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 successions span time from Late Miocene through Late Pleistocene. The occurrence of some Asian elements makes the Plio-Pleistocene fauna comparable to contemporaneous West European faunas. Within the succession of faunal complexes considered, the most striking faunal restructuring took place at the boundary of Early and Middle Pleistocene, and at the beginning of the middle Pliocene.

RIASSUNTO — La sequenza delle faune a mammiferi plio-pliosicani della regione del Mar d’Azov (Russia meridionale) — La regione del Mar d’Azov e aree adiacenti (Russia meridionale) contengono successioni sedimentarie che hanno prodotto abbondanti resti fossili. Queste successioni coprono il periodo dal Miocene superiore al Pleistocene superiore. La presenza di elementi asiatici fa comparare le faune a mammiferi plio-pliosicani alla contemporanea fauna europea occidentale. Nell’intermedio di successioni è notevole la rimodellazione fauna a seguito della transizione tra il Miocene medio e iniziale 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, Yeniseysky 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 faunal development, and phylogenetic history of many mammalian groups.

LATE MIOCENE

The oldest known deposits, which have yielded remains of terrestrial vertebrates in the Azov and the Lower Don area, 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 Moeskaz railway station (1 in Text-fig. 1). A rich vertebrate fauna from the locality includes remains of fishes, reptiles, birds and mammals, including Pseudocricetodon, Hypsipalorchus, Scincus, Castoridae indet., Nationalodon sp., Carnegieosaurus mar-virens, Cricetinae indet., Parapodemus sp., Dendrocnites sp., Felis cf. attica, Deinotherium cf. bartoniensis, and Hippopotamus sp. These fossils were discovered in strata deposited on the eroded surface of the Middle Saratyn limestone. This material is so far believed to represent a synchro- mous association of Turolian age. An almost complete skeleton of Deinotherium giganteum and isolated finds of Zygolophodon beurlani, Paracastorinae sp. and "Halictotherium" hipposphalx are known from the Blizhne deposits of possibly Miocenian age at Obukhova sand pit, near Novocherkassk (Rahmehl, 1969, p. 153; Bagnecheva & Titov, 1998) (2 in Text-fig. 1). Remains of late Turolian (MN15) mammals are also known in the early Pliocene marine deposits. This, off-shore sandy limestones of Pliocene age (Novorossiisk substage) outcropping at Razdonskaya in the Lower Don area yielded remains of Hypsipalorchus ignu- mcen (Aniscionian, 1996), together with numerous remains of fishes, turtles, and mammals (3 in Text-fig. 1). Another locality of this age near Sinyavskaya railway station (northeastern Azov Region) in Text-fig. 1 produced remains of Hippopotamus sp. and Paracastorinae sp.

EASY PROCENSE

The Rasciician is represented in the Azov Region by the reddish sands of the lower beds of the Obukhova sand pit (Topochnevsky et al., 1988). This alluvial assemblage is referred to the late Rasciician MN15a unit and includes: Ferocias sp., Unio sp., Paracastorinae sp., Hypsipalorchus cf. brevicrassus, Trichechus zubatov, Prionotherium eximium, Ochindra cf.
Middle Pliocene

The association of vertebrates from the Khapy strata suite corresponds to the level of the typical middle Villarranian Saint-Vallerian fauna unit in Western Europe. The Khapy strata are exposed along the northeast coast of the Sea of Azov (6 in Text-fig. 1). The complex of large mammals includes:  

*Neoceratotherium*, *Cetus* cf. *zeuglensis*, *Ursus* cf. *argenteus*, *Equus* sp., *Pliohippus* sp., *Equus* sp., *Hippopotamus sp.*, *Equus* sp., *Anoplotherium* sp., *Pliohippus* sp., *Equus* sp., *Hippopotamus* sp., *Equus* sp., and *Equus* sp. The association of vertebrates suggests a Late Pliocene age for the Khapy strata suite. The Khapy fauna is characterized by the presence of large herbivores such as *Equus* cf. *zeuglensis* and *Hippopotamus* sp., which are typical of this age in the region. The vertebrate assemblage is indicative of a warm and humid climate, similar to the modern-day Mediterranean region. The Khapy fauna is considered to be a key reference for understanding the paleoenvironmental conditions of the late Pliocene in the region.

Text-fig. 1. - Distribution of some mammal localities in the Ann region and adjacent areas. The distribution of the Khapy strata suite is shown in the figure.
continent (Tian, 2000). Finally, a group of so called "Asian" forms, like *Struthio* (Mikhailov & Karshchik, 1988), *Parasornuris* (Havocsek, 1954), and *Elsimutheorhinus* emphasizes the similarity of the Khapys faunistic complex to middle Villafanchan faunas of the Black Sea region, the Northern Caucasus, West Kazakhstan and southern West Siberia.

The large mammal fauna of the Livideshow sand pit (the parastratotype of the Khapys faunistic complex; 6 and 7 in Text-fig. 1) is accompanied by a rich small mammal fauna. The rodent association includes *Myosurus plagioleucodon*, *Boruska psistophorocoris sinolonicus*, and *Mysunum* ex gr. *taricus* (Tesakov, 1993b, 1995, 1996). This complex allows correlation of the Khapys fauna to the MN17 unit and to middle Villafanchan.

The transitional period spanning the end of the late Pleistocene and the beginning of the Early Pleistocene (MN17-MQ1) is characterized in East Europe by the Sokupsk complex. The megafauna of the type localities corresponds to the West European Senan fauna unit. The Sokupsk fauna organizes from fluvialite deposits of the Sokups River in the northwestern Caucasus (Baksinskaya and Saratovskaya localities, 9 and 10 in Text-fig. 1). The Sokups faunas are distinguished by the occurrence of an association of advanced *Archidiskodon meridonialis*, *Anancus* sp., *Equus* cf. major, *Stephanotherium etruscum*, *Parasornuris* cf. *abienis*, *Sus* cf. *stolonii*, *Eucladoceros striolatus*, E. cf. *stolonii* and *Struthio* sp. and a new bison, *Bison* cf. *sushovichii* (Alexcev, 1977b).

Very likely, *Archidiskodon* coexists with *Phanogadunomus mammotinae* (Gazit, 1995). An isolated mandible of A. meridonialis is known from the environs of Berdiansk town at Zakarova Balta (11 in Text-fig. 1). The small mammal fauna of the Sokups complex includes *Mysunum* ex gr. *veidei*, *Pryzimpinos prisypatides*, *Boruska sp.*, *Clebromys bogdani*, *Althebactes* cf. *elthi*, *Apodemus sp.*, *Natalopcus cf. okhotinensis*, *Spermophilus sp.*, *Berunenodus fideles*, and *Pteropus hovorovii* (Vorogheni et al., 1990; Tesakov, 1995). This association is known from a locality near Saratovskaya village (Sokups River) and in the uppermost beds of the Livideshow sand pit. The increasing role of arcticoids with useless cheek dentition marks small mammalian fauna of the second half of the Sokups complex.

The complex of *Anancus*, *Archidiskodon*, *Equus* ex gr. *teonius*, *Stephanotherium*, *Elasmotherium* and *Parasornuris*, which was typical for Early European faunas in the late Pleistocene, persisted into the early Pleistocene of this region. Transitional faunas were characterized by *Canis etruscus*, *Pustreba gomazesquei* and *Equus teonius teonius*, which appeared at the end of the Villafanchan (Terre et al., 1992). These associations are correlated with West European faunas of the Olfaud 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 Transcaucasia: Palm-Tukan (Azerbaijan) and Dmanisi (Georgia). The latest *Nyeternotherium megamandibulum* is recorded in these communities (Somkova & Sablin, 1993; Vekua, 1995).

Early Pleistocene

The Early Pleistocene of Eastern Europe is characterized by the Taman faunistic complexes (correlate to late MQ1, as defined by Fettig & Meinrich, 1990). The type Tamanian fauna originates from localities Sinyaya Balta and Tsimbal (12 and 13 in Text-fig. 1) in the Taman Peninsula (Vereshchagin, 1957) and contain an association of *Archidiskodon tamunicus* and *Elasmotherium caucasicum*. The latest representative of *Anancus* ex gr. *teonius* is known from the Tsimbal locality (Duhovych, 1963). Tamanian fauna of the Sembliski locality (the south bank of the Taganrog Gulf of the Sea of Azov) is represented by *Mammuthus* sp., *Trogoletherium cavius*, *Homoheberis* cf. *renatudens*, *Palaeochoerus* cf. *brevirostris*, *Archidiskodon tamunicus*, *Equus major*, *Eucladoceros* cf. *orientalis*, *Bison tamunicus* and *Postcranosaurus* (Bjaglewera, 2000). In the Azov region the small mammal faunas of the Taman complexes are known in the locality of Sembliski-3 (14 in Text-fig. 1) where there have been reported: *Clebromys bogdani*, *Podogadunomus budaevi*, *Mysunum pauciloricum*, *M. intermedium*, *Allophacodon pliosicus,* and *Meryxus taimerus* (Rekoves, 1994). A similar fauna is known at Post-Kaoton (15 in Text-fig. 1) where remains of *Ursus* sp., *Lutra* sp. and *Equus* sp. are also present (Duhovych & Alexcev, 1964; Buginesheva, 1976). Small mammals of the locality include *Podogadunomus budaevi*, *Liponyx anasae*, *Euliponyx arganbey*, *Meryx decumbens*, *M. simutnovi*, *M. paullini* and *Allophacodon* (Markevich, 1998). Both associations are referable to the late stage of the Taman complex. Another locality that yielded numerous remains of *Archidiskodon tamunicus* is situated in the surroundings of the Azov town (16 in Text-fig. 1), near the village of Samarskoe (Buginesheva, 1984a).

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 *Mammuthus* sp., *Mysunum satini*, *Mammothoth trogrotheri*, *Equus teonius teonius*, *Bison hebetorvi* and *Megaloceros* sp. Two almost complete skeletons of *Mammothoth trogrotheri* 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 deformed resemble the tro-
The late Pleistocene is characterized by a rapid climatic oscillation, with periods of glacial maxima and interglacial minima. During the last glacial maximum, about 20,000 years ago, North America and Europe were covered by extensive ice sheets, while in Asia, the Tibetan Plateau acted as an ice-free area. This led to the development of distinct biogeographic regions, with the separate evolution of faunal and floral assemblages.

The late Pleistocene is divided into several stages, each with its own distinctive characteristics. The Last Glacial Maximum (LGM), occurring around 26,000 years ago, marked the peak of ice advance. The Last Interglacial (LIG), which followed the LGM, was a period of warmer climate, and is characterized by the expansion of tropical and sub-tropical faunal assemblages into cooler regions.

The late Pleistocene saw the development of new species, some of which are still in existence today, while others are known from fossil records. This period was crucial for the evolution of humans, as it facilitated the development of complex societies and technological advancements. The late Pleistocene also witnessed the extinction of many large mammal species, such as the woolly mammoth and the saber-toothed cat, which are known from fossil records.

The study of the late Pleistocene has provided valuable insights into the history of life on Earth, and has helped shape our understanding of the diverse and dynamic processes that have shaped our planet over time.
can be interpreted as gradual responses to increasing aridization. Considerable changes in mammalian fauna occurred between the Taman and Perekop faunistic complexes. At the Early to middle Pliocene transition, these changes resulted in formation of typical Pleistocene faunas.

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 Arno area shares a considerable number of Asian elements (Pananaloe, Elasmotherium, Palaeotherium) 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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