river basin), Konevich (Dniepr basin) and Posudichi (Dniepr basin). These sites are in alluvial deposits of the second terrace (David & Lungu, 1972; Kalinovski, 1981, 1983; Motuzko, 1985; Agadjanian & Glushankova, 1986a;

Markova, 1986; Adamenko et al., 1996). The Posudichi fossiliferous bed corresponds to the lower part of the channel deposits in the second terrace of the Sudost' river and overlies the lacustrine deposits containing the typical Mikulino palynological sequence (Gurtovaya & Faustova, 1977). This locality represents the end of the Mikulino interglacial (Agadjanian & Glushankova, 1986b).

Localities in tufa

The Borisova Gora locality (in the Zapadnaya Dvina Basin) was found in the tufa that overlies the Dniepr till. The Middle Valdai solifluction deposits and the Valdai till rest on these travertines (San'ko & Motuzko, 1991). According to San'ko and Motuzko, this locality represents the beginning of the Mikulino interglacial.

Localities in lacustrine and bog deposits

Among the localities of this type, the Timoshkovichi and Netiesos sites (Nemunus Basin) and the Cheremoshnik locality (the Rostov Lowland) date from the Mikulino (= Merkine) stage. ESR dates have been obtained from the Netiesos sequence: the lower samples gave 112 ± 25 ka, and the upper samples 101.5 ± 11.5 ka (Gaigalas & Molod'kov, 1997). The Netiesos lake deposits also have OSL dates of 95 ± 12 ka and 86 ± 7 ka for the lower bed, and 70 ± 3 ka and 70 ± 8 ka for the upper part (Gaigalas & Hutt, 1997). In the Timoshkovichi site, the Mikulino (= Muravino) peats are overlain by Valdai-age glacial deposits. The peats yield typical Mikulino pollen spectra, as well as a warm interglacial insect fauna (Kalinovski, 1983; Nazarov, 1986).

The Netiesos locality includes a peat lens (containing a rich Mikulino-age seed and pollen flora) overlain by alluvial channel deposits that reach up to 12–13 m thick (Velichkevich, 1982).

The Cheremoshnik small mammal fauna was recovered from the Mikulino peat deposits of the Rostov Lowland. The fossiliferous bed is overlain by a Middle Pleistocene till unit. Rich plant remains (pollen and seeds) were found in the peat and described as being of typical Mikulino character (Grichuk, 1989). Cold, Valdai-age small-mammal faunal remains have been found in deposits overlying the peat (Agadjanian & Erbaeva, 1983).

Localities in fossil soils

The Gadiach fauna (in the Psel river basin) was recovered from 'crotovines' within the Mezin pedocom-

Table 1. Species composition of the mammals from the Mikulino localities.

Species	Localities														
	Timoshkovchi	Borisova Gora	Konevich	Pesudichi	Niastos	Cheremoshnik	Malutino	Chernyanka	Mikhailovka 5	Gadyach	Shkuriat	Novonekrasovka	Karagash	El'tigen	Zaskal'naya IX, lower layer
Insectivora:															
<i>Erinaceus</i> sp.		10													
<i>Talpa</i> cf. <i>europaea</i> Linnaeus		7						16							
<i>Sorex araneus</i> Linnaeus		6						19							
<i>Sorex caecutiens</i> Laxmann		2													
<i>Sorex minutus</i> Linnaeus		2						1							
<i>Sorex isodon</i> Turov		1													
<i>Sorex</i> sp.	2			3		1		1	8						
<i>Neomys fodiens</i> Pennant		9													
<i>Desmana moschata</i> Linnaeus	1			1											
Lagomorpha:															
<i>Lepus</i> sp.															1
<i>Ochotona pusilla</i> Pallas		3						5	2	3				2	
Rodentia:															
<i>Sciurus vulgaris</i> Linnaeus.		2													
<i>Marmota bobac</i> Muller															1
<i>Marmota</i> sp.						3			+						
<i>Spermophilus</i> cf. <i>suslicus</i> Guldenstaedt								18							
<i>Spermophilus</i> sp.						4	5	4		27	14			10	5
<i>Allactaga major</i> Pallas											1				
<i>Allactaga</i> sp.															8
<i>Pygeretmus (Alactagulus) acontion</i> Kerr											1				
<i>Spalax microphthalmus</i> Guldenstaedt						2		29						2	
<i>Castor</i> sp.					1										
<i>Cricetulus migratorius</i> Pallas									1						
<i>Cricetus cricetus</i> Pallas		1				2		2							
<i>Glis</i> sp.		2													
<i>Apodemus (Sylvimus) flavicollis</i> Melchior							1	1							
<i>Apodemus</i> ex gr. <i>sylvaticus-flavicollis</i>		128				1		6							
<i>Mus musculus</i> Linnaeus		2													
<i>Lemmus sibiricus</i> Kerr		267		4	10										
<i>Myopus vel Lemmus</i>	3		4												
<i>Dicrostonyx</i> sp.		1													
<i>Ellobius talpinus</i> Pallas							1							13	
<i>Clethrionomys glareolus</i> Schreber	8	273	13	1	2	2		2	30						
<i>Eolagurus</i> cf. <i>luteus</i> Eversmann						5	6	5	1		81			9	
<i>Lagurus</i> aff. <i>lagurus</i> Pallas					2		14			12	126			3	
<i>Arvicola</i> ex gr. <i>terrestris</i> Linnaeus	8	60	1	20	4	29	21	29	95		10	180		4	
<i>Microtus (Terricola) subterraneus</i> Selys-Longchamps		6							12						
<i>Microtus (Stenocranius) gregalis</i> Pallas			1	1	15	2	21	2	2	7	45			3	
<i>Microtus (Microtus) agrestis</i> Linnaeus	3	14	1			2	5	2	107	2	2				

Table 1. Continued.

Species	Localities														
	Timoshkovchi	Borisova Gora	Konevich	Posudichi	Niatesos	Cheremoshnik	Malutino	Cherryanka	Mikhailovka 5	Gadyach	Shkurlat	Novonekrasovka	Karagash	El'tigen	Zaskal'naya IX, lower layer
<i>Microtus (Microtus) arvalis</i> Pallas	1	4			9	1	2	1	8		1	9			
<i>Microtus obscurus</i> Eversmann															210
<i>Microtus (Pallasiinus) oeconomus</i> Pallas		3	3			2	15	2			2				
<i>Microtus</i> sp.	6	154	9	13		47	34	47	132	13	52	8			
Carnivora:															
<i>Ursus</i> sp.		1													
<i>Canis lupus</i> Linnaeus															6
<i>Vulpes vulpes</i> Linnaeus		1													9
<i>Vulpes corsak</i> Linnaeus															5
<i>Crocota (Crocota) spelaea</i> Godfuss															1
<i>Panthera (Leo) spelaea</i> Goldfuss											+				
Proboscidea:															
<i>Mammuthus primigenius</i> Blumenbach (early type)											+		+		
<i>Palaeoloxodon antiquus</i> Falconer et Cautley (advanced type)											+		+		
Perissodactyla:															
<i>Equus ex gr. caballus</i> Linnaeus											+				1
<i>Coelodonta antiquitatis</i> Blumenbach											+				
Artiodactyla:															
<i>Sus</i> sp.		1													
<i>Bison priscus</i> Bojanus											+				1
<i>Bos trochoceros</i> Meyer													+		
<i>Cervus elaphus</i> Linnaeus													+		
<i>Saiga tatarica</i> Linnaeus															29

plex formed during the Mikulino interglacial. In the Gadyach section, the Mezin soil, overlain by a Valdai-age loess series, rests on top of the Dniepr Till (Markova, 1986).

The Michailovka 5 locality (Svapa river basin) was found in remnants of the Mezin fossil soil, which overlies Dniepr fluvioglacial sediments and is overlain by Valdai periglacial deposits (Agadjanian & Glushankova, 1986b).

Localities in calcareous deposits

The Novonekrasovka (the lower Danube basin) and

the El'tigen (Crimea, the Kerch' peninsula) sites were found in the Karangat (= Eemian) coquina, together with a rich mollusc fauna, associated with the Karangat transgression of the Black Sea. Palaeomagnetic studies of the El'tigen section allows identification of the Blake Event in the fossiliferous strata. A few dates have also been obtained from these sediments by using the U-Th method: 127 ± 8.9 ka for cycle I, and 107 ± 7.7 ka for cycle II of this sequence (Markova & Mikhailesku, 1990; Dodonov et al., 2000 – this issue). The fauna was recovered from cycle I deposits (substages Ib and Ic).

Table 2. Sizes of the *m*₁ of *Atricolta* from Middle and Late Pleistocene localities on the Russian Plain.

Geochronology	Localities	L ₁ , mm			W ₁ , mm			SDQ		
		n	lim	x	n	lim	x	n	lim	x
modern time	Ukraine	11	3.45-4.30	4.01	11	1.35-1.85	1.65	11	59.88-100	76.92
Valdai glaciation	Troitsa II 32,500 ± 700 year BP	3	3.67-4.1	3.91	3	1.60-1.70	1.65	3	71.43-83.33	80
	26,860 ± 30 year BP									
	27,000 ± 350 year BP									
Late Pleistocene	Shkurlat	3	3.8-4.2	3.91	3	1.5-1.8	1.65	3	63.89-76.67	70.3
	Malutino	4	3.75-4.2	3.97	4	1.5-1.65	1.59	4	42-100	61.4
	Chernianka	4	3.8-4.2	4	4	1.5-1.6	1.55	4	90-111	99
	Mikulino interglacial	18	3.5-4.1	3.84	18	1.5-1.75	1.66	18	60-140	87
	Novonekrasovka (upper layer)	14	3.6-4.0	3.78	14	1.5-1.75	1.66	14	59.9-110	92
	Novonekrasovka (lower layer)									
	Chigirin	48	3.2-3.9	3.49	62	1.3-1.65	1.47	62	101.67-166.67	129
	Verkhnyaya Emancha	33	3.0-3.75	3.38	48	1.25-1.6	1.35	33	100-200	125
	Gun'ki 1	23	3.15-3.7	3.43	35	1.5-1.55	1.45	35	120-303.03	125
	Gun'ki 2	12	3.2-3.45	3.38	9	1.3-1.65	1.49	12	120.48-303.03	132
	Likhvin interglacial									

Table 1. Continued.

Species	Localities														
	Timoshkovchi	Horisova Gora	Konevich	Posudichi	Niatesos	Cheremoshnik	Malutino	Chernyanka	Mikhailovka 5	Gadyach	Shkurlat	Novonekrasovka	Karagash	El'tigen	Zaskal'naya IX, lower layer
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Table 3. Sizes of the m1 and the A/L index of *Lagurus* cf. *lagurus* from Mikulino localities.

Localities	L, mm		W, mm		L of ACC, mm		L of AC2, mm		A/L	
	lim	n	lim	n	lim	n	lim	n	lim	n
Gadiach	2.1-2.4-2.7	3	0.85-0.9-0.95	3	1.3-1.367-1.4	3	0.7-0.733-0.75	3	51-57-61	3
Malutino	2.1-2.434-2.75	16	0.7-0.866-0.75	16	1.15-1.368-1.6	16	0.7-0.81-1.0	16	54-56-58	16
Chernianka	2.35	1	0.85	1	1.25	1	0.75	1	53	1
Shkurlat	2.2-2.491.-2.8	35	0.6-0.845-1.05	35	1.15-1.329-1.6	35	0.7-0.798-0.9	35	52-53-57	35

Table 4. Morphotypes of the m1 *Lagurus* from Middle and Late Pleistocene localities on the Russian Plain.

Geochronology	Mammal assemblages	Species	Localities	Morphotypes of ACC of m1, %			
				'transiens'		'lagurus'	
				%	n	%	n
Valdai glaciation	Mammoth	<i>Lagurus</i> aff. <i>lagurus</i>	Luchki	—	—	100	4
			Arapovichi	11.12	2	88.88	16
Mikulino interglacial	Shkurlatian		Gadiach	33.33	1	66.676	2
			Chernianka	—	—	100	1
			Shkurlat	17.24	5	82.76	24
Dnieper glaciation		<i>Lagurus</i> ex gr. <i>lagurus</i>					
Romny warming	Khazarian						
cooling (glaciation)							
Kamenka Interglacial			Priluki	43.75	7	56.25	9
Likhvin interglacial	Gun'kovian	<i>Lagurus</i> ex gr. <i>transiens</i>	Gun'ki 2	57.67	29	42.33	23
			Chigirin	74.99	9	25.11	3

Faunas from cultural layers of Palaeolithic sites

Mammalian remains have been collected from the lower cultural layer at the Zaskal'naya IX Palaeolithic site (grotto on the Ak-Kaya plateau, Crimea). From this site, Mousterian artefacts of an archaic type were described from the lower layer (Kolosov, 1986; Kolosov et al., 1993). Remains of mammoths and arctic foxes have not been discovered here, although they are very typical of other Mousterian sites in the Crimea. Both the archaeological data and the mammal fauna therefore unambiguously indicate that the lower layer at Zaskal'naya IX is one of the earliest Mousterian sites in the Crimea and that it might be correlated with a warm interglacial event (Kolosov, 1986).

The mammalian faunas

Small mammals¹

Arvicola ex gr. *terrestris* Linnaeus – water vole *Arvicola* teeth from Mikulino localities show the following morphological characteristics (Table 2):

¹ Terminology: in the present contribution, the following terminology – introduced by Van der Meulen (1973) – was used for the parts of the occlusal surface of molars of voles. L = the length of molars; W = the width of molars; AC 2 = the anterior cap; ACC = the anteroconid complex; A = the length of anteroconid complex; T1-T5 = the dentine fields of occlusal surface of molars; B = the shortest distance between AC 2 and T4 and T5; BRA = the buccal re-entrant angle; LRA = the lingual re-entrant angle; C = the shortest distance between the BRA 3 and the LRA 3 angles. We also used the SDQ index after Heinrich (1978), which shows the ratio between the thickness of the enamel on the posterior wall of the molar salient angles and the thickness of the enamel on the anterior part of the salient angles. In th we used the measurements of the enamel of three central angles of the m1 (LSA2, LSA3, BSA2).

- (1) the teeth of the Mikulino water voles are smaller than those of modern representatives, but larger than those of the late Middle Pleistocene water voles;
- (2) the SDQ index shows a positive enamel differentiation of the molars, but the enamel is less differentiated than the enamel of the modern *Arvicola* teeth.

Judging from the complex of morphological characteristics, the water vole remains from Mikulino sites are closer to those of *A. terrestris* than to those of *A. cantianus* and may be attributed to *Arvicola* ex gr. *terrestris*.

Lagurus cf. *lagurus* Pallas – steppe lemming

The sizes of the m1 do not differ significantly from those of the modern *Lagurus lagurus*. Differences are more pronounced when comparing them with samples from earlier localities (Table 3). The 'lagurus' morphotypes of the m1 and the M3 dominate in the populations of this age and reach 70% and even more. The 'transiens' morphotypes persist at very low proportions (Table 4).

Eolagurus cf. *luteus* Eversmann – yellow steppe lemming

The sizes of Mikulino *Eolagurus* teeth (Table 5) are a bit smaller than modern ones, but larger than Middle and Early Pleistocene ones. Dentine fields of m1 and M3 of Mikulino yellow steppe lemmings are not completely separated. ACC characteristics show a rather low differentiation. The tooth size and the coefficient showing the degree of confluence between the angles at the base of anteroconid are most diagnostic (Table. 5).

Microtus (*Stenocranius*) *gregalis* – narrow-skulled vole

The typical 'gregalis' morphotypes of the ACC dominate over the 'arvalis'-like morphotypes, which are more characteristic of the Valdai glacial faunas (Table 6). T4 and T5 are practically separated. AC 2 is also separated from T4 and T5.

Large mammals

The Mikulino localities of the Russian Plain are char-

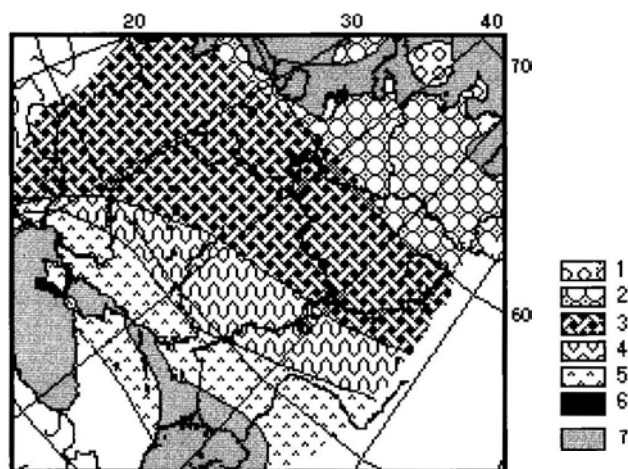


Fig. 2. Vegetation types and types of mammal communities during the Mikulino interglacial.

1 = birch and pine open woodland (after Grichuk, 1989), no mammal finds; 2 = the fir/birch woodland with some oak and hornbeam in the South (after Grichuk, 1989), no mammal finds; 3 = mammal community of mixed and broad-leaved woodland; 4 = forest/steppe mammal community; 5 = steppe mammal community; 6 = mountain-steppe mammal community; 7 = sea basins.

acterised by the presence of remnants of *Mammuthus primigenius* (early type), *Palaeoloxodon antiquus* (advanced type), *Coelodonta antiquitatis*, *Bison priscus*, *Bos trochoceros* and two cave carnivores, *Panthera* (*Leo*) *spelaea* and *Crocota spelaea*. The bone morphology of other species of carnivores (*Ursus arctos*, *Vulpes vulpes* and *V. corsak*) does not differ from that of modern species (Alexeeva, 1980; David & Lungu, 1972).

Mammal communities

The characteristics of the Mikulino fauna have been inferred primarily from small mammal assemblages (only three sites have yielded larger mammal remains). All localities are concentrated in the central and southern parts of the Russian Plain and on the Crimea peninsula. No mammal localities of Mikulino age have been found north of 60° NL.

Table 5. Sizes of fossil and modern *Eolagurus*.

Geochronology	Localities	n	L. m ₁ (mm)		B/L		C/L		Species
			x	m _n	x	m _n	x	m _n	
Valdai glaciation	Malyi Gai	3	3.15	±0.126	1.67	±0.086	1.6	±0.19	<i>Eolagurus</i> aff. <i>luteus</i>
Mikulino interglacial	Shkurlat	8	3.05	±0.082	1.67	±0.12	1.7	±0.23	
	Malutino	2	3.075	±0.2704	2.275	±0.6008	2.903	±0.4422	
Likhvin interglacial	Gun'ki II	17	2.92	±0.0411	2.9	±0.29	3.2	±0.26	<i>Eolagurus</i>
	Chigirin	13	2.95	±0.0302	2.66	±0.97	3.5	±0.87	<i>luteus volgensis</i>
early Middle Pleistocene	Tikhonovka	12	3.025	±0.0279	2.85	±0.4961	5.863	±0.6374	<i>Eolagurus gromovi</i>
	Platovo	7	3.025	±0.0279	2.85	±0.4961	5.863	±0.6374	
end of Early Pleistocene	Karai-Dubina	35	2.77	±0.02237	2.9	±0.188	7.03	±0.187	<i>Eolagurus</i> cf. <i>argyropuloi</i>

Table 6. Measurements and A/L index of the m1 of the *Microtus* (*Stenocranius*) lineage.

Geochronology	Localities	Species	L m1, mm				A/L			
			n	min	x	max	n	min	x	max
Valdai glaciation	Khotylevo 2	<i>M. (S.) gregalis</i>	40	2.35	2.8	3	20	52	54.1	56.4
Mikulino interglacial	Malutino	<i>M. (S.) gregalis</i>	20	2.35	2.7	3	17	50.9	54.1	56.5
	Shkurlat	<i>M. (S.) gregalis</i>	22	2.25	2.6	2.95	10	49.6	52.2	55.7
	Chigirin	<i>M. (S.) cf. gregalis</i>	24	2.35	2.7	3.1	10	48.4	51.9	54.4
Likhvin interglacial	Gun'ki 2	<i>M. (S.) cf. gregalis</i>	61	2.25	2.6	2.75	25	47.9	51.5	53.9
Muchkap interglacial	Suvorovo	<i>M. (S.) gregalis</i> -	8	2.37	2.5	2.68	8	47.5	50.5	54.7
	(upper layer)	<i>M. (S.) gregaloides</i>								
very end of Early Pleistocene	Karai-Dubina	<i>M. (S.) hinoni</i>	90	2.2	2.5	2.8	23	44.3	47.3	50.6

Mixed and broad-leaved forest community

Mammal communities dominated by forest species were distributed on the Russian Plain between 60-52° NL and, possibly, even further north. *Erinaceus europaeus*, *Sciurus vulgaris*, *Castor fiber*, *Apodemus*, *Clethrionomys glareolus*, *Microtus (Terricola) subterraneus* and *M. (Microtus) agrestis* were widely distributed. This assemblage has been termed the 'mixed and broad-leaved forest community' (Figure 2). From the early phase of the Mikulino interglacial, a small number of cold-tolerant animal remains (*Dicrostonyx* sp.) were found in the Borisova Gora locality (Table 2). *Lemmus sibiricus* and *Lemmus* vel *Myopus* remains have also been discovered from sites located at 53-55° NL. The records of the fossil *Lemmus* remains may indicate less strict environmental requirements for this species during the Pleistocene (when they were also typical of boreal forests) than at present.

Forest-steppe mammal community

The distribution area of the so-called 'forest-steppe mammal community' was situated further south: south of 52° NL. The steppe species (*Ochotona pusilla*, *Spermophilus*, *Marmota bobac*, *Spalax microphtalmus*, *Ellobius talpinus*, *Cricetus cricetus*, *Cricetulus migratorius*, *Lagurus* cf. *lagurus*, *Eolagurus* cf. *luteus*, *Microtus (Stenocranius) gregalis*), forest species (*Clethrionomys glareolus*, *Microtus (Microtus) agrestis*), meadow species (*Microtus (Microtus) arvalis*) and 'intra-zonal' species (*Arvicola* ex gr. *terrestris*, *Microtus (Pallasinus) oeconomus*) occurred in this zone. The southern limit of this community was about 45° NL in the central part of the Russian Plain (Fig. 2).

Steppe mammal community

The 'steppe mammal community' existed in the Northern Black Sea coastal region and in the Crimea, where only steppe species lived during the Mikulino in-

terglacial. The species included *Ochotona pusilla*, *Spermophilus*, *Spalax*, *Sicista subtilis*, *Allactaga major*, *Ellobius talpinus*, *Lagurus*, *Eolagurus*, *Microtus (Stenocranius) gregalis*, *Microtus (Microtus) obscurus* and others.

Conclusions

It is possible to reconstruct at least the following three biomes in the central and southern parts of the Russian Plain on the basis of mammal faunas from the Mikulino localities (unfortunately there are no records from the Northern part of Eastern Europe).

- (1) The zone of mixed and broad-leaved forests with a rich fauna of forest mammals from 60° to 52° NL. The northern boundary of this zone was farther to the north during the Mikulino than at the present-day. The southern limit occurred close to the modern one.
- (2) The southern forest/steppe zone, where high concentrations of steppe mammals (rodents, insectivores, lagomorphes, proboscidea, artiodactyla and perrisodactyla) were found. Several forest species also inhabited this region. The geographical position of this zone during Mikulino times resembles that at the present-day.
- (3) The steppe zone into the extreme South of Eastern Europe. The steppe mammals (primarily small mammals) inhabited this region, not only during the Mikulino, but also during earlier warm intervals of the Middle Pleistocene (the Il'inka, Muchkap, Likhvin and Kamenka interglacials) and even during the Early Pleistocene (Markova, 1992). All this evidence demonstrates the antiquity of the steppe biome on the Russian Plain.

The East European Mikulino mammalian assemblages are not very rich, but as a whole they indicate warmer climatic conditions during this stage than today. The existence of a wider broad-leaved forest zone on the Russian Plain, with numerous forest mammals, supports this conclusion.

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