Large mammal faunas of the European part of Russia in Quaternary

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ABSTRACT. The article presents the results of a study of a unique osteological material from archaeological sites and settlements in the European part of Russia. In total, more than 119 thousand bones of large Quaternary mammals were studied. The closest analogue of the Early Pleistocene faunal complex Muhkai 2 is a community of animals from the dry African savannah. Data to distinguish between the early and late (1.1 Mya) stages of the Taman fauna are presented. It was confirmed that in the Late Pleistocene, the climate was responsible for changes in the number of large mammals and their habitats. It was shown that the domestication of the dog occurred in the early Upper Paleolithic, and in the Holocene, the indigenous European population of *Canis familiaris* was largely replaced by migrants from the east. Data are given that support that throughout the Quaternary at archaeological sites and settlements in the European part of Russia, there was a practice of complete utilization of hunted or raised animals.


KEY WORDS: large mammals, faunas, osteological material, European part of Russia, Quaternary.

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Фауны крупных млекопитающих европейской части России в антропогене

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РЕЗЮМЕ. В статье изложены результаты исследования уникального остеологического материала из археологических стоянок и поселений европейской части России. Всего было изучено более 119 тыс. костей крупных четвертичных млекопитающих. Показано, что ближайшим аналогом ранне плейстоценового фаунистического комплекса Мухкай 2 является сообщество животных сухой африканской саванны. Представлены данные, позволяющие различать раннюю и позднюю (1.1 млн. лет) стадии таманской фауны. Подтверждено, что в позднем плейстоцене именно климат был ответственен за изменения численности крупных млекопитающих и ареалов их обитания. Показано, что одомашнивание собаки произошло в эпоху ранней поры верхнего палеолита, а в голоцене автохтонная европейская популяция *Canis familiaris* в значительной степени заменилась мигрантами с Востока. Приведены данные, что на протяжении всего антропогена на археологических стоянках и поселениях европейской части России присутствовала практика тотальной утилизации человеком добытых или выращенных им животных.

КЛЮЧЕВЫЕ СЛОВА: крупные млекопитающие, фауны, остеологический материал, европейская часть России, антропоген.

Introduction

Comprehensive studies of the fauna of large Quaternary mammals in the European part of Russia on the basis of an in-depth study of the richest osteological collections of some archaeological sites have not been carried out before, and published works have covered only a small part of the fossil material. The absolute age of a number of sites and settlements and their economic structure often remain unclear. Moreover, sometimes conclusions have been based on erroneous species determinations. New osteological material, as well as recent molecular genetic studies, has shown that a number of basic concepts need to be reviewed. The poor knowledge of old collections and the appearance of new bone collections of large Quaternary mammals from the European part of Russia have determined the need for this work.
Material and methods

In total, more than 119 thousand bones of large Quaternary mammals from sites and settlements in the European part of Russia were studied. The methods for studying osteological material are diverse. Particular attention in this study was given to the correct determination of animal species. For this, in some cases, classical morphometry was involved. We used literature data on the morphology, paleogeography, and systematics of extinct and recent mammals, as well as standard statistical methods. Trace evidence and taphonomy were involved as necessary but were not the main research methods in this work. For genetic and isotopic study, radiocarbon dating was performed using materials from museum collections and from material that the author collected during the field work.

Results

Large mammals in the European part of Russia in the Early Pleistocene

The site Muhkai 2 (Inner Dagestan, northeastern Caucasus) has a complex geomorphology, which is reflected in the stratigraphy and nomenclature of the cultural layers. The bulk of the bones and stone implements lay in the deposits of a once shallow, drying and highly silted reservoir with weakly flowing or standing water. In our opinion, animals died here due to natural causes; for example, they drowned in a short autumn “rainy season” with catastrophic heavy rainfall after a long drought (Sablin et al., 2018). The composition of this faunal complex allows us to consider the animal community of dry African savannah as its closest analogue (Sablin et al., 2013; Sablin, 2016a, 2016b). The composition of the fauna is as follows: *Archidiskodon meridionalis*; *Palaeotragus priaiosovicus*; *Libralces gallicus*; *Eucladoceros senezensis*; *Eguaus (Allohippus) stenonis*; *Gallogoral meneghinii*; *Gazellespora torticornis*; *Gazella bouvrainae*; *Acinonyx pardinenis*; *Pliocrocuta perrieri*; *Lynx issiodorensis*; *Vulpes alpeceoides*; *Meganteeron cultridens*; *Canis etruscus*. The geological age of Muhkai 2 is estimated by us to be in the range of 2.1–1.77 Mya (Sablin et al., 2013; Amirkhanov et al., 2014, 2016, 2017).

Until recently, it was customary to consider the Taman faunal complex as a whole until the onset of the Jaramillo reversal, i.e., 1.1 Mya (Vangengeim et al., 1991). Its stratotype is located at the Bogatyry/Sinyaya Balka (Taman Peninsula): hundreds of bones of large mammals and stone tools were collected there (Shchelinsky, 2010; Kulakov, 2019). Our studies indicate that the probable absolute age of this site is 1.6 Mya (Sablin, 2008, 2010a). We believe that it is necessary to expand the age limits of the complex: it is necessary to distinguish between the early and late (1.1 Mya) stages of the Taman fauna.

Most researchers of the second half of the 20th century believed that the arrival of the genus *Homo* in Eurasia did not happen earlier than 1.0 Mya (Dennell & Roebroeks, 1996). Our studies of Early Pleistocene faunas allowed clarification of the time of that genus possible exit out of tropical Africa to about 2.2 Mya (Sabin & Girya, 2009, 2010; Sablin, 2011).

Large mammals in the European part of Russia in the Late Pleistocene

Our revision of osteological material from the lithological layer IV (36 Kyr cal BP) of the Kyik-Koba Grotto (eastern Crimea) from the 1924–1925 excavations generally confirmed the conclusions made by V.I. Gromova and V.I. Gromov in 1937 (Sablin, 2013). The composition of the fauna is as follows: *Mammuthus primigenius*; *Coelodonta antiquitatis*; *Equus ferus*; *Equus hydruntinus*; *Cervus elaphus*; *Megaloceros giganteus*; *Bison priscus*; *Saiga tatarica*; *Ovis sp.*. We believe that the Kyik-Koba Grotto was not the primary place of slaughtering animals but should be considered a base camp where ancient people carried out the full-scale processing of carcasses and their subsequent disposal. In this regard, the presence of a large number of highly fragmented, indefinable bone residues in the cultural layer seems logical.

The molecular genetic studies in which the author took part indicate dissimilar population dynamics in the evolutionary history of the large mammals in the Late Pleistocene, including in the European part of Russia. We found a positive correlation between changes in the range-size and the genetic diversity for six Late Pleistocene herbivores — woolly mammoth, woolly rhinoceros, wild horse, reindeer, steppe bison and musk ox (Lorenzen et al., 2011). A multiple increase in the number of these animals is recorded on the Eurasian continent 34–19 Kyr BP. Our other study showed that the ancient endemic European woolly mammoth began to be replaced by Siberian woolly mammoth about 32 Kyr BP, and this process lasted at least 10 Kyr BP (Palkopoulou et al., 2013). We have also shown that modern European *Vulpes lagopus* is not a descendant of the Late Pleistocene *V. lagopus* since it migrated from Siberia to Europe only after the end of the Ice Age (Dalén et al., 2007).

The fossil material from Kostenki 21, layer III (27–25 Kyr cal BP), which we studied in detail, provides additional information on the fauna of large mammals in the Late Pleistocene in the center of the Russian Plain (Reynolds et al., 2019). The composition of the fauna is as follows: *Lepus timidus tanaicicus*; *Canis lupus*; *Vulpes lagopus rossicus*; *Ursus arctos*; *Lynx lynx*; *Mammuthus primigenius*; *Coelodonta antiquitatis*; *Equus ferus*; *Rangifer tarandus*; *Bovidae* gen. et sp. indet.; *Saiga tatarica*. There are three main hypotheses about the relationship between ancient people and mammoths. The first one is related to the idea of using the carcasses and bones of the giants who died from various natural causes. The second hypothesis defends the theory of the active hunting of mammoths. The third is a synthesis of the first and second hypotheses. From our point of view, the existence of an active hunt for mammoths in the
Late Pleistocene seems a quite possible event (Sablin, 2019). We believe that human hunting for mammoths did not have any effect on the latter’s populations. As our studies showed, people mainly hunted small females weighing less than two tons and cubs (Germontpré et al., 2008a, 2008b; Sablin, 2014a, 2019). The cuts found on the bones of mammoths from Kostenki 21, layer III and Eliseevichi 1 (15–13 Kyr BP) are evidence of the cutting of their carcasses in the settlements (Sablin, 2017a; Demay et al., 2017, 2019).

The discovery by the author of two skulls of dogs among osteological material from the Upper Paleolithic Eliseevichi 1 site was conclusive evidence of the presence of this animal in the center of the Russian Plain in the Late Pleistocene. Skulls were found back in 1935–1936, but a comprehensive morphometric analysis of these specimens using modern statistical methods was carried out only recently (Sablin & Khlopachev, 2001, 2002, 2003; Sablin, 2007a, 2016c, 2017a). Their absolute age, determined by AMS, was 13.9 Kyr BP and 13.4 Kyr BP. Molecular genetic studies have shown the complex evolutionary history of Canis familiaris (Thalmann et al., 2013; Frantz et al., 2016). It has been shown that none of the recent wolf populations can be considered ancestral to dogs. Apparently, domestication attempts began even in the early Upper Paleolithic and then did not stop for at least 20 thousand years. The final separation of the lines of the wolf and the dog occurred about 15 thousand years ago.

Large mammals in the European part of Russia in the Holocene

The beginning of the Holocene started as the Preboreal period (about 11.7 Kyr BP). In the north of the European part of Russia, extensive natural zones of the tundra and forest-tundra were preserved; in the south, steppes prevailed, where people staged massive driven hunts. Wild horses were harvested here, as in the Pleistocene, in strictly defined places along the migration routes, most likely from herds crossing rivers (Kitagawa et al., 2018).

The Atlantic period was the climatic optimum of the Holocene. At this time, large areas of broadleaved forests spread to the north of the European part of Russia, which contributed to the widespread distribution of wild boar. Having studied the osteological material from the grave No. 114 of the Yuzhny Oleniy Ostrov (Karelia, northwestern Russia), for the first time in this Mesolithic cemetery, we managed to find the bones of Sus scrofa (Mannermaa et al., 2019).

Analysis of osteological material from the early Neolithic layers of the Rakushechny Yar (Rostov Region, southwestern Russia) settlement showed that in the Middle Holocene, hunting for red deer and roe deer was actively conducted there, and cattle breeding played an insignificant role. We found that domestic pigs, a cow and a sheep penetrated the south of the European part of Russia with immigrants from Asia Minor at the very end of the 7th millennium cal years BC (Sablin, 2018).

Pile settlements became common in the northwest of the European part of Russia at the end of the Atlantic period, beginning of the Subboreal period. At this time, the climate became cooler and drier. We found that elk, wild boar, marten, and brown bear were the main prey for people. Our data indicate that domestic horses and cows appeared in the northwest of the European part of Russia in the second half of the 3rd millennium cal BC and, at its end, so did pigs and small cattle (Sablin & Syromyatnikova, 2009; Sablin et al., 2011; Sablin, 2014b, 2018). In the transition from the Subboreal to the Subatlantic period of the Holocene at the turn of the 2nd to 1st millennium BC, the climate became relatively wetter and warmer. Analysis of osteological material from the settlement of Anashkino (Pskov Region, northwestern Russia) showed that marten hunting from the 8th to the 1st century BC became decreasingly demanded in the life of the inhabitants of the settlement and that hare hunting, on the contrary, became more active (Korotkevich et al., 2010; Sablin, 2010b; Korotkevich & Sablin, 2014).

All this may indicate the appearance of significant open spaces such as fields and pastures after deforestation in the vicinity of the settlement.

At the end of the VII century BC in the south of the European part of Russia in the Northern Black Sea region, the first Antique settlements appear. The settlement of Golubitskaya 2 (Taman Peninsula) existed in the VI–III centuries BC. The domestic animal bones make up 98.8% of the total number of identifiable bones of the large mammals in the osteological material (Sablin, 2016d). The composition of the fauna is as follows: Lepus europaeus; Canis lupus; Canis familiaris; Felis catus; Sus scrofa; Sus scrofa domestica; Equus caballus; Cervus elaphus; Bos taurus; Ovis aries/Capra hircus.

In the middle of the Subatlantic period of the Holocene (the second half of the 1st millennium AD), the Middle Ages began in the European part of Russia. Having studied the osteological collection from the Ryurikovo Gorodishche (Novgorod Region, northwestern Russia) for the first time with well stratified bone material, we traced the dynamics of the composition of the fauna at IX–XII centuries AD. Most of the bones were found in the multimeter deposits of the ancient moat. Twenty-one well-preserved Equus caballus skulls (adult stallions aged 5 to 15 years old) were found in the layers of the IX–X centuries AD (Sablin, 2007b, 2017b). A large fragment of the skull of Macaca sylvanus, dated to the XII century AD, was also discovered on the Ryurikovo Gorodishche. Currently, this species is distributed in the mountainous regions of northwest Africa and Gibraltar, from which this monkey could have been brought alive to the Ryurikovo Gorodishche via the Eastern Mediterranean. It should be noted that this find is the oldest on the continent for this epoch (Sablin, 2007b, 2017b).

Our molecular genetic studies, together with those of our colleagues, showed that the autochthonous European population of dogs belonged to mitochondrial clade C, and only at the very end of the 7th millennium cal BC did dogs of mitochondrial clade D come here with their masters, immigrants from Asia Minor. As a result of the
next wave of mass migrations of people in the Middle Bronze Age from the zone of Eastern European steppes, the local dog population was almost completely replaced by migrants carrying mainly clades A and B (Frantz et al., 2016; Ollivier et al., 2018). Our other study showed that around the 7th millennium cal BC, the genome of European C. familiaris appeared with fixed beneficial mutations that allowed them to easily consume the large amounts of starch contained in human food (Ollivier et al., 2016). Therefore, the transition to agriculture created dogs capable of assimilating crop products. It should be noted that the effective population size of C. familiaris in Europe increased sharply in the Holocene, which was directly related to the increase in the number of people. Moreover, the effective size of the wolf population remained virtually unchanged (Thalmann et al., 2013).

Many dogs in the Middle and Late Holocene settlements were sacrificed and deliberately buried (Losey et al., 2011, 2013, 2018a, 2018b; Zhuravlev et al., 2016; Sablin, 2016d). Complex postmortem manipulations of people with parts of bodies and, especially, with the heads of these animals are clearly recorded in the available osteological material. The sacred killing of a dog and the more or less solemn burial of it remains by an ancient person should not be surprising. Complicated ceremonies using C. familiaris were apparently a common practice at that time, since the dog was, for many primitive peoples, a kind of dual nature creature, a guard on the border of the world of the dead. However, the fact that this animal was the subject of a cult does not at all preclude a pragmatic and, at times, quite cruel human attitude towards it (Losey et al., 2013, 2014).

Discussion

The variety of osteological materials obtained during archaeological excavations involves their in-depth processing involving various scientific approaches. At present, an extensive set of facts has been accumulated, the interpretation and analysis of which is necessary for a correct understanding of the features of the existence of faunas of large mammals in the European part of Russia in the Quaternary. This is fully consistent with the trends of modern science, where the most important role is played by interpretation and reconstruction and not just the quantitative accumulation of data. The extraction of the greatest possible amount of information from already accumulated osteological material is of utmost importance. A new view of seemingly obvious facts often leads to unexpected results, which are described above.

Large mammals and the genus Homo have coexisted because the appearance of the latter. A number of recent discoveries have aroused increased interest in elucidating the features of such an interaction. The European part of Russia is ideal for studying such interactions, since it was here that during the Quaternary, the most intensive changes in natural climatic zones took place. Large mammals were forced to consistently adapt to living in dry, hot Early Pleistocene savannahs, Late Pleistocene periglacial steppes and tundra, and wet Holocene forests. In our research, we clearly show that ancient people were completely dependent on the state of the animal world, its composition and its dynamics over time.

Another extremely relevant point in our study is the domestication of animals and everything connected with that action. Domestication is not just the formation of symbiosis (mutually beneficial cohabitation) between species. It is both a natural and socio-cultural phenomenon. It should be emphasized here that both the origin of some species of domestic animals and the ways of their distribution in the territory of the European part of Russia still remain extremely poorly developed issues, and the existing ideas about this apparently need a radical revision. We have touched on only some aspects of this problem in our research.

Obviously, the study of a complex system of human-beast relationships is impossible without a sufficiently broad view of this problem. It is necessary to study the bones of large mammals at the sites of sacrifice. The ritual component is extremely important here, and it should be investigated separately in the study of osteological materials.

The data obtained by us are important for assessing and analyzing the biological diversity of ecosystems in the European part of Russia during the Quaternary, which, in turn, can be used to solve specific problems, particularly in the field of paleogeography. The data have theoretical significance in the context of a comprehensive study of the history of faunas and make a significant contribution to understanding the role of large mammals in the formation of the foundations of modern civilization. Our research will undoubtedly cause great practical interest among archaeologists, since it allows analyzing in sufficient detail the economic structure of human populations and reconstructing paleoecosystems. Data are given that support that throughout Quaternary at the sites and settlements in the European part of Russia, there was a practice by humans of total utilization of animals they had hunted or raised. Our research also changes a number of traditional ideas about the basic laws of interaction between human populations and their natural environment, which cannot but have practical significance in the long term.

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