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Pleistocene mammal faunas of Eastern Europe

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Abstract

Systematic studies of the Pleistocene mammal assemblages of Eastern Europe have been carried out for more than a century, and they elucidated evolutionary changes and ascertained chronological sequence of the faunas. The available evidence on fossil mammals from Eastern Europe allows differentiation of 7 complexes of large mammals. These complexes represent 15 assemblages and their phases distinguished for small mammals. The appearance of new taxa of different rank provides the basis for identification of the principal stages in mammal evolution. Multi-disciplinary studies of fossil mammal localities have made it possible to correlate theriological data with the main events of the Pleistocene (such as glacials and interglacials) by comparison between geological, geochronological and palaeontological data.

Interglacial and periglacial mammal faunas of different age have been defined on the basis of their structural characteristics and geographical distribution. Two types of mammal assemblages are recognised: zonal interglacial and periglacial assemblages specific to glacial periods. In the first type, each zonal assemblage is dominated by a single ecological group of mammals. A distinctive feature of the second type is the co-existence of animals belonging to different ecological groups and inhabiting different natural environments.

1. Introduction

Studies of the Pleistocene mammal faunas in Eastern Europe began over a 100 yr ago. Fossil mammal remains recovered from over 400 Eastern European localities have allowed the differentiation of the principal stages in the mammal evolution throughout the Pleistocene and establishment of a biostratigraphical subdivision based on evolutionary changes, supported by both geological and geochronological information.

Seven large-mammal complexes have been recognised in the Pleistocene: the Psekupsian, Tamanian, Tiraspolian, Singilian, Khozarian, Shkurlatian and the Mammoth. Fifteen small mammal assemblages (including phases) can be correlated with the large-mammal complexes. The assemblages have been identified on the basis of the first appearance of new taxa of different rank in the faunas. The fossil mammals reviewed were recovered from sections studied using a wide range of techniques; which include geological, palaeopedological, malacological, palynological, palaeomagnetic and radiocarbon evidence.

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In the present paper the subdivision of the Pleistocene adopted follows the international stratigraphic scale in which the base of the Pleistocene beginning is defined by the upper boundary of the Olduvai palaeomagnetic Subchron (at 1.81 Ma BP), the base of the Middle Pleistocene is placed the Brunhes/Matuyama Chron boundary (0.85 Ma BP), and the Late Pleistocene at the base of the Eemian (Mikulino) Stage Interglacial (135 ka BP).

2. Mammal assemblages of Eastern Europe

2.1. Early Pleistocene

2.1.1. Psekupsian mammal complex

Faunas immediately preceding the oldest ones of the early Pleistocene have been described from the locality on the Psekups River (Northern Caucasus); they include *Archidiskodon meridionalis meridionalis, Mastodon avernensis*, *Equus stenonis*, *Dicerorhinus etruscus*, *Cervus pliotarandoides*, *Mimomys pitymyoides* and *Mimomys* ex gr. *reidipusillus, Mimomys pliocaenicus, Borsodia fejervaryi* and *B. arankoides* (Gromov, 1948; Alexandrova, 1977; Tesakov, 2004). Small-mammal fossils recovered later from the same

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strata appeared to represent only voles with rooted molars. These faunas were identified as the Psekupsian assemblage. Their occurrence in the layers containing Akchagylian molluscs suggests the fauna predates the Olduvai Subchron that is older than 1.9 Ma BP (Vangengeim et al., 1990).

Mammal assemblages similar in evolutionary level to that from Psekups River sections have been found in the upper series of the Liventsovka section, near the city of Rostov-na-Donu (Alexandrova, 1976) and at the Svapa locality in the upper reaches of the Dnieper River (Agadjanian, 1992). Faunas of a similar evolutionary level are also present in the Tegelen and Zuurland 91–95 localities, in the Netherlands (Kolfschoten, 1988, 1990a).

2.1.2. Odessian small mammal assemblage

The later phase of the Psekupsian assemblage, with *Archidiskodon m. meridionalis*, can be correlated with the Odessian small mammal assemblage; the latter having been identified by Shevchenko (1965) who studied the assemblage from the Kryzhanovka locality (Kuyalnik Liman). This assemblage is distinct because it contains the highly diversified forms of *Mimomys*, and also because it includes the first appearance of rootless-toothed cemented and cementless voles (*Allophaiomys*, *Lagurodon*) (Shevchenko, 1965). The Odessian assemblage is coeval with the lower and middle Gurian strata of the Black Sea, and the lower and middle Apsheronian sediments of the Caspian Sea (Nikiforova and Alexandrova, 1991).

2.1.2.1. Early phase of the Odessian small-mammal assemblage. The earliest small-mammal faunas which contain remains of rootless voles (*Allophaiomys deucalion*) are known from a number of localities, such as Mikhailovka 1 in the Upper Dnieper region (Agadjanian, 1992) and Tiligul, the Tiligul Liman in the northern Black Sea coastal region (Topachevski and Skorik, 1977; Rekovets, 1994) (Fig. 1). No remains of large mammals have been recovered from these sites. The faunas do not yield voles with rootless molars of the genera *Prolagurus* and *Lagurodon*. At that time cementless voles of the *Borsodia* gen., with rooted molars, are noted for their increasing hypsodonty. *Mimomys* are represented by the same species as in the Psekupsian faunas. The genus *Allophaiomys* is represented by an archaic species *A. deucalion*. Similar faunas have been described from the Villány V locality in Hungary and Kamyk in Poland (Kretzoi, 1969; Kowalski and Nadachowski, 1990).

The stratigraphical position of the faunas of this evolutionary level is still debatable. Until recently, the first appearance of *Allophaiomys* was dated to the beginning of the Pleistocene. Most of the known localities correlate with the early and middle Gurian sediments of the Black Sea and with early and middle Apsheronian sediments of the Caspian. No *Allophaiomys* has been recovered from the Psekupsian assemblage stratotype. It is worth noting that large-mammal assemblages, including *A. m. meridionalis*, existed longer, spanning both the Psekupsian and Odessian small-mammal assemblages ranges. The early Odessian faunas may be equivalent to those of the Eburonian in Western Europe, with faunas from the Zuurland localities (borehole 50–58 m) in the Netherlands (Kolfschoten, 1988, 1990a); Kolińany, Včeláre 5, 10 and 10 B (Fejfar and Horáček, 1990); Kamyk and Kadzelnya in Poland (Garapich and Nadachowski, 1996).

2.1.2.2. Late phase of the Odessian small-mammal assemblage. The small-mammal faunas attributable to the later phase of the Odessian assemblage are marked by the appearance of the first cementless rootless toothed voles of *Prolagurus* (*P. ternopolitanus*) and *Lagurodon* (*L. arankae*) genera (Markova, 1998a, b). Faunas of this evolutionary level are also found from a number of localities: Kryzhanovka (the upper layer) and Zhevakhova Gora (layers 5,9), near Odessa; Uspenka, Korotoyak (the lower layer), Log Denisov on the Don river; Khadzhimus on the Dniester river; Chortkov (the Seret river basin) and Melekino in the Azov region (Shevchenko, 1965; Agadjanian, 1992; Iosifova et al., 1992; Mikhailesku and Markova, 1992; Iosifova and Krasnenkov, 1994; Rekovets, 1994; Markova and Kozharinov, 1998) (Fig. 1). The Kryzhanovka locality has yielded some large-mammal remains, including *A. m. meridionalis*, *E. stenonis*, *Elasmotherium sibiricum* and others. Here the small mammals are represented by *Allophaiomys deucalion*, *Prolagurus ternopolitanus* and *Lagurodon arankae*.

Among the *Mimomys* voles, *Mimomys* ex gr. *reidi—pusillus* still occur together with some later representatives of *M. pliocaenicus*. Fluvial deposits underlying the 9th terrace of the Dniester river in Khadzhimus site (with small-mammal fossils) have been dated by thermoluminescence method at 1300 ± 350 Ma (Kulikov and Chepalyga, 1985). Possibly the age of this strata is even older.

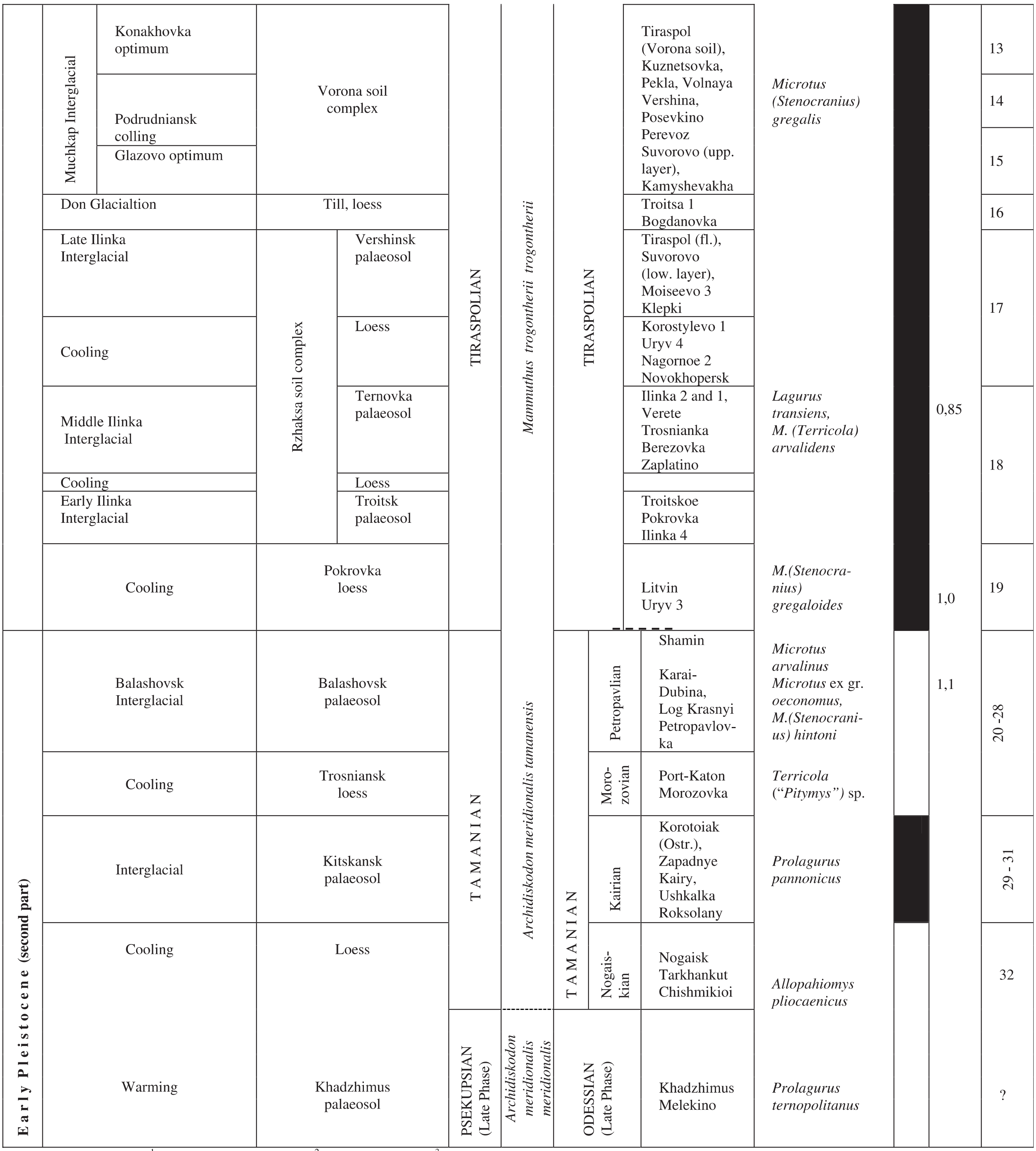
Faunas of this evolutionary level are of similar composition to those recovered from a number of localities in Europe: e.g. Betfia XIII in Rumania, which includes early *Allophaiomys* and *Lagurodon arankae* (Terzea, 1995); Mokrá in Slovakia (Fejfar and Horáček, 1990), Žabia Cave in Poland (Garapich and Nadachowski, 1996); Zuurland (42–46 m) in the Netherlands (Kolfschoten, 1988); Nagyharsányhegy 2 in Hungary (Kretzoi, 1956); Venta Micena in Spain (Agusti, 1991). These assemblages may possibly be attributed to the early Biharian Mammal Stage (Kretzoi, 1961).

2.1.3. Tamanian mammal complex

The index fossil for the Tamanian mammal complex is *Archidiskodon meridionalis tamanensis* (Gromov, 1948; Dubrovo, 1964; Garrut and Tikhonov, 2001). The Tamanian complex stratotype at the village Sinyaya Balka has yielded the remains of *A. m. tamanensis*, *Elasmothrium caucasicum*, *Equus süssenbornensis* and others (Gromov, 1948) (Fig. 1). The large-mammal faunas typical of this assemblage existed throughout a considerable time interval

Chronology	Glaciations, Interglacials (Breslav et al., 1992; Shik, 1993)		Tills, loesses, palaeosols (Velichko et al., 1992, Sycheva, 1997)	Large-mammal assemblages	Elephantidae philogeny	Small-mammal assemblages	Small-mammal localities	The first appearance of species	PM[1]	MA[2]	M I S[3]
1	2		3	4	5	6	7	8	9	10	11
Hol.	Holocene		Holocene soil	Holo-cene	*Mammuthus primigenius*	Holo-cene					1
L a t e P l e i s t o c e n e	Valdai Glaciation	Late Valdai	Till, loess Trubchevsk palaeosol Till, loess	'MAMMOTH'		SU NGIRIAN	Tatinki, Yudinovo Khotylevo 2 Eliseevichi	*Dicrostonyx torquatus*		0,01	2
		Middle Valdai	Briansk, Alexandrovka, Streletsk paleosoils				Arapovichi, Sungir, Troitsa 2				3
		Early Valdai	Loess Krutitsk palaeosol Loess				Betovo, Kabazi 2 (III/3) Gadiach	*Dicrostonyx gulielmi*			4
	Mikulino Interglacial		Salyn palaeosol	Shkurlatian		Shkur-latian	Malutino, Chernianka, Mikhailovka 5, Shkurlat, Eltigen, Novonekra-sovka	*Arvicola* ex gr. *terrestris, Microtus (Terricola) subterraneus*			5
M i d d l e P l e i s t o c e n e	Dniepr Glaciation	Moscow stage Kursk Interstadial Dnieper stage	Till, loess Kursk palaeosoil Till, loess	CHOZARIAN	*Mammuthus trogontherii chosaricus*	CHOZARIAN	Pavlovka-on-Desna, Kobyliaki, Zhukevichi, Alpatievo, Spasskoe, Volgino, Strigovo, Chekalin (fluviogl. layer.), Yagodnoe	*Dicrostonyx simplicior*		0,13	6
	Warming		Romny palaeosol								7
	Cooling		Orchik loess								8
	Kamenka Interglacial		Kamenka palaeosol				Priluki, Plavni, Uzunlar, Rasskazovo, Chernyi Yar	*Lagurus* ex gr. *lagurus, Arvicola chosaricus*			9
	Cooling		Borisoglebsk loess				Topka				10
	Likhvin Interglacial		Inzhava palaeosol	S I N G I L I A N		G U N K O V I A N	Chekalin (gittia), Gunki Chigirin Ver.Emancha Naravai, Rybnaya Sloboda, Otkaznoe Uzmari, Tiraspol (Inzh.soil), Mikhailovka 2, Smolenski Brod	*Arvicola cantianus*		0,36	11
	Oka Glaciation		Oka till, loess				Chekalin (Oka glacial layer) Mikhailovka 2	*Dicrostonyx simplicior okaensis*		0,43 0,47	12

Fig. 1. The stratigraphical scheme of Eastern Europe and mammalian faunas (Glaciations, Interglacials (Breslav et al., 1992; Shik, 1993), Tills, loesses, palaeosols (Velichko et al., 1992; Sycheva, 1997)).



[1] – palaeomagnetic data, [2] – million years, [3] – marine isotope stages

Fig. 1. (*Continued*)

which may be correlated with the upper Gurian of the Black Sea and the late Apsheronian of the Caspian (Nikiforova and Alexandrova, 1991). Comparison of the fossil-bearing localities and the palaeomagnetic record, suggest that the duration of the interval may be tentatively estimated at 300 ky, from 1.1 to 0.8 Ma BP (Vangengeim et al., 1991). Four distinct phases can be distinguished in the small-mammal evolution during the existence of the Tamanian mammal complex, the Nogaiskian, Kairian, Morozovkian and Petropavlovkian faunas.

2.1.3.1. Nogaiskian small-mammal faunas. The earliest small-mammal faunas coeval with the Tamanian large-mammals complex have been identified as belonging to a separate evolutionary stage, on the basis of fossils from the Nogaisk type locality in the northern Azov region

(Topachevski, 1965). The discoveries from some localities on the Russian Plain may be also attributed to this type; such are those from the Tarkhankut site (Topachevski, 1973), the upper strata at Korotoyak 3 (Agadjanian, 1992), Chishmikioi (Shushpanov, 1977), and the Demsk and Davlekanovsk horizons in Akkulaevo (Sukhov, 1970) (Fig. 1). The Nogaisk locality has yielded the remains of *Archidiskodon meridionalis* (*tamanensis*?), *Equus* sp., *Elasmothrium* sp., *Megaloceros* sp. and others (Topachevski, 1965). Characteristically, this assemblage includes advanced voles of genus *Allophaiomys* (*A. pliocaenicus*). An important characteristic, indicative of the evolutionary level of the voles, is the A/L for M_1 of *Allophaiomys* (>42) (Rekovets, 1994; Markova and Kozharinov, 1998). Among the steppe lemmings, *Lagurodon arankae* and *Prolagurus ternopolitanus* (="*P. praepannonicus*") are still present (Topachevski, 1965, Fig. 35, p. 129). The Nogaiskian faunas also include *Mimomys* ex gr. *reidi-pusillus*, as well as the voles *M. savini* (="*intermedius*"), *Ellobius* (*E. paleotalpinus*, *E. tauricus*, *E. tarchancutensis*) and abundant *Clethrionomys sokolovi* (Topachevski, 1965; Rekovets, 1994). Archaic *Eolagurus argyropuloi* remains were found for the first here (Topachevski, 1973). Of the West European faunas, those from Vćelare 3B/1 (Check Republic) are the closest to those from Nogaiskian (Horáček, 1985).

2.1.3.2. Kairian small-mammal faunas. The next stage in the mammal fauna' evolution is marked by the appearance of more advanced lagurids *Prolagurus pannonicus* descending from *Prolagurus ternopolitanus*. Faunas of this level have been recovered from the Dnieper (Zapadny Kairy and Ushkalka localities), Dniester (Roksolany locality) and Don (Korotoyak locality, Ostrogozh Suite) drainage basins (Markova, 1982, 1998b; Mikhailesku and Markova, 1992; Iosifova and Krasnenkov, 1994) (Fig. 1). Besides *Prolagurus pannonicus*, faunas of this age typically include *Allophaiomys pliocaenicus* with advanced dental morphotypes (enamel of 'Microtus' type, A/L index of 44–45) (Markova, 2005). *Lagurodon arankae*, *Clethrionomys sokolovi* and *Eolagurus argyropuloi* still persist, whilst *Mimomys* genus is represented by *M. savini* and *M. pusillus*. The remains of *Archidiskodon*, *Bison priscus*, *E. stenonis* and *Paracamelus alutensis* have been also found at the Zapadny Kairy locality (Pidoplichko and Topachevski, 1962).

This stage in small-mammal evolution is considered to be a separate phase and it has been named after the type locality of Zapadny Kairy (alluvium of the so-called Kairy Terrace of the Dnieper river). The Brunhes/Matuyama Chron boundary in the section occurs above two palaeosols that overlie the bone-bearing fluvial sediments (Markova, 1982, p.19–22; Velichko et al., 1983).

In the Korotoyak section, palaeomagnetic evidence allows small mammals in the Ostrogozh layer to be correlated with the Jaramillo Subchron (Semenov, 1994). Therefore, the Kairian faunas may be dated approximately to 1.0–1.1 Ma BP. In Western Europe, similar faunas, including *Allophaiomys pliocaenicus*, *Prolagurus pannonicus* and *Lagurodon arankae*, are known from the localities of Deutsch-Altenburg $2C_1$, Betfia IX and Colle Curti (Rabeder, 1981; Terzea, 1995; Abbazzi et al., 1998). These faunas are equated with the early phase of the Netherlands' Waalian Stage.

2.1.3.3. Morozovkian small-mammal faunas. The index fossil for this phase is the Tamanian elephant *Archidiskodon meridionalis tamanensis*, recovered from the Port-Katon section on the Azov Sea coast (Baigusheva and Titov, 2001). A feature characteristic of small-mammal faunas attributed to this evolutionary level (the Morozovkian faunas) is the appearance of the more advanced voles *Microtus* (*Stenocranius*) *hintoni* and *M.* (*Terricola*) sp. The faunas of that evolutionary level have been described from the Morozovka 1 section at the Khadzhibei Liman (Alexandrova, 1976; Topachevski et al., 1987). Similar faunas have also been found at Port-Katon (the Azov Sea coast), Luzanovka and Bolshevik 2 (near the city of Odessa) (Markova, 1990; Rekovets, 1994) (Fig. 1).

Typically, the Morozovkian faunas abound with late *Allophaiomys* and late *Mimomys* (*M. savini* and *M. pusillus*). Steppe lemmings are represented by *Prolagurus pannonicus* and *Lagurodon arankae* and *Eolagurus argyropuloi* is also present. The index A/L for M_1 of *Allophaiomys* exceeds 47. The Morozovkian faunas are correlated with the Tamanian large-mammal assemblage (with *Archidiskodon meridionalis tamanensis*).

2.1.3.4. Petropavlovkian small-mammal faunas. Other Early Pleistocene faunas those from the Petropavlovkian ones, are still more evolutionarily advanced. They are distinct since they include the first appearance of archaic *Microtus* (*Pallasiinus*) ex gr. *oeconomus*. The faunas have been named from the Petropavlovka locality in the Don drainage basin, described by Alexandrova (1976) and Agadjanian (Krasnenkov and Agadjanian, 1975) (Fig. 1). A small-mammal fauna similar in evolutionary level to that from Petropavlovka has been discovered in the lower Dnieper basin, near the village of Karai-Dubina (Markova, 1982; Rekovets, 1994), as well as in the upper reaches of the Don–Log Krasny locality near Uryv village (Kazantseva, 1990).

The Petropavlovkian faunas are dominated by *Prolagurus pannonicus, Eolagurus argyropuloi*, *Microtus* (*Stenocranius*) *hintoni*. Also present are some *Mimomys savini* and *M. pusillus*, as well as late forms of *Borsodia*. Occasional remains of *Allophaiomys* teeth from those localities are of an advanced morphotype. The enamel has a *Microtus* type. Of the Western European faunas, that from Holštejn, in Czech Republic, is close to those discussed here in evolutionary level (Fejfar and Horáček, 1990). Untermassfeld small-mammal fauna, described by Maul (2001), resembles the Petropavlovkian one by the evolutionary level of the voles (Kolfschoten and Markova, 2005).

It was during this interval that *Mammuthus trogontherii* first appeared (Dubrovo, 1985); its remains were discovered in sediments of the 6th (Mikhailovka) Terrace of the Dniester river. The Brunhes/Matuyama Chron boundary occures within these alluvial sediments.

It follows from palaeomagnetic analysis of the sections containing the Petropavlovka faunas, that the bone-bearing strata belong to the uppermost part of the Matuyama reversed polarity Chron of reversed polarity. The Petropavlovkian faunas are the last in the sequence of the Early Pleistocene faunas of the Russian Plain.

2.2. Early Middle Pleistocene

2.2.1. Tiraspolian mammal complex

The Tiraspolian mammal complex was first defined on the fossil record recovered from 'Tiraspolian gravels' (that is, fluvial deposits of the Dniester 6th Terrace, Kolkotova Balka section near Tiraspol). The up-to-date list of large mammals found in the stratotype of the Tiraspolian mammal complex is as follows: *Archidiskodon wusti* (= *Mammuthus trogontherii*), *Equus* (*Allohipus*) aff. *süssenbornensis*, *Equus* (*Equus*) cf. *mosbachensis*, *Dicerorhinus etruscus*, *D. kirchbergensis*, *Paracamelus* sp., *Bison schoetensacki schoetensacki*, *Alces latifrons*, *Praemegaceros verticornis*, *Praedama* cf. *süssenbornensis*, *Cervus acoronatus* and *Cervus* cf. *elaphoides* (Nikiforova, 1971). The characteristics of the small mammals indicate their evolutionary level, and abundance in locations all over Eastern Europe, allow the differentiation of several phases in the development of the Tiraspolian mammal complex (Markova, 1998a).

2.2.1.1. Early Tiraspolian small-mammal faunas. Small-mammal faunas of more advanced evolutionary level, in comparison to those of the preceding Petropavlovkian, are attributed to the beginning of the Middle Pleistocene, that is the uppermost part of the Matuyama Chron. Of localities of those occurrences the Shamin locality in the lower Don region should be mentioned first. Besides yielding *Microtus* ex gr. *oeconomus*, teeth of another species of *Microtus* gen.—*M. arvalinus* are also found here. Some archaic *Microtus* (*Stenocranius*) *hintoni* have also been recovered together with the steppe lemmings *Prolagurus posterius* (descendant of *P. pannonicus*) (Fig. 1), *Mimomys pusillus*, *Eolagurus* ex gr. *argyropuloi* and *Allophaiomys pliocaenicus nutiensis*. The species composition of the faunas allows them to be attributed to the Early Tiraspolian (Markova, 1992, 1990).

The fauna from the Litvin locality on the Taman Peninsular is similar to that from Shamin in the evolutionary level of mammals. The Litvin mammal remains have been recovered in the Chauda marine sediments. This fauna, however, occurs within the Brunhes normal polarity Chron. It contains remains of *Mimomys savini*, *Allophaiomys pliocaenicus nutiensis*, *Prolagurus pannonicus*, *Eolagurus simplicidens gromovi*, *Microtus* (*Stenocranius*) *hintoni* and *Microtus* (*Mictotus*) *arvalinus* (Markova, 1990). The Early Tiraspolian faunas may therefore be correlated with the final part of Matuyama Chron and the beginning of Brunhes Chron. Similar faunas were described from some West European localities, namely Villány VI, Betfia-7, Pirro-Nord, Stránska Skala, Atapuerca, levels TD3-6 and others (Kretzoi, 1956; Feifar, 1972; Cuenca Bescos et al., 2001; Kowalski, 2001).

2.2.1.2. Phase of advanced Tiraspolian small-mammal faunas. More advanced mammal faunas of the Tiraspolian assemblage are attributed to the beginning of the Brunhes Chron (Fig. 1) (e.g. Agadjanian, 1992; Alexandrova, 1976; Markova, 1982, 1992; Rekovets, 1994). The appearance of the more advanced steppe and yellow steppe lemmings *Lagurus transiens* and *Eolagurus simplicidens gromovi* have been recorded in low numbers. *Microtus* (*Terricola*) *arvalidens*, *M.* (*Stenocranius*) *gregaloides, Microtus* (*Pallasiinus*) *oeconomus* and *M.* (*Microtus*) *arvalinus* become the core species of this assemblage. *Prolagurus posterius* continues to be common. The genus *Mimomys* is represented by younger (in the evolutionary context) species *M. savini* and *M. pusillus.* Faunas of this evolutionary level, including that from the Tiraspolian complex stratotype, have been recovered from the 6th Terrace alluvium of the Don, Dniester and Danube rivers. In Western Europe the faunas may be correlated to those from the localities West Runton, Somssich Hill-2, Hohen-Sülzen, Podumcy I, Voigtstedt, Rifreddo (e.g. Stuart, 1982; Yánossy, 1986; Malec and Rabeder, 1984; Kahlke, 1965; Masini et al., 2005).

2.2.1.3. Late Tiraspolian small-mammal faunas. The late Tiraspolian small-mammal faunas are differentiated into two groups on the basis of their environmental setting: first, faunas belonging to the Donian glacial Stage, and the younger faunas equivalent to the Muchkap interglacial Stage. Both groups include numerous *Lagurus transiens* and *Prolagurus posterius*, *Eolagurus luteus volgensis* and voles with rooted molars, *Mimomys savini* and *M. pusillus*, *Microtus* (*Terricola*) *arvalidens*, *M. arvalis*, *M.* (*Stenocranius*) *gregaloides* and *M. oeconomus*.

2.2.1.4. Faunas of the Donian glacial Stage. Faunas attributable to the Donian glaciation are distinct because of the presence of the subarctic species: *Lemmus* ex gr. *sibiricus, Dicrostonyx* sp. and *Microtus* ex gr. *hyperboreus* and narrow-headed vole *Microtus* (*Stenocranius*) *gregaloides* (Agadjanian, 1992; Markova, 1982, 1992). Therefore, a single event has been identified in the Tiraspolian faunal succession, which indicates a considerable cooling that has been recognised as far south as the lower reaches of the river Don (Fig. 1).

2.2.1.5. Faunas of the Muchkap interglacial Stage. The Don Till and Don loess units are overlain by a sediment series of complex structure which may be correlated with the Muchkap interglacial Stage. Mammal faunas of this age lack subarctic small-mammal species (Agadjanian, 1992; Markova, 1982, 1992). A distinctive feature of the Muchkap interglacial faunas is the appearance of a more advanced species in the narrow-skulled vole lineage, that is *Microtus* (*Stenocranius*) *gregalis*, not found in the earlier faunas. This interglacial was also marked by the formation of the Vorona palaeosol complex; developed on sediments in valleys of the Russian Plain 5th river terraces (Breslav et al., 1992). The Muchkap (Roslavl) deposits in the type region are of complex structure; the sequence includes two warm optima (Konakhov and Glazov) and separated by an intervening cool phase (Podrudnyansky) (Biryukov et al., 1992) (Fig. 1). All the units of the type region have yielded advanced voles with rooted molars, e.g. *Mimomys intermedius* (= *M. savini*). Water vole remains of *Arvicola* gen. (descendant of later *Mimomys*) have not been found even in the youngest Muchkap interglacial strata. Agadjanian (Biryukov et al., 1992) identified the following species recovered from the sediments correlated with the second or Konakhov climatic optimum: *Sorex* sp., *Desmana* cf. *moschata*, *Spermophilus* sp., *Cricetus* ex gr. *cricetus*, *Mimomys intermedius*, *Clethrionomys* sp., *Microtus gregaloides*, *M. oeconomus*, *M.* cf. *hyperboreus* and *Lemmus* sp.

2.2.1.6. Faunas of the Oka glacial Stage. There are very rare records of fossil small mammals that inhabited the Russian Plain during the Oka Stage glaciation. Only two localities have been confidently attributed to this Stage, Chekalin (Alexandrova, 1982) and Mikhailovka 2 (Agadjanian, 1992) (Fig. 1). This interval is marked by the appearance of pied lemming (*Dicrostonyx simplicior okaensis*), determined by Alexandrova (1982) from the Oka units exposed at the Chekalin locality. Typically, *Lagurus transiens* and *Microtus gregalis* are present in these faunas. It is still questionable whether *Mimomys* voles with rooted molars existed at that time. Neither *Arvicola* remains, nor its ancestral form *Mimomys savini*, have as yet been found from the localities of Oka age. Judging from the West European records, *M. savini* had already evolved into *Arvicola cantianus* by this time (Koenigswald, 1973; Kolfschoten, 1990a; Maul et al., 2000).

2.3. Late Middle Pleistocene

2.3.1. The Singilian mammal complex and the Gunkovian small-mammal assemblage

One of the most pronounced climatic warm periods of the Middle Pleistocene was the Likhvin Stage interglacial which is the equivalent of the Holsteinian Stage in Western Europe. It is well represented in the sediments of the Russian Plain such as Inzhavino palaeosol, fluvial deposits of the 4th terraces and the Early Euxinian transgression sediments of the Black Sea (Breslav et al., 1992; Mikhailesku and Markova, 1992) (Fig. 1).

Among the large-mammal species typical of this Singilian assemblage, are *Palaeoloxodon antiquus*, *Bison priscus*, *Saiga tatarica*, *Camelus* cf. *knoblochi*, *Megaloceros* sp., *Cervus ex gr. elaphus*, *Equus* sp. (ex gr. *caballus*) and *Elasmotherium sibiricum* (Gromov, 1948; Alekseeva, 1977). Impoverished fauna of small mammals, including *Lagurus transiens—L. lagurus*, *Eolagurus luteus*, *Microtus gregalis*, *M. arvalinus*, *M. oeconomus*, *Ellobius* sp. and *Spermophilus* sp., has been recovered from the Volga alluvium exposed at the Singilian stratotype, near Raigorod village (Volgograd region) (Tesakov, personal communication).

Many localities of this age are known from the Russian Plain where they are distributed from 55° N to the northern Black Sea region. Among them are Gunki, Chigirin and Pivikha in the Dnieper drainage basin; Chekalin in the Oka basin; Verkhnyaya Emancha, Strelitsa and Vladimirovka 2 in the Don basin; Mikhailovka 3 in the Svapa basin; Rybnaya Sloboda in the Volga basin; Kolkotova Balka (Inzhavino palaeosol) in the Dniester basin; Ozernoye in the Danube basin; Uzmari in the Prut basin; Otkasnoye in the Kuma basin (North Caucasus), and Smolensky Brod in the Zapadnaya Dvina basin (Motuzko, 1985; Agadjanian, 1992; Markova, 1992, 1996, 2004). The most typical feature of the Likhvin faunas is the appearance of the archaic water vole of the genus *Arvicola* (*A. cantianus*) which replaced the ancestral form of the rooted-toothed voles *Mimomys savini*. Dental morphology of the steppe lemmings suggests some prevalence of the 'transiens' morphotype in the faunas of that age (Markova, 1982). *Microtus* voles (*M. arvalis*, *M. oeconomus*, *M. gregalis, M. agrestis*) are found in the Likhvin deposits in abundance, while *M. arvalidens* and *M. gregaloides* voles disappear almost completely.

The author disagrees with Pevzner et al. (2001) who attributed the Verkhnyaya Emancha and Strelitsa faunas to a later Middle Pleistocene interval, notwithstanding that they are quite comparable with the rest faunas on the basis of the vole morphology. Geological evidence provides additional support for the Likhvinian age of these faunas.

Abundant data available on small mammals from the Likhvin provide insight into the structure and distribution of these interglacial assemblages. It indicates that the Likhvin mammal assemblages have a zonal pattern; they include assemblages that inhabited broadleaf and mixed forests, forest-steppes and steppe. Unfortunately, information from the Northern Eastern Europe is still insufficient (Markova, 1998a).

It has been suggested that the Likhvin small-mammal faunas should be united into a Gunkovian small-mammal assemblage (Markova, 1992, 1996), which existed simultaneously with the Singilian large-mammal complex (Alekseeva, 1977). In Western Europe, faunas of similar were recovered from the sediments synchronous to the Holsteinian (Hoxnian) Stage interglacial (Heinrich, 1990; Koenigswald and Tobien, 1990; Kolfschoten, 1990a; Kowalski, 2001; Schreve, 2001).

2.3.2. Khozarian mammal complex

The Khozarian mammal complex was first defined by Gromov (1948) from finds from the Lower Volga region near Cherny Yar village. It includes the following large mammals *Mammuthus trogontherii*, *Camelus knoblokhi*, *Cervus* (*Megaceros*) *germaniae*, *Bison priscus* var. *longicornis*, *Equus caballus chosaricus* and others (Gromov, 1948). Later, the elephant from the Cherny Yar locality was re-identified as *Mammuthus trogontherii chosaricus* by Dubrovo (1966). The age of the bone-bearing strata in the early Khozarian alluvial sediments is still under discussion (Kirillova and Tesakov, 2004).

The Likhvin deposits from the Pre-Dnieper loess-palaeosol sequence on the Russian Plain are overlain by two loess horizons and two palaeosols. Small-mammal remains, including lagurids with predominantly 'lagurus-like' dental morphotypes, have been recovered from the Kamenka fossil soil (Markova, 1982, 1992) at localities of the Dnieper and Don river drainage basins. Similar faunas have been defined from liman and marine sediments in the northern Black Sea region, attributed to the Uzunlar transgression, and from the 3rd terrace of the River Danube. Water-vole remains found there belong to *Arvicola chosaricus* species which replaced *Arvicola cantianus* (Mikhailesku and Markova, 1992) (Fig. 1). The faunas are correlated with the Khozarian assemblage of large and small mammals (including *Mammuthus trogontherii chosaricus* and *Arvicola chosaricus*), which was identified on the basis of materials from the Cherny Yar locality on the Volga (Gromov, 1948; Alexandrova, 1976). In Western Europe, faunas of this age are known from the localities of Ariendorf I, Wageningen-Fransche Kamp I, Maastricht-Beloédère 2.2, 3A-3, 4 and others (Kolfschoten, 1990b, 1991).

The subsequent Dnieper glaciation caused considerable changes in small-mammal species composition and distribution across the Russian Plain. The faunas from Igorevka locality (the Seim basin) and Alpatyevo (the Oka basin), several localities in the Desna and Volga drainage basins (Motuzko, 1985; Agadjanian, 1992; Markova, 1992) where typical Subarctic and steppe species were found: *Dicrostonyx simplicior*, *Lemmus sibiricus*, *Lagurus* ex gr. *lagurus* and *Microtus gregalis* are attributed to this interval. These faunas were also referred to the Khozarian mammal assemblage on the basis of bone morphology. During the second half of the Dnieper Stage, the elephant phylogenetic line experienced a transformation, with *Mammuthus trogontherii chosaricus* being replaced by an early type of woolly mammoth *Mammuthus primigenius* (Alekseeva, 1980; Dubrovo, 1985).

2.4. Late Pleistocene

2.4.1. Shkurlatian mammal complex

The first half of the Late Pleistocene—the Mikulino (Eemian) Stage interglacial is reflected in the loess-soil series of the Russian Plain as the first phase of the Mezin palaeosol complex and fluvial sediments of the second river terraces. These continental sediments are correlated with the Karangat transgression of the Black Sea.

A wide range of large-mammal remains have been recovered from the stratotype of the Shkurlatian mammal complex (near Shkurlat village, Voronezh Region, the Don river drainage basin), including woolly mammoth *Mammuthus primigenius* (early form), straight-tusked elephant *Palaeoloxodon antiquus* (advanced form), horse *Equus* ex gr. *caballus*, woolly rhinoceros *Coelodonta antiquitatis*, bison *Bison priscus* and cave lion *Panthera* (*Leo*) *spelaea* (Alekseeva, 1980). Small mammal remains have been also collected (Markova, 2000).

The author (Markova, 1982, 2000) also studied small-mammal faunas of the same age from a number of localities from various regions of the Russian Plain the deposits of which widely varied in taphonomic setting and depositional environments (fluvial, liman and marine deposits, palaeosols). The Mikulino small-mammal faunas are dominated by species are morphologically close to those of modern type, although there are certain morphological variations (mostly at subspecies level) that can be traced in some phylogenetic lines. The Mikulino interglacial faunas are referred to the Shkurlatian mammal assemblage with *Mammuthus primigenius* of early type and *Palaeoloxodon antiquus* (Alekseeva, 1980). Small-mammal fauna from the stratotype section, near the village of Shkurlat, has been defined by the author; it includes remains of water vole, not unlike the modern *Arvicola* ex gr. *terrestris*, together with *Lagurus* cf. *lagurus*, *Eolagurus* cf. *luteus*, *Microtus gregalis*, *Microtus arvalis* and others (Markova, 1992).

The fossil mammalian data has allowed the reconstructing of their structure and geographical position of the Mikulino mammal assemblages on the Russian Plain and in the Crimea. The zonation of the assemblages appears to be typical of that of interglacials (Markova, 2000).

There are similar faunas in Central and Western Europe described from localities including, for example, La Fague, Tornewton, Solymar, Süttö, and others (Chaline, 1972; Sutcliffe and Kowalski, 1976; Janossy, 1986; Nadachowski et al., 2003).

2.4.2. Mammoth mammal complex and Sungirian small-mammal assemblage

The second half of the Late Pleistocene was marked by a drastic cooling that resulted in expansion of the Valdaian ice Stage. Faunas of the mammoth assemblage were widespread at that time. They included woolly mammoth *Mammuthus primigenius* (later type), woolly rhinoceros *Coelodonta antiquitatis*, reindeer *Rangifer tarandus*, musk ox *Ovibos moschatus*, saiga antelope *Saiga tatarica*, horse *Equus ferus*, steppe lemming *Lagurus lagurus* and yellow vole *Eolagurus luteus*, pied lemming *Dicrostonyx gulielmi*, Siberian lemming *Lemmus sibiricus*, narrow-skulled vole *Microtus* (*Stenocranius*) *gregalis* and others (Markova et al., 1995, Table 1; Agadjanian, 2001; Baryshnikov and Markova, 2002).

It has been established that the response of various mammal species to the cooling differed essentially in direction and scale; that resulted in appearance of totally new ecosystems having no modern analogues. Tundra species penetrated as far south as 48° N, while steppe species extended far west and northwards, into the modern forest zone. The ranges of environmentally tolerant forest and forest-steppe species, as well as ranges of taiga mammals, changed only slightly, which implies the persistence of separate forested areas. Broadleaf forests practically disappeared from the Russian Plain, except for a few refugia in mountain and elevated regions (Markova, 1998a).

A recent synthesis and analysis of theriological and floral materials obtained from numerous localities, dated to the Valdai maximum, have allowed reconstruction of the principal Eastern European ecosystems, using GIS and mathematical methods (Markova et al., 2002a, b). The Valdai cooling exerted a marked influence on the environments. Latitudinal differentiation of ecosystems (from the ice sheet in the north to the sea coast in the south) was much less pronounced in comparison to that during interglacial intervals. Five principal ecosystems have been reconstructed for Europe based on these palaeobiological data (Markova et al., 2002b).

3. Conclusions

From the synthesis presented here it is demonstrated that fossil mammal faunas underwent conspicuous changes during the Pleistocene. These changes have been recognised from a series of large stages in their evolution, as reflected in the mammal assemblages, together with smaller divisions, reflecting phases in the assemblage development. The stages have been recognised primarily on the basis of the appearance of new taxa (at genera and species level). Secondary divisions are based on less significant evolutionary changes, such as the appearance of new subspecies, and on modifications of the prevailing morphotypes in the mammal-bone remains, primarily in the dental system. Regular studies of Pleistocene mammal faunas in Eastern Europe, spanning over a century, have made it possible to trace the evolutionary changes and ascertain the chronological sequence of the fauna' developments.

At least 15 large chronological divisions (small-mammal assemblages and their phases) have been distinguished through the Pleistocene. They correspond to the Psekupsian, Tamanian, Tiraspolian, Singilian, Khozarian, Shkurlatian and Mammoth large-mammal complexes. The multidisciplinary studies of the mammal localities have provided the basis for correlation between the theriological evidence and the main natural events of the Pleistocene (such as glacial and interglacial events) determined from geological, geochronological and palaeontological materials (Fig. 1).

The structural characteristics of the interglacial and periglacial mammalian faunas of various ages have been established, their location in geographical space being ascertained. Maps of mammal assemblages have been compiled and ecosystems of Eastern Europe reconstructed (Markova et al., 2001a, b, 2003) for the time intervals best represented by fossil mammal materials. Two types of the mammal assemblages have been recognised, zonal assemblages of interglacials and periglacial assemblages specific to glacials. In the first type, each zonal assemblage was dominated by a single ecological mammal group. A distinctive feature of the second type was the co-existence of animals belonging to different ecological groups and inhabiting different natural zones (non-analogue assemblages).

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