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The sequence of Plio-Pleistocene mammal faunas from the south Russian Plain (the Azov Region)

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ABSTRACT – The Azov Region and adjoining areas are rich in sedimentary successions that have yielded abundant remains of fossil mammals. These encompass the time span from Late Miocene through late Pleistocene. The occurrence of some Asian elements makes the peri-Azovian faunas somewhat peculiar compared to contemporary West European faunas. Within the succession of faunal complexes considered, the most striking faunal restructuring took place at the boundary of Early and Middle Pliocene, and at the beginning of the middle Pleistocene.

RIASSUNTO – [La successione delle faune a mammiferi plio-pleistoceniche nella regione del Mar d'Azov (Russia meridionale)] – La regione del Mar d'Azov e delle aree adiacenti (Russia meridionale) è caratterizzata da successioni sedimentarie ricche in resti di mammiferi fossili. È possibile individuare una serie di complessi faunistici successivi, che abbracciano un intervallo di tempo dal Miocene superiore al Pleistocene superiore. La presenza di alcuni elementi ad affinità asiatiche caratterizza in maniera peculiare le faune dell'area del Mar d'Azov, se confrontate con le contemporanee associazioni faunistiche dell'Europa occidentale. Nell'intervallo temporale documentato, i momenti di maggior rinnovamento faunistico si collocano al passaggio tra Pliocene inferiore e medio e all'inizio del Pleistocene medio.

Numerous investigators have conducted paleontological studies of the territory of the Azov Region over several decades. Today we can attempt an overview of the history of development and change of mammal associations of the region during Plio-Pleistocene time. Fossil collections from that territory are kept in the Rostov and Azov regional museums, and in several institutes of the Russian Academy of Sciences (Geological Institute, Paleontological Institute, Vernadsky State Geological Museum in Moscow, and Zoological Institute in St. Petersburg). The regional record has produced abundant fossil material including a number of complete skeletons. These materials are important for the correlation of European and Asian faunas, for the reconstruction of faunistic development, and phylogenetic history of many mammalian groups.

LATE MIOCENE

The oldest known deposits that have yielded remains of terrestrial vertebrates in the Azov and the Lower Don areas are dated to the Late Miocene. These are estuarine and coastal deposits exposed on the north coast of the Taganrog Gulf of the Sea of Azov near Morskaya railway station (1 in Text-fig. 1). A rich vertebrate fauna from the locality includes remains of fishes, turtles, birds and mammals, including *Petenya hungarica*, *Hypolagus igromovi*, Castoridae indet., *Nannospalax* ex gr. *compositodontus-maccovei*, Cricetinae indet., *Parapodemus* sp., *Promephitis* sp., *Felis* cf.

attica, *Deinotherium* cf. *bavaricum*, and *Hipparion* sp. These fossils were discovered in strata deposited on the eroded surface of the Middle Sarmatian limestone. This material is so far believed to represent a synchronous association of Turolian age. An almost complete skeleton of *Deinotherium giganteum* and isolated finds of *Zygolophodon borsoni*, *Paracamelus* sp. and "*Palaeoryx*" *longicephalus* are known from the fluvial deposits of possibly Maeotian age at Obukhovka sand pit, near Novochoerkassk (Krahmalnaya, 1996, p. 153; Bajgusheva & Tishkov, 1998) (2 in Text-fig. 1). Remains of late Turolian (MN13?) mammals are also known in the early Pontian marine deposits. Thus, off-shore sandy limestones of Pontian age (Novorossian substage) outcropping at Razdorskaya in the Lower Don area yielded remains of *Hypolagus igromovi* (Averianov, 1996), together with numerous remains of fishes and turtles (3 in Text-fig. 1). Another locality of this age near Sinyavskaya railway station (northeastern Azov Region; 4 in Text-fig. 1) produced remains of *Hipparion* sp. and *Paracamelus* sp.

EARLY PLIOCENE

The Ruscinian is represented in the Azov Region by the rodent fauna of the lower beds of the Obukhovka sand pit (Topachevsky *et al.*, 1988). This faunal assemblage is referred to the late Ruscinian MN15a unit and includes: *Erinaceus* sp., *Talpa* sp., *Paranourosorex* sp., *Hypolagus* cf. *brachygnathus*, *Trischizolagus* sp., *Proochotona eximia*, *Ochotona* cf.

antiqua, *O. cf. pseudopussila*, *Pliolagomys* sp., *Dryomimus* cf. *eliomyoides*, *Paralactaga* sp., *Nannospalax maccovei*, *Estramomys* cf. *simplex*, *Orientalomys* sp., *Rhagapodemus* cf. *frequens*, *Apodemys* sp., *Myomimus* sp., *Cricetinus* sp., *Germanomys* sp., *Baranomys* sp., *Promimomys moldavicus*, and *Trogotherium* cf. *minus*.

MIDDLE PLIOCENE

Mammals of this age are scarcely represented in the region. A few remains likely representing an early Villafranchian fauna were discovered at Nizhnevodyanoy (5 in Text-fig. 1), where the following taxa have been collected: *Melinae* indet., *Mustelidae* indet., *Anancus* cf. *arvernensis*, *Hipparion* sp., *Stephanorhinus* sp. and *Gazella* sp. (Alexeeva, 1977a). The fauna is tentatively referred to the MN16 unit; poor preservation of fossils and insufficiently known geological settings, however, do not exclude a different biochronological attribution. Rodent remains of early Middle Pleistocene age have been recovered in the lowermost beds of the Liventsovka sand pit. The association of *Pitymimomys* sp., *Borsodia praeungarica*, *Mimomys livenzovicus*, *M. polonicus*, *Dolomys milleri*, and *Pliomys ucrainicus* is typical for the end of MN16b (Tesakov, 1993).

LATE PLIOCENE

The association of vertebrates from the Khapry fluviatile suite corresponds to the level of the typical middle Villafranchian Saint-Vallier faunal unit in Western Europe. The Khapry strata are exposed along the northeast coast of the Sea of Azov (6 in Text-fig.

1). The complex of large mammals includes: *Nyctereutes megamastoides*, *Canis* cf. *senezensis*, *Ursus* cf. *etruscus*, *Lutra* sp., *Pannonictis nestii*, *Pliocrocota perrieri*, *Lynx issiodorensis*, *Acinonyx pardinensis*, *Homotherium crenatidens*, *Anancus alexeevae*, *Archidiskodon gromovi*, *Hipparion* cf. *moriturum*, *Equus (Allohippus) livenzovensis*, *E. (A.) ex gr. stenonis*, *Stephanorhinus* ex gr. *jeanvireti*, *Elasmotherium* cf. *caucasicum*, *Sus* cf. *strozzi*, *Paracamelus alutensis*, *P. gigas*, *Cervus (Rusa) cf. philisi*, *Eucladoceros* cf. *dicranios*, *Arvernoceros* sp., *Libralces gallicus*, *Palaeotragus (Yuorlovia) priasovicus*, *Leptobos* sp., *Gazellospira* cf. *gromovae*, *Tragelaphini* gen., *Gazella* cf. *subgutturosa* (Bajgusheva, 1971, 1984; Alexeeva, 1977a; Godina, 1979, Titov, 2000; Sotnikova *et al.*, 1998). Among other vertebrates, a find of *Struthio* cf. *asiaticus* is of special interest (Bajgusheva, 1971).

The Khapry large mammal fauna can be subdivided into several groups. The bulk of forms known in the Khapry fauna have a wide stratigraphic range or appear in central and western parts of Europe at the beginning of the Middle Villafranchian. Another group comprises mammal forms that are either typical for the Early Villafranchian (*Arvernoceros* and *Palaeotragus*), or unknown later than Middle Villafranchian (*Nyctereutes megamastoides*, *Stephanorhinus* ex gr. *jeanvireti*). We interpret the presence of some archaic elements from their wide stratigraphical range in eastern Europe. Again, there is a group of elements which would rather indicate Late Villafranchian communities of western and Central Europe (*Canis*, *Cervus* cf. *philisi philisi*, *Eucladoceros* cf. *dicranios*, *Libralces gallicus*). Their presence may be interpreted as an earlier appearance in the south of Eastern Europe compared to the western part of the



Text-fig. 1. - Distribution of some mammal localities in the Azov Region and adjoining areas.

Morskaya 1; 2) Obukhovka; 3) Razdorskaya; 4) Sinyavskaya; 5) Nizhnevodyanoy; 6) Khapry; 7) Liventsovka; 8) Volovaya Balka; 9) Saratovskaya; 10) Bakinskaia (Psekups); 11) Zukalova Balka; 12) Sinyaya Balka; 13) Tsymbal; 14) Semibalki; 15) Port-Katon; 16) Samarskoe; 17) Kagalnik; 18) Lebiazhenskiy; 19) Kamensk; 20) Margaritovo; 21) Kamennaia Balka.

continent (Titov, 2000). Finally, a group of so called "Asian" forms, like *Struthio* (Mikhailov & Kurochkin, 1988), *Paracamelus* (Havesson, 1954), and *Elasmotherium* emphasizes the similarity of the Khapry faunistic complex to middle Villafranchian faunas of the Black Sea region, the Northern Caucasus, West Kazakhstan and southern West Siberia.

The large mammal fauna of the Liventsovka sand pit (the parastratotype of the Khapry faunistic complex; 6 and 7 in Text-fig. 1) is accompanied by a rich small mammal fauna. The rodent association includes *Mimomys praepliocaenicus*, *Borsodia praehungaricus cotlovinensis*, and *Mimomys* ex gr. *reidi* (Tesakov, 1993, 1995, 1996). This complex allows correlation of the Khapry fauna to the MN17 unit and to middle Villafranchian.

The transitional period spanning the end of the late Pliocene and the beginning of the Early Pleistocene (MN17- MQ1) is characterized in East Europe by the Psekups faunistic complex. The megafauna of the type localities corresponds to the West European Seneze faunal unit. The Psekups fauna originates from fluvial deposits of the Psekups River in the northwestern Caucasus (Bakinskaya and Saratovskaya localities, 9 and 10 in Text-fig. 1). The Psekups faunas are distinguished by the occurrence of an association of advanced *Archidiskodon meridionalis*, *Anancus* sp., *Equus* cf. *major*, *Stephanorhinus etruscus*, *Paracamelus* cf. *alutensis*, *Sus* cf. *strozzi*, *Eucladoceros orientalis*, *E.* cf. *senezensis* and *Struthio* sp. and a new bison, *Bison* cf. *suchovi* (Alexeeva, 1977b). Very likely, *Archidiskodon* coexists with *Phanagoroloxodon mammantoides* (Garutt, 1995). An isolated molar of *A. meridionalis* is known from the environs of Berdiansk town at Zukalova Balka (11 in Text-fig. 1). The small mammal fauna of the Psekups complex includes *Mimomys* ex gr. *reidi*, *Pitymimomys pitymyoides*, *Borsodia* sp., *Clethrionomys kretzoi*, *Allocrietus* cf. *ehiki*, *Apodemus* sp., *Nannospalax* cf. *odessanus*, *Spermophilus* sp., *Beremendia fissidens*, and *Petenya hungarica* (Vangengeim *et al.*, 1990; Tesakov, 1995). This association is known from a locality near Saratovskaya village (Psekups River) and in the uppermost beds of the Liventsovka sand pit. The increasing role of arviculids with rootless cheek dentition marks small mammalian faunas of the second half of the Psekups complex.

The complex of *Anancus*, *Archidiskodon*, *Equus* ex gr. *stenonis*, *Stephanorhinus*, *Elasmotherium* and *Paracamelus*, which was typical for East European faunas in the late Pliocene, persisted into the early Pleistocene of this region. Transitional faunas were characterized by *Canis etruscus*, *Panthera gombaszogensis* and *Equus stenonis stenonis*, which appeared at the end of the Villafranchian (Torre *et al.*, 1992). These associations are correlated with West European faunas of the Olivola faunal unit. No representative localities of this age are so far known in Eastern

Europe. However, Plio-Pleistocene transitional faunas are well known in the neighbouring territory of Transcaucasus: Palan-Tukan (Azerbaijan) and Dmanisi (Georgia). The latest *Nyctereutes megamas-toides* is recorded in these communities (Sotnikova & Sablin, 1993; Vekua, 1995).

EARLY PLEISTOCENE

The Early Pleistocene of Eastern Europe is characterised by the Taman faunistic complex (correlatable to late MQ1, as defined by Fejfar & Heinrich, 1990). The type Tamanian faunas originate from localities Sinyaya Balka and Tsimbal (12 and 13 in Text-fig. 1) in the Taman Peninsula (Verestshagin, 1957) and contain an association of *Archidiskodon tamanensis* and *Elasmotherium caucasicum*. The latest representative of *Anancus* ex gr. *arvernensis* is known from the Tsimbal locality (Dubrovo, 1963). Tamanian fauna of the Semibalki locality (the south bank of the Taganrog Gulf of the Sea of Azov) is represented by *Marmota* sp., *Trogotherium cuvieri*, *Homotherium* cf. *crenatidens*, *Pachycrocuta* cf. *brevirostris*, *Archidiskodon tamanensis*, *Equus major*, *Eucladoceros* aff. *orientalis*, *Bison tamanensis* and *Pontoceros ambiguus* (Bajgusheva, 2000). In the Azov region the small mammal faunas of the Taman complex are known in the locality of Semibalki-3 (14 in Text-fig. 1) where have been reported: *Clethrionomys glareolus*, *Prolagurus pannonicus transylvanicus*, *Mimomys pusillus*, *M. intermedius*, *Allophaiomys plio-caenicus*, and *Microtus hintoni* (Rekovets, 1994). A similar fauna is known at Port-Katon (15 in Text-fig. 1), where remains of *Ursus* sp., *Lutra* sp. and *Equus* sp. are also present (Dubrovo & Alexeev, 1964; Bajgusheva, 1976). Small mammals of the locality include *Prolagurus pannonicus*, *Lagurodon arankae*, *Eolagurus argyropuloi*, *Microtus hintoni*, *Mimomys savini*, *M. pusillus* and *Allophaiomys* sp. (Markova, 1998). Both associations are referable to the late stage of the Taman complex. Another locality that yielded numerous remains of *Archidiskodon tamanensis* is situated in the surroundings of Azov town (16 in Text-fig. 1), near the village of Samarskoe (Bajgusheva, 1984).

MIDDLE PLEISTOCENE

In the Azov area Middle Pleistocene faunistic associations are traditionally considered within the framework of the Tiraspol faunistic complex. Typical Tiraspol faunas of the area include *Marmota* sp., *Mimomys savini*, *Mammuthus trogontherii*, *Equus süssenbornensis*, *Bison schoetensacki*, *Alces latifrons* and *Megaceros* sp. Two almost complete skeletons of *Mammuthus trogontherii* were collected at the Kagalnik sand pit (Azov town, south bank of the Don River delta; 17 in Text-fig. 1). Upper and lower third molars of these elephants resemble the *tro-*

gontheri mammoth described by Pavlow (1910) as *Elephas* (= *Mammuthus*) *wusti* (Bajgusheva & Garutt, 1987; Bajgusheva, 2000; Garutt & Bajgusheva, 1999). Deposits with *M. trogontherii* are underlain by strata with an early Tiraspol rodent association (*Lagurus transiens*, *Microtus gregaloides*). The complex of small mammals from the site Semibalka -1 is also referred to the early Tiraspol complex (Markova, 1998). The successive Singil faunistic complex is characterized by the presence of *Ursus spelaeus*, *Panthera (Leo) spelaea*, *Mammuthus chosaricus*, *Equus latipes*, *Asinus* sp., *Stephanorhinus kirchbergensis* (= *S. merki*), *Coelodonta antiquitatis*, *Camelus knoblochi*, *Cervus elaphus*, *Megaceros giganteus*, *Bison priscus* and *Saiga tatarica*. The succeeding fauna of the Khazar faunistic complex includes *Equus chosaricus*, *Bos primigenius*, *Bison priscus* and *Mammuthus chosaricus*. The Khazar mammal association corresponds to the beginning of the Last Glacial Maximum in the territory of Eastern Europe. This fauna was formed in conditions of falling temperature and increasing aridity. In the Azov area mammal remains of these associations are confined to isolated finds from flood plain deposits of the Don River.

LATE PLEISTOCENE

Most well-studied late Pleistocene faunas in the region are associated with late Palaeolithic archaeological sites. These faunas are considered within the late Palaeolithic faunistic complex. Numerous materials of the "Mammoth" fauna are known from the exposure near the Lebiashenskoe farm (18 in Text-fig. 1) thanks to the collections by V.P. Litvinenko and are referable to the Odintsovian-Moskovian glaciation. The fauna includes *Marmota* cf. *bobac*, *Castor* cf. *fiber*, *Canis* sp., *Ursus rossicus*, *Panthera (Leo) spelaea*, *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Equus* cf. *caballus*, *Equus hidruntinus*, *Megaceros giganteus*, *Rangifer tarandus*, and *Bison priscus*. Other important localities of the Late Pleistocene faunas are known near Kamensk (19 in Text-fig. 1) on the left bank of the Severskiy Donets River, where a primitive *M. primigenius* was unearthed (Bajgusheva, 1980), and at Margaritovo (20 in Text-fig. 1). In this locality the fossiliferous deposits correlated to the Valday Glaciation yielded remains of *Mammuthus primigenius* together with small mammals (*Lagurus lagurus* and *Microtus gregalis*). The end of the late Palaeolithic faunistic complex is characterised by a rapid decrease of mammoth, woolly rhinoceros and cave predators. Abundant remains of *Marmota* sp., *Canis lupus*, *Ursus arctos*, *Equus latipes*, *Bos primigenius*, *Bison priscus*, *Rangifer tarandus*, *Cervus elaphus* and *Ovis* sp. are associated with kitchen refuse at the late Palaeolithic archaeological site "Kamennaia Balka" (21 in Text-fig. 1) (Leonova & Minkov, 1988).

CONCLUSIONS

In the Azov region the best-represented mammalian faunas are those of Middle Pliocene, Late Pliocene and Pleistocene age. Late Miocene and early Pliocene sites are rare and poorly studied.

The Late Miocene is represented by the late Turolian faunas of Morskaya and Razdorskaya, and the only Early Pliocene fauna referable to the late Ruscian is Obukhovka. Several Middle Pliocene faunas (MN 16, early Villafranchian) were recovered at Obokhuvka, Liventsovka (lower beds) and, possibly, Nizhnevodyanoy.

Late Pliocene faunas are included in the Khapry faunistic complex, correlatable to the middle Villafranchian. The Khapry faunas are known from Khapry, Liventsovka, Morskaya 1 and Volovaia Balka, all belonging to the same fluvial suite. The serial collection of large and small mammals from the Khapry deposits allows attribution of this association to zone MN17. Geologically younger faunas of the Psekups faunistic complex are known in the localities Bakinskaia, Saratovskaia, Liventzovka (upper beds) and Zukalova Balka. These associations are transitional between Late Pliocene and Early Pleistocene and correlate with early Late Villafranchian (MN17-MQ1).

The Early Pleistocene stage of mammalian history is presented by faunas of the Taman faunistic complex (Semibalki, Port-Katon and Samarskoe), and small mammals from these localities are attributable to the early Biharian (MQ1). The Tiraspol faunistic complex (latest MQ1) is known from Kagalnik and Semibalki, while the late Middle Pleistocene localities of Singil and Khazar (MQ2) are still insufficiently known. Late Pleistocene Late Palaeolithic faunal assemblages (MQ2) marked by representatives of the Mammoth fauna are known from Lebiashenskiy, Kamensk, and Kamennaya Balka.

Systematic analysis of East European faunas of the Azov region reveals major stages of faunal development. The most notable change is evident at the boundary of Early and Middle Pliocene. At this level there were major changes in composition of proboscideans, hipparions, antelopes and leporids, while mimomyine and pliomyine voles with rooted dentitions were widespread.

Some changes in faunal composition occurred at the Middle to Late Pliocene transition. At this time an increase in steppe and forest-steppe animals, like *Archidiskodon*, *Equus*, *Eucladoceros*, is recorded. The sequence of Late Pliocene and Early Pleistocene faunas is represented by the Khapry, Psekups and Taman faunistic complexes. These associations are dominated by similar elements, like *Anancus*, *Archidiskodon*, *Equus* ex gr. *stenonis*, *Stephanorhinus*, *Elasmotherium* and *Paracamelus*. This is probably evidence of a lack of considerable climatic fluctuation in the south Russian Plain during this period. Most changes of faunal communities and different phyletic lineages

can be interpreted as gradual responses to increasing aridisation. Considerable changes in mammalian fauna occurred between the Taman and Tiraspol faunistic complexes, at the Early to middle Pleistocene transition. These changes resulted in formation of typical Pleistocene faunas.

During the time span considered (from Late Miocene to the end of the Pleistocene) the East European faunas were influenced both by West European and Asian mammal associations. Mammal forms of west European affinities formed the background of the fauna. At the same time the Azov area shares a considerable number of Asian elements (*Paracamelus*, *Elasmotherium*, *Palaeotragus*) with faunas of West Kazakhstan and southwest Siberia. Most Asian forms appeared in Eastern Europe earlier than in the western part of the continent.

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