

Original article

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## STRATIGRAPHIC DISTRIBUTION OF LARGE QUATERNARY MAMMALS IN THE TERRITORY OF THE WEST SIBERIAN PLAIN

Andrei Valerievich Shpansky

National Research Tomsk State University, Tomsk, Russia, andreyshpansky@yandex.ru



**Abstract.** New data on the stratigraphic distribution of large mammals in the territory of the West Siberian Plain allowed distinguishing three main stages in the development of the Quaternary fauna. The first is the ancient stage (Paleopleistocene, Eopleistocene) that reflects warm and humid conditions, mosaic landscapes, and an ecologically diverse fauna composition. The second stage is transitional (Early Neopleistocene) that reflects changes in the landscape, climatic conditions, and in fauna composition. The third is the tundra-steppe stage (Middle and Late Neopleistocene) that reflects the maximum cold aridization of landscapes and the dominance of species related to open landscape.

**Keywords:** Large mammals, Quaternary, Western Siberia, Biochronology, faunal complex

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## СТРАТИГРАФИЧЕСКОЕ РАСПРОСТРАНЕНИЕ КРУПНЫХ ЧЕТВЕРТИЧНЫХ МЛЕКОПИТАЮЩИХ ТЕРРИТОРИИ ЗАПАДНО-СИБИРСКОЙ РАВНИНЫ

Андрей Валерьевич Шпанский

Национальный исследовательский Томский государственный университет, Томск, Россия, andreyshpansky@yandex.ru

**Аннотация.** Новое обобщение данных по стратиграфическому распределению четвертичных крупных млекопитающих территории Западно-Сибирской равнины позволило уточнить время существования отдельных таксонов и видовые составы фаунистических комплексов. В связи с понижением неоген-четвертичной границы и включением в состав квартера гелазия, подпуск-лебяжбинский комплекс стал самым древним для Западной Сибири. Для палеоплейстоцена, эоплейстоцена отмечается достаточно высокая степень экологического разнообразия таксонов, что может отражать определенную мультиландшафтность на территории равнины. Изменения в составе фауны млекопитающих раннего неоплейстоцена привели к формированию фауны с преобладанием таксонов, тяготеющих к открытым ландшафтам. Новые радиоуглеродные датирования показали более позднее (во второй половине позднего неоплейстоцена) вымирание некоторых доминантных таксонов среднего неоплейстоцена. Увеличившаяся степень близости видовых составов фаун среднего и позднего неоплейстоцена позволила автору предложить новый фаунистический комплекс – «тундро-степной» для всего объема среднего и позднего неоплейстоцена. Ранее выделявшиеся для этого интервала прииртышский, хазарский и мамонтовый фаунистические комплексы понижены до ранга подкомплексов. Объединяющим их является высокая доля общих таксонов и высокая степень специализации к тундро-степным ландшафтам.

**Ключевые слова:** крупные млекопитающие, четвертичный период, Западная Сибирь, биохронологии, фаунистические комплексы

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## Introduction

The Late Cenozoic is characterized by dynamic natural processes, such as the differentiation of the relief due to orogenic activity, the emergence and disappearance of land connections between continents and periodic changes in their outlines due to glaciations and associated marine transgressions and regressions. This dynamics was causing changes in climate and landscapes, leading to rapid changes in terrestrial ecosystems. The mammals were the most susceptible to those changes. Many groups have experienced adaptive radiation over the past 3–4 million years, and new subfamilies appeared with large generic and specific differentiation. In addition, the ecological structure of the mammal fauna that formed in the second half of the Pliocene is mostly a successor of the Hipparion fauna that had been spread in the second half of the Miocene and the beginning of the Pliocene [Shpansky, 2008].

The ecological structure of the mammal fauna in the Quaternary was related to the predominance of open arid landscapes and was preserved until the end of the Pleistocene in the form of mammoth fauna. This structure is largely similar to the modern African savanna fauna [Vereshchagin, Baryshnikov, 1983; Shpansky, 2010, 2018a] with a large number of fast-running ungulates and a high variety of medium- and large-sized carnivorans.

Due to the recent lowering of the Neogene–Quaternary boundary to 2.6 million years and a large body of new data, including those with radiocarbon dating, a certain rethinking of the biostratigraphic basis for the division of Quaternary sediments of the West Siberian Plain is required. In the General Stratigraphic Scale of Russia, the Gelasian interval has not received a clear status. Thus, the author uses the term “Paleopleistocene” proposed by A.S. Tesakov [2013] and “regional Irtysh horizon” for sediments. Subdivisions of the Regional Stratigraphic Scale of the West Siberian Plain are used for the remaining periods [Unificirovannaya..., 2000]. The review presents data on the stratigraphic distribution of only large mammals. The research is based on data obtained as a result of the author’s own research and on the analysis of published works. Data on 30 multi-species localities of large mammals of the West Siberian Plain, some of which consist of several bone-bearing layers, and a number of other findings we analyzed. In addition to the territory of the West Siberian Plain, large localities from the Minusinsk Basin (Kurtak), the Pre-Altai Plain (the lower course of the Chumysh River), and the Kuzneck Basin (Kemerovo Province) are also considered. In the Pleistocene, these territories were similar to the West Siberian Plain in terms of landscape and climatic conditions.

## Faunal complexes of Western Siberia after V.I. Gromov and E.A. Vangengeim

The first well-reasoned biostratigraphic scheme on mammals based on significant factual data was published by V.I. Gromov in 1939. For the Late Pliocene and Quaternary of the European part of the USSR, he identified nine faunal complexes: Khaprovsky, Psekupsky (divided into lower and upper), Taman, Tiraspol, Khazar and Upper Paleolithic (with the Late Mousterian) [Gromov, 1939, 1948]. V.I. Gromov proposed with a high degree of confidence the Khazar and Upper Paleolithic complexes for the West Siberian Plain. The older complexes only indicate the presence of “separate leading elements”. V.I. Gromov understood the faunal complex as a combination of animal species common for “certain more or less significant stratigraphic units of the Quaternary and for certain territories” [1939, p. 200]. V.I. Gromov proposed a phylogenetic tree of mammoth elephants (*Archidiskodon–Mammuthus*) as a leading group. Later, he compared faunal complexes of Eastern Europe with the existence time of various forms of mammoth elephants. The comparison became decisive for the assessment of the stratigraphic volume of the complexes [Gromov, 1961; Gromov et al., 1965]. Thus, the faunal complexes became biochrons of elephants of the *Archidiskodon–Mammuthus* phylogenetic lineage. This understanding of the faunal complexes is preserved to the present day.

V.I. Gromov’s ideas on the biostratigraphy of Northern Asia in general and the West Siberian Plain in particular were developed in the 1960s–1970s. Diverse geological and surveying, exploring and biostratigraphic works were carried out at this time by the effort of many geological organizations. Many localities of Neogene and Quaternary large and small mammals were identified. The extensive factual data were collected in the course of their implementation. Localities of ancient faunas (older than 1 million years) were found only in the southern part of Western Siberia, in the upper and middle courses of the Irtysh, Ob, and Ishim rivers. Miocene–Pliocene and Quaternary sediments are exposed in natural outcrops there. For the Late Pliocene and Eopleistocene, E.A. Vangengeim and V.S. Zazhigin [1965] proposed the Beteke, Lebyazhie, and Razdolian complexes. Later, the Kizikha and Vyatka complexes were identified mainly for small mammals [Vangengeim, Zazhigin, 1972; Zazhigin, 1980]. A summary of these data can be found in the monograph by E.A. Vangengeim [1977]. She included Betekey and Podpusk-Lebyazhie complexes, which until recently have been considered characteristic for the Middle and Late Pliocene, in the West Siberian “anthropogenic” mammalian complexes. She developed the basic principles of constructing biochronological scales for mammals for the Pliocene and Pleistocene [Vangengeim, 1982;

Vangengeim, Tesakov, 2008] and gave a clear definition for the term “faunal complex” [Vangengeim, 1977, 1982]. The important “condition – presence of a standard locality” is added to the already traditional “Gromov” criteria for the allocation of complexes [Vangengeim, 1977, p. 71].

Estimates of the Middle Neopleistocene fauna have remained unclear until today. There is a case when within one zoogeographic province two conditionally identical complexes are distinguished – Priirtysh [Kozhamkulova, 1969] and “Tatarka fauna” [Vangengeim, 1977]. According to the authors, they correspond to the first half of the Middle Neopleistocene and are comparable with the Singilsky complex of Eastern Europe. V.S. Kozhamkulova defined the Pavlodar Priirtyshye as a type locality for the Priirtysh complex. The locality near the village of Tatarka is also situated within this area. In addition, B.S. Kozhamkulova estimated the existence interval of the Priirtysh complex very widely – from the end of the Early Neopleistocene to the beginning of the Late Neopleistocene. The “Tatarka fauna” is a local fauna, the data of which mainly comes from R.A. Zinova’s beach collections (1966–1967, Geological Institute RAS, collection 895).

### Stratigraphic distribution of Quaternary large mammal taxa in Western Siberia

A brief overview of the stratigraphic distribution of Quaternary mammal taxa within the West Siberian Plain is given at family level.

#### Elephantidae

The most common elephant findings within the West Siberian Plain are the remains of the *Archidiskodon–Mammuthus* clade. The teeth of elephants are common and well diagnosed. The remains of *Archidiskodon meridionalis gromovi* Garutt et Alexejeva, *A. m. meridionalis* (Nesti), *Mammuthus trogontherii trogontherii* Pohlig, *M. t. chosaricus* Dubrovo, *M. primigenius* Blumenbach are found within the West Siberian Plain (Fig. 1). The remains of an earlier form of the archidiskodontic elephant, *A. rumanus*, known from the early European Villafrancian sediments, have not been found in the West Siberian Plain.

The most ancient findings of mammoth elephants in the territory of the West Siberian Plain come from sediments of the Irtysh formation in Lebyazhye 2, Podpusk 1 and 2. The remains of the nominate southern elephant (*A. m. meridionalis*) are rare; fragments of teeth and a phalanx from the upper part of the Irtysh formation in Lebyazhye 2 and Moiseyevka 1 (Pavlodar Province) and teeth from sediments of the Kochkovsky horizon near the village of Ust-Talovka (Altai Priirtyshye region) are found [Vislobokova, 1973; Zhylykibaev, 1975]. In the south-west of Western Siberia, remains from the lower

part of the Zhunshilik formation (Late Eopleistocene) are found near Arkalyk [Kozhamkulova, 1969; Zhylykibaev, 1975]. A fragment of an ancient elephant tooth is noted by I.A. Vislobokova [1973] from Moiseyevka 2 on the Irtysh River. She suggested that it belonged to the progressive form *A. m. tamanensis* Dubrovo. The distribution time of the southern elephant is estimated to be within the second half of the Paleopleistocene and the first half of the Eopleistocene.

The remains of *Mammuthus* Burnett elephants are much more common and not only in the form of isolated teeth. For *M. trogontherii trogontherii*, the author described two skeletons – from Pyatiryzhsk on the Irtysh River [Shpansky et al., 2008] and Ust-Tarki on the Om River [Shpansky et al., 2015]. The last molars of the elephant from Ust-Tarka are strongly worn and look more primitive in their structure. They also appeared to be a transitional type between *A. meridionalis* and *M. trogontherii*. It can be assumed that the geological age of this elephant is earlier (the beginning of the Early Neopleistocene) than the elephant from Pyatiryzhsk. Both skeletons belong to adult specimens, which can reflect greater intraspecific variability. In addition, the Pyatiryzhsk skeleton is 70 cm higher than the Ust-Tarka skeleton.

*M. trogontherii* was replaced by *M. t. chosaricus* at the border of the Early and Middle Neopleistocene. *M. t. chosaricus* is already present in the Priirtysh complex of Grigoryevka [Shpansky et al., 2007]. To the same elephant, the author [Shpansky et al., 2015] refers the skeleton from Chembakchino, described by P.A. Kosintsev as *M. t. trogontherii* [Kosintsev et al., 2004]. The latest findings of *M. t. chosaricus* are the remains from layer 6 of Krasny Yar (Novosibirsk Province) [Vasiliev, 2005]. The age of these sediments is estimated as Kazantsevsky (MIS 5e). An elephant with a structure of teeth of a transitional type between *M. t. chosaricus* and *M. primigenius*, defined by L.I. Alekseeva as an early type of mammoth, had already existed in Eastern Europe as part of the Shkurlat complex during the Mikulinsky period [Alekseeva et al., 1984; Alekseeva, 1990]. Nevertheless, the main morphological features of elephant teeth (frequency of plates per 10 cm, enamel thickness) from Shkurlat and Mezhevikhino are within the range of variation of *M. t. chosaricus* from other localities. In addition, the findings of *M. trogontherii chosaricus* and *M. intermedius* are indicated in the sediments of the Mikulinsky Interglacial (MIS 5e) of the early Late Neopleistocene for Eastern Europe [Dubrovo et al., 2007; Bajgusheva, Titov, 2021]. An even more recent finding is a skull from Asino (Tomsk Province) [Shpansky, 2000]. AMS dates  $41.865 \pm 1990$  ka BP (UBA-38453) and  $42.670 \pm 1310$  ka BP (UBA-39395) were obtained by them [Shpansky, Kuzmin, 2021].

The Late Pleistocene is characterized by numerous remains of the typical mammoth *Mammuthus primigenius*

with fine enamel and high plate frequency of 10 cm. At the same time, large accumulations of mammoth bones or skeletons are confined to the deposits of the Late Pleistocene (25–15 thousand years) [Puchkovskaya, Shpansky, 2023].

In addition to the well-studied mammoth elephant line *Archidiskodon–Mammuthus*, *Elephas* Falc. et Cautl. elephants, belonging to the group of forest elephants of the subgenus *Palaeoloxodon* Matsumoto, were distributed within the West Siberian Plain. The most ancient finding of *Elephas (Palaeoloxodon)* cf. *namadicus* (Falc. et

Cautl.) is a tooth fragment recovered from the greenish-gray and blue-gray loam soil of the Erestnaya formation (Upper Eopleistocene) near Barnaul [Vislobokova, 1973]. The remains of a more progressive forest elephant *E. (Palaeoloxodon) antiquus* (Falc.) were found in Zhana-Aul, Krasnoyarsk (Pavlodar Province) in the early Middle Neopleistocene [Dubrovo, 1960]. There is a general trend in changes in the teeth structure among forest elephants as well as in mammoth elephants. The frequency of plates increases by 10 cm of the crown length and enamel thickness decreases.

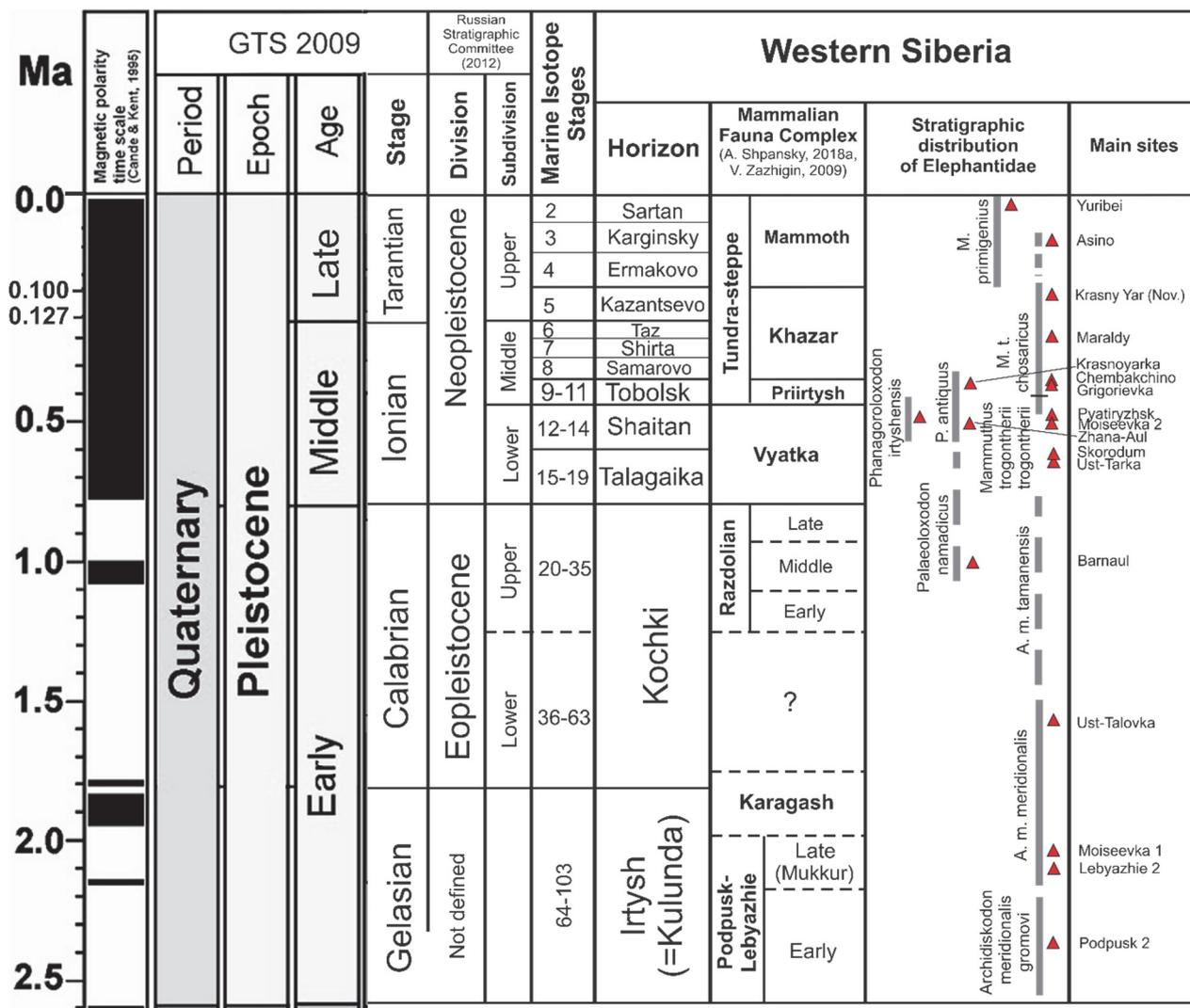


Fig. 1. Scheme of stratigraphic distribution of elephants of the family Elephantidae within the West Siberian Plain

Рис. 1. Схема стратиграфического распространения слонов семейства Elephantidae в пределах Западно-Сибирской равнины

With the help of the skull found in the Early Neopleistocene sediments of Pyatiryzhsk (Irtysh River, Pavlodar Province), which also has features different from mammoth and forest elephants, the author could identify a new

species referred to *Phanagoroloxodon irtyshensis* Shpansky [2005b]. According to V.E. Garutt [Garutt, Tikhonov, 2001], the Phanagora elephant line is ancestral to mammoth elephants in Eurasia.

**Rhinocerotidae**

Remains belonging to representatives of three rhino genera are found in the territory of the West Siberian Plain – *Stephanorhinus*, *Coelodonta* (subfamily Dicero rhinae), and *Elasmotherium* (subfamily Elasmotheriinae).

The phylogeny of the genus *Elasmotherium* Fischer remains unclear. A.K. Shvyreva [2015, 2016] notes the presence of four species in southern Eastern Europe – *Elasmotherium peii* Chow (Late Pliocene–Paleopleistocene), *E. chaprovicum* Shvyreva (Paleopleistocene, first half of Middle Akchagyl), *E. caucasicum* Borissiak (Late Paleopleistocene–Eopleistocene, Apsheron), and *E. sibiricum* Fischer (Early-Late Neopleistocene). Remains of *Elasmotherium* are quite numerous in Central and Northern Kazakhstan and also in the south of the West Siberian Plain. B.S Kozhamkulova [1981] notes 30 localities of different geological age from the Gelasian (Podpusk) to the Middle Neopleistocene (main group).

A series of findings dated to the Karginsky Interglacial has been added to them recently [Shpansky et al., 2016a; Kosintsev et al., 2019]. The oldest findings of *Elasmotherium* within the West Siberian Plain come from the sediments of the Irtysh formation (Gelasian) near the village of Podpusk (Pavlodar Province). Their genus is currently difficult to define due to the scarce data. I.A. Vislobokova notes the similarity of the remains to *E. sibiricum* [Vislobokova, 1996]. The data available to the author shows that the *Elasmotherium* from Podpusk was smaller than *E. caucasicum*, but larger than *E. sibiricum*. According to the geological age, these remains are comparable to the existence time of the Chinese *E. reii* or the Liventsovian *E. chaprovicum*. The importance of specific interpretation of the findings in Pavlodar Province increases due to the very large distance among ancient representatives of *Elasmotherium* since they are geographically located approximately in the middle. *E. sibiricum* is established for the Neopleistocene of Western Siberia (Fig. 2).

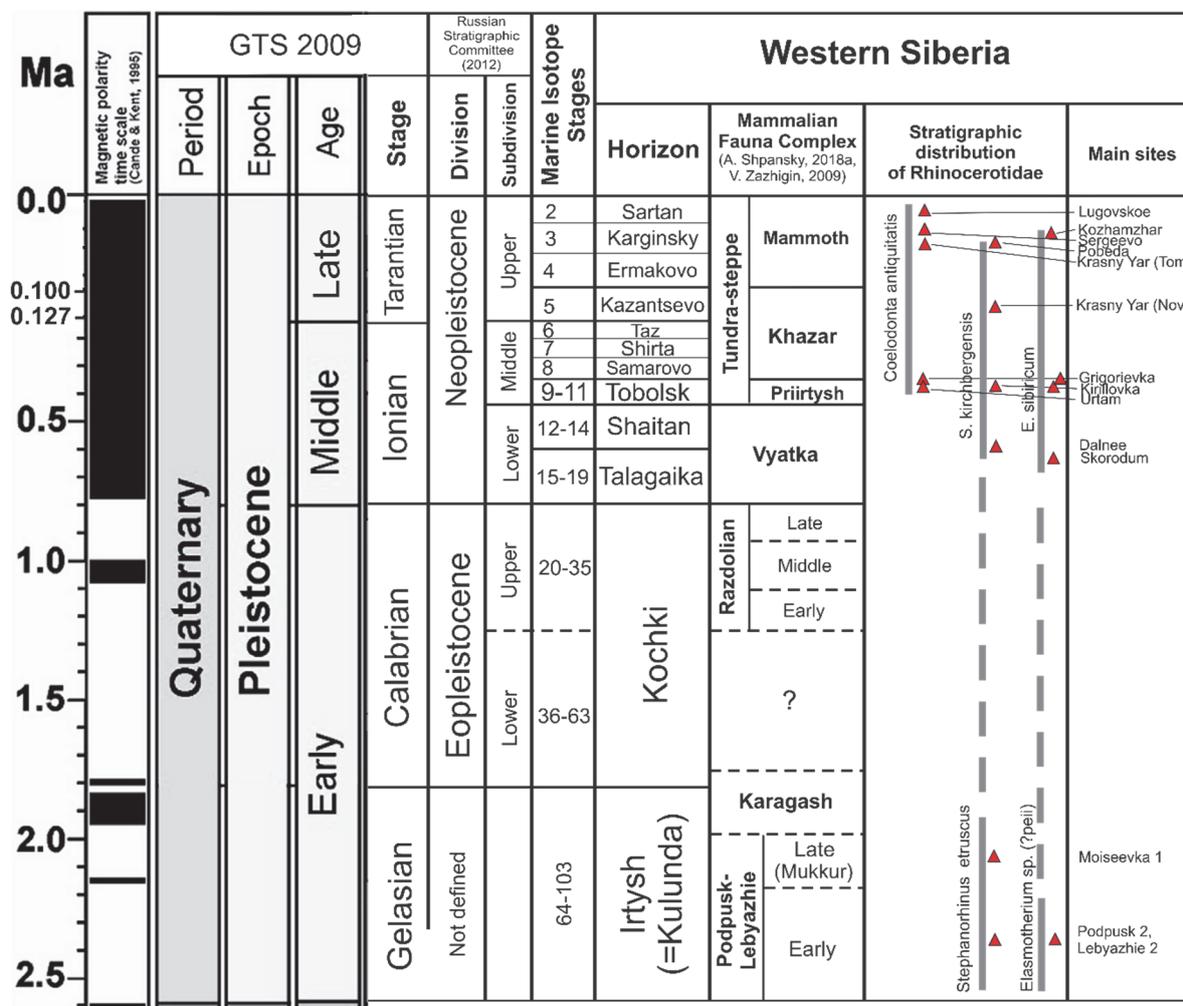


Fig. 2. Scheme of stratigraphic distribution of rhinos of the genera *Coelodonta*, *Stephanorhinus*, and *Elasmotherium* within the West Siberian Plain

Рис. 2. Схема стратиграфического распространения носорогов родов *Coelodonta*, *Stephanorhinus* и *Elasmotherium* в пределах Западно-Сибирской равнины

The findings of *Elasmotherium* in Grigoryevka (Pavlodar Province) are dated to the sediments of the Middle Neopleistocene Tobolsk horizon. They are found together with the remains of *Coelodonta antiquitatis* Blum as part of the Priirtysh faunal complex [Shpansky et al., 2007; Shpansky, 2018b]. This is the first co-occurrence of *Elasmotherium* and woolly rhino (*Coelodonta antiquitatis*).

A skeleton fragment found on the Burluk River near the village of Kirillovka in 2016 is an important finding of *Elasmotherium* (North-Kazakhstan Province) [Shpansky et al., 2017]. The upper tooth of *Stephanorhinus kirchbergensis* was found together with the *Elasmotherium* skeleton. The co-occurrence of these rhino species is noted for the first time. The geological age of the remains is between Early and Middle Neopleistocene.

The genus *Stephanorhinus* Kretzoi within the West Siberian Plain has been intensively studied only in the last few years [Shpansky, Billia, 2012]. The genus is represented in the territory of the West Siberian Plain by two species – *S. etruscus* Falconer and *S. kirchbergensis* Jäger. The most ancient remains of *S. etruscus* come from sediments of the Irtysh formation in Lebyazhye 2 and Moiseyevka 1 (Fig. 2) [Shpansky, Ilyina, 2020].

About 20 record localities of *S. kirchbergensis* were identified in the territory of the West Siberian Plain, including several lower jaws with teeth [Shpansky, 2016, 2017; Lobachev et al., 2021]. The geological age of the localities within the West Siberian Plain is from the second half of the Early Neopleistocene to the Karginy horizon of the Late Neopleistocene (see Fig. 2). The most ancient finding is a lower jaw recovered from sediments of the upper sub-formation of the Zhunshilik formation (the second half of the Early Neopleistocene) in the northeast of the Turgay trough (Akmolinsk Province). More ancient localities (the first half of the Early Neopleistocene) are found in the south of Kazakhstan – Koshkurgan and Kapchagay. Most findings of *S. kirchbergensis* in Western Siberia and in Eurasia in general come from the Middle Neopleistocene [Shpansky, 2017]. Within the West Siberian Plain, the most recent finding is the lower jaw from alluvium near the village of Pobeda on the Chumysh River (Altai Krai). The radiocarbon age of the finding is 43.3–44.4 ka cal BP [Kirillova et al., 2021].

Only the remains of *C. antiquitatis* Blumenbach that existed during the Middle–Late Neopleistocene are found for the genus *Coelodonta* Bronn within the West Siberian Plain (Fig. 2). Findings of *C. cf. tologojensis* Bel., defined by I.V. Foronova [2001] in the upper part of the Sergey formation (the beginning of the Early Neopleistocene) in the Bachatsky and Mokhovo quarries of Kuzbass are doubtful since the author has not specified the data and not provided a description. The older species *C. thibetana* Deng et al. was not found within the West

Siberian Plain. From the Kurtak locality (left bank of the Yenisei River), metatarsale III and IV, closest to the Chinese *C. nihowanensis* Kahlke of Eopleistocene age, have been described [Klementiev, Laptinok, 2021]. The most ancient findings of *C. antiquitatis* are obtained from the sediments of the Tobolsk horizon in Grigoryevka (Pavlodar Province) on the Irtysh River. According to B.S. Rusanov [1968], the subspecies identified as *C. antiquitatis pristinus* Russ., *C. a. jacuticus* Russanov and *C. a. humilis* Russ. lived in the Early, Middle, and Late Neopleistocene, respectively. Later, P.A. Lazarev [2008] identified *C. jacuticus* as an independent species from the Middle Neopleistocene. Revision of these taxa allowed reducing them to junior synonyms of the nominative species *C. antiquitatis* [Shpansky, Boeskorov, 2018].

### Equidae (Equinae)

Horses of the genus *Equus* first appear in the sediments of the Aksorskaya formation (end of the Upper Pliocene) in the territory of the West Siberian Plain. The limb bones of the archaic horse *Equus (Allohippus)* sp. were found in Lebyazhye 1 [Vislobokova, 1996]. The remains of two horse forms were found in the sediments of the Irtysh formation (Podpusk 1, 2, Lebyazhye 2) – large *Equus livenzovensis* Bajgusheva and small *Equus* sp. 1 (Fig. 3). Numerous teeth and remains of a postcranial skeleton are referred to *E. livenzovensis* [Vislobokova, 1996]. Earlier, L.A. Makarova [1955] and I.A. Vislobokova [1973] referred these remains to *E. cf. stenonis* Cocchi. Other researchers have referred this horse to *Equus ex gr. robustus* Pomel [Vangengeim, Zazhigin, 1965] or *Allohippus robustus* [Kozhamkulova, 1969, 1981]. I.A. Vislobokova [1973] obtained the remains of a large horse, close to the Sussenborn horse *E. cf. sussenbornensis* Wüst, from the upper part of the Irtysh formation in Podpusk 1 and 2. More recent findings of this horse are reported from the sediments of the Sergey formation (Upper Eopleistocene) in Kuzbass [Foronova, 2001]. Distal limb bones of the small horse *Equus* sp. 2 were found together with *E. cf. sussenbornensis* in Podpusk. According to I.A. Vislobokova [1973, p. 124], they may belong to the “early form of the *Asinus* subgenus”. Reliable remains of horses are not found for the first half of the Eopleistocene in the territory of the West Siberian Plain. I.V. Foronova [1990] identified a new species *Equus singularis* for Kuzbass from sediments of the Mokhovo formation. Findings of the phalanges of a large “broad-toed” horse, identified by V.E. Ryasina [1962] as *E. ex gr. robustus*, were obtained for the end of the Eopleistocene from the upper part of the Erestnaya formation of the Pre-Altai Plain (Vyatkin, Belovo). Later, I.A. Vislobokova [1973] identified it as *Equus* sp. 3 suggesting that these remains could belong to a new species.

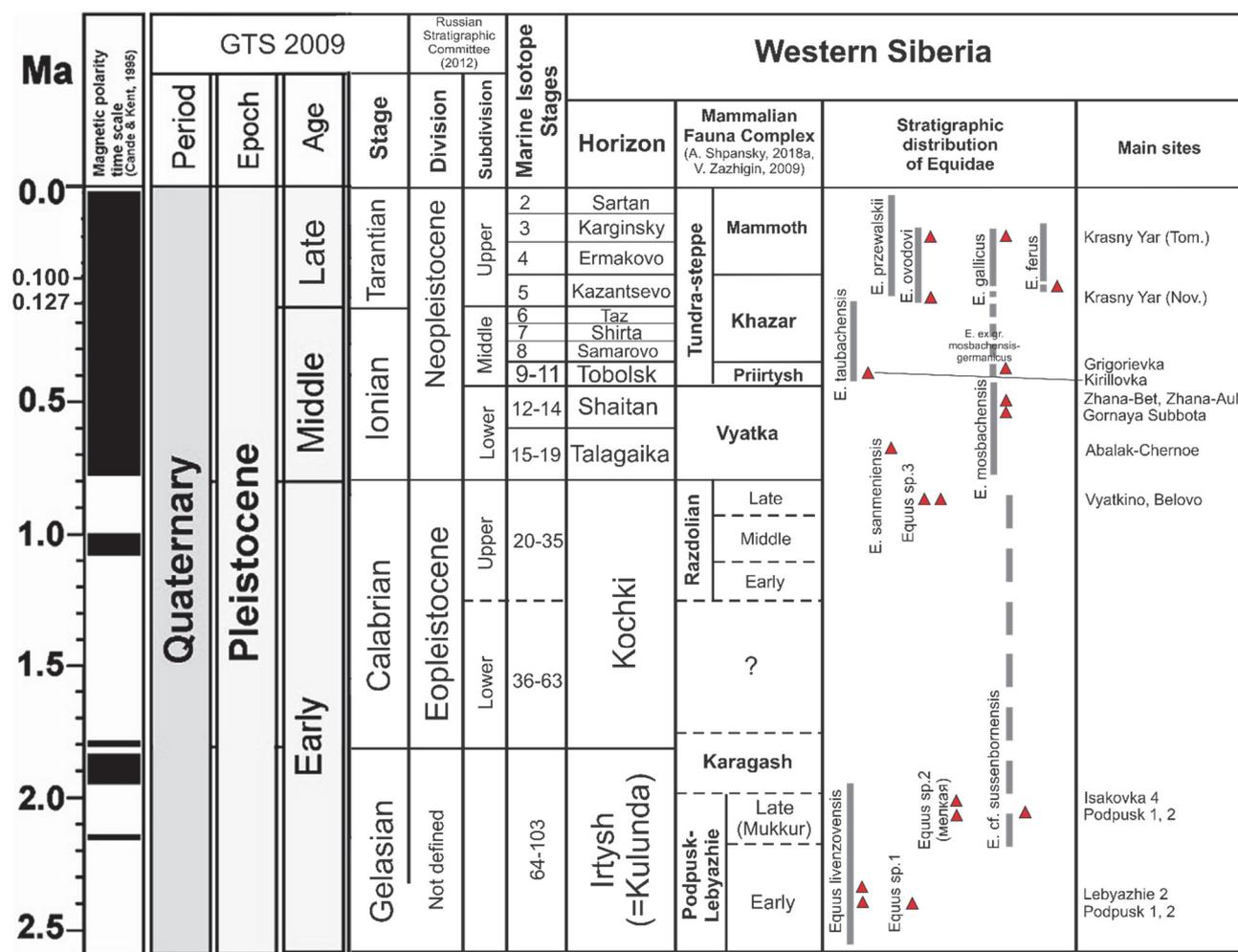


Fig. 3. Scheme of stratigraphic distribution of representatives of the family Equidae

Рис. 3. Схема стратиграфического распространения представителей семейства Equidae

The Early Neopleistocene is characterized by the findings of *Equus ex gr. mosbachensis* Reich. Its most northern findings were reported from near Tobolsk [Kaplyanskaya, Tarnogradskiy, 1974] and the village of Gornaya Subbota [Kozhamkulova, 1981]. In the south of the West Siberian Plain, its remains are found on the Irtys River near the village of Zhana-Bet [Kozhamkulova, 1981] and in Kuzbass [Foronova, 2001]. In the lower reaches of the Irtys River, A.N. Motuzko [1975] found the remains of *Equus ex gr. sanmeniensis* Teilh. et Piv. in the sediments of Tobolsk sands exposed between the villages of Abalak and Chernoe. The existence time of this horse is estimated as Late Eopleistocene and Early Neopleistocene [Vangengeim, 1977].

The horse remains of the Middle–Late Neopleistocene in multi-species localities of Western Siberia make up 19–40 % of the total number of mammalian remains and together with bison are the most widespread [Kosintsev, Vasiliev, 2009; Shpansky et al., 2016b; Shpansky, 2018a]. Several horse species are proposed by different

authors for the Middle–Late Neopleistocene. B.S. Kozhamkulova [1981] includes all large horses of Kazakhstan and the south of Western Siberia in one group of caballoid horses *E. caballus* subsp. explaining this by the lack of series data from different localities. She divides the horses of the Late Neopleistocene into *E. gmelini* Antonius, *E. przewalskii* Poljakow and distinguishes separately the kulans and donkeys *E. hemionus* Pallas, *E. (Asinus) hydruntinus* Regalia. According to the majority of researchers, two horse morphotypes (small and large) lived at the same time within the West Siberian Plain in the Late Neopleistocene. Earlier, small horses from the territory of Western Siberia were classified as *E. hydruntinus* or *E. hemionus* [Kozhamkulova, 1981; Foronova, 1990]. Currently, all small horses that lived in the late Pleistocene in the territory of the south-east of the West Siberian Plain belong to two species – *Equus (Sussemionus) ovodovi* Eisenmann et Vasiliev and *Equus hemionus* Pallas [Plasteeva et al., 2019]. There is no consensus on the species of large horses in Western Siberia.

Some researchers unite them with the Gallic horse of Europe, *E. ex gr. gallicus* Prat. [Fononova, 1990; Shpansky, 1999]. I.E. Kuzmina [1997] suggests the occurrence of the broad-toed horse *E. latipes* Grom in the south of Western Siberia. N.A. Plasteveva notes the distribution of the wild horse (tarpan) *E. ferus* Boddaert. She also notes the succession of Pleistocene and Holocene horses [Kosintsev et al., 2013]. It is assumed that the more ancient horses *E. ex gr. mosbachensis-germanicus* and *E. aff. taubachensis* [Fononova, 1990] are ancestral forms of *E. ex gr. gallicus* and *E. przewalskii* for the Kuznetsk Basin at the beginning of the Late Neopleistocene. The mass presence of very large remains (according to metapodials and ungulate phalanges), corresponding to *E. ex gr. mosbachensis-germanicus* and even *E. mosbachensis* in their morphometric parameters in

Krasny Yar (Tomsk Province) together with the remains typical for *E. gallicus* (with the same preservation) [Shpansky, 1999], raises doubts about the methodological basis for the allocation of these taxa and rather suggests a large intraspecific variability in the size of horse bones.

It can be noted that two morphotypes of horses occurred during the entire Pleistocene in the territory of the West Siberian Plain – a large caballoid type and a small donkey-kulan type.

### Bovinae

Bovids were highly diverse in faunas of the Quaternary period, and within the West Siberian Plain were represented by three subfamilies: Antilopinae, Caprinae, and Bovinae (Fig. 4).

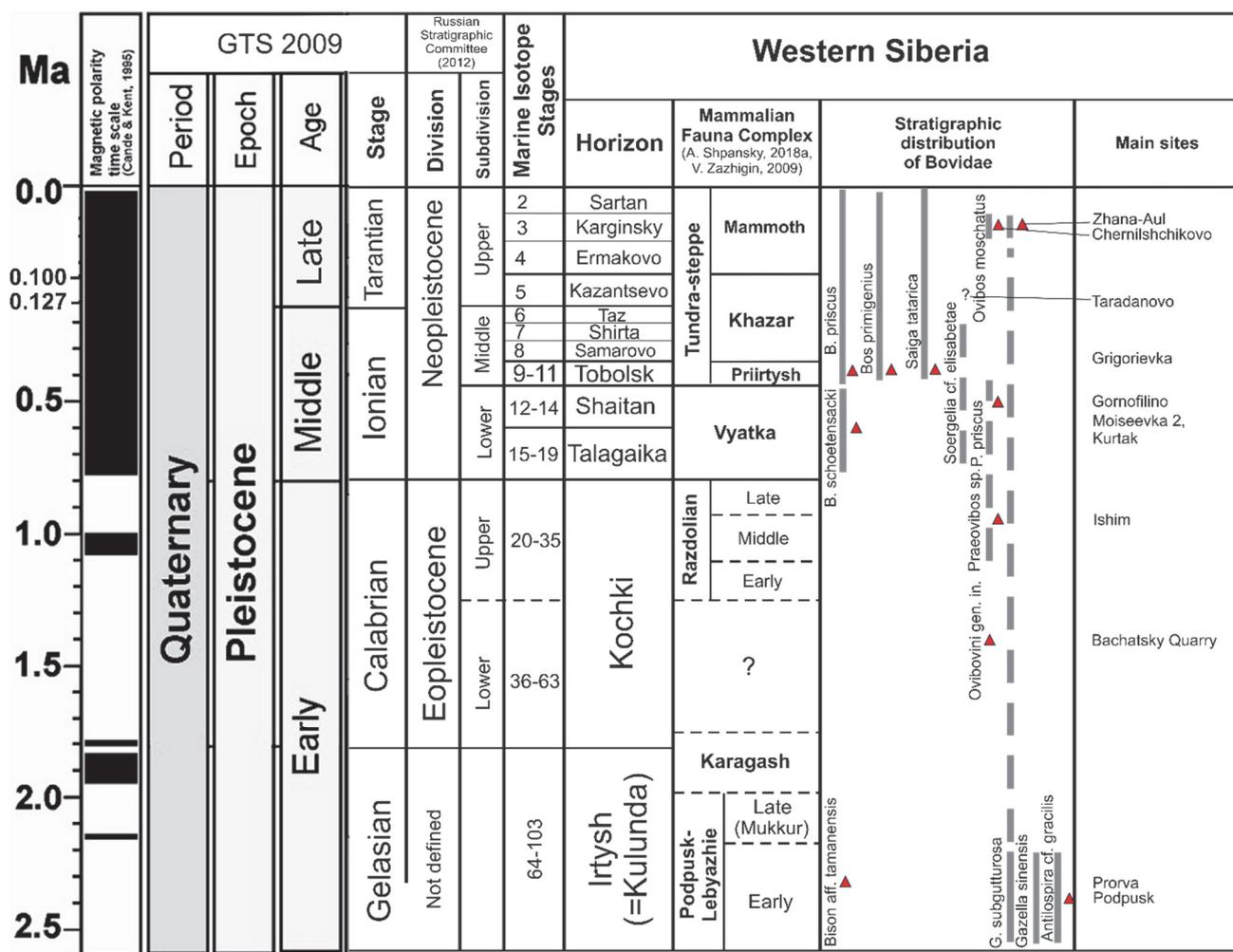


Fig. 4. Scheme of stratigraphic distribution of representatives of the family Bovidae  
 Рис. 4. Схема стратиграфического распространения представителей семейства Bovidae

Two horn cores of the most ancient spiral horned antelope are described by R.K. Kambartdinov [1969] from the sediments of the Irtysh formation in Podpusk. According to B.S. Kozhamkulova [1981], they are close to *Antilospira cf. gracilis* Teil. de Chard. et Young. I.A. Vislobokova [1973, 2008] refers the remains to *Antilospira* sp.

Gazelles of the genus *Gazella* Blanville are represented by the Chinese gazelle (*G. sinensis* Teil. de Chardin et Piveteau) and the black-tailed gazelle (*G. subgutturosa* Güld.). Both species are found in Pavlodar Priirtysh: from the sediments of the Irtysh formation near Podpusk (complete skeleton of *G. sinensis* [Motuzko, 1971]) and 4 km

to the north-east from Podpusk (*G. subgutturosa* [Kozhamkulova, 1969, 1981]). The remains of jeyran are found from the Upper Neopleistocene sediments – 40 km to the north-west from Arkalyk (Kustanay Province) and near the village of Zhana-Aul (Pavlodar Province) [Kozhamkulova, 1969, 1981].

The subfamily of caprines (Caprinae Gill) is represented by two tribes: goats (Caprini Simpson) and musk oxen (Ovibovini Simpson). There are no reliable findings of the remains of representatives of the genus *Capra* L. in the territory of the West Siberian Plain, although *Capra sibirica* Pallas is quite common in Paleolithic cave complexes of the Altai Mountains [Agadjanian, Shunkov, 2018]. The situation is similar with the remains of argali *Ovis ammon* L., but B.S. Kozhamkulova [1969] notes the findings of postcranial bones in Pavlodar Priirtysh in Upper(?) Neopleistocene sediments. These findings require confirmation. The genus *Saiga* Gray is represented by a single species *S. tatarica* L. The most ancient remains of saiga were obtained by the author from Grigoryevka (Tobolsk horizon) on the Irtysh River (Pavlodar Province) [Shpansky et al., 2007]. Extensive comparative and morphological studies of saiga skulls of different geological ages have shown that during the Middle–Late Neopleistocene the modern type species *S. tatarica* existed [Ratajczak et al., 2016]. Previously, it was believed that the fossil remains of saiga belonged to a separate species – *S. borealis* Tschersky. The subspecies of saiga *S. ricea krasnojariika* Shpansky, previously identified by the author based on a skull from Krasny Yar (Tomsk Province) [Shpansky, 1998], was referred to *S. tatarica* in the result of detailed morphological analysis and thorough comparison [Ratajczak et al., 2016]. In addition, the cranial remains from Krasny Yar, as well as the remains of the saiga from the Middle Neopleistocene (Grigoryevka), somewhat differ from the typical *S. tatarica*. It can be suggested that these differences may exist on subspecific level [Ratajczak et al., 2016].

One of the earliest findings of musk ox remains in the territory of the West Siberian Plain is an incomplete skull of *Praeovibos* sp. obtained by R.A. Zinova [1972] above the mouth of the Ishim River and referred to the Late Eopleistocene. An even earlier finding may be an upper jaw fragment of Ovibovini gen. indet., recovered from the Bachatsky quarry from sediments of the Mokhovo formation (Kuzbass) [Fonova, 2001; Vislobokova, 2008], comparable with the first half of the Eopleistocene. N.E. Bobkovskaya [2002] mentions the discovery of two fragments of *P. priscus* skulls from the Lower Neopleistocene sediments in Gornofilino. The remains of *Ovibos moschatus* Zimm are found in sediments of the second half of the Upper Neopleistocene. Earlier, it was suggested that the fossil remains of musk oxen belonged to an independent species – *O. pallantis* H. Smith, but a comparative analysis of morphometric parameters of the

skulls showed a high degree of similarity between the fossils and the modern musk oxen [Stefaniak et al., 2021]. The southernmost dispersal of the musk ox in the West Siberian Plain is observed at the end of the Karginsky Interglacial (up to 56° N) and especially during the Sartan period (up to 54° N) [Malikov et al., 2020].

The genus *Soergelia* Schaub is represented by rare findings of *S. cf. elisabetae* Schaub in sediments of the second half of the Eopleistocene and Lower Neopleistocene [Kozhamkulova, 1981; Vislobokova, 2008]. The remains of *Soergelia* are not found in the Middle Neopleistocene sediments. Nevertheless, its remains are again present in Novosibirsk Priobye – the alluvial locality of the Upper Neopleistocene [Vasiliev, 2010, 2011]. More than 50 specimens were found in Taradanovo. According to S.K. Vasiliev [2010, 2011], the radiocarbon date obtained by the AMS method (more than 41,060 ka BP, AA-79331) on the skull of *Soergelia* from Taradanovo is exorbitant.

The subfamily Bovinae Gill within the West Siberian Plain is represented by the tribe Bovini Simpson and two genera – *Bison* and *Bos*. Representatives of the genus *Bison* H. Smith appear in the territory of the West Siberian Plain from the Paleopleistocene. A horn core from the sediments of the Irtysh formation in Prorva (Pavlodar Province) was identified as *B. (Eobison) aff. tamanensis* N.Ver. [Kozhamkulova, 1981]. Bison of the subgenus *Bison* have appeared since the Early Neopleistocene. The earliest findings of *B. (Bison) cf. schoetensacki* Freud. are obtained near Moiseevka and Krasnokutsk on the Irtysh River (Pavlodar Province) [Kozhamkulova, 1981] and near the village of Maly Atmas (Omsk Province) [Motuzko, 1971]. The author found the horn core in the dense sand and pebble sediments in Berezhkovo (Kurtak) on the Yenisei River (Krasnoyarsk Krai) [Shpansky et al., 2020]. Earlier finds of *B. schoetensacki* were recorded in the Nazarov Depression [Puminov, Buzulutskov, 1968]. *B. priscus* Boj has become ubiquitous since the Middle Neopleistocene. The share of its remains in multi-species localities reaches 20–42% [Shpansky et al., 2016b]. The extinction time of bison is close to the extinction time of mammoths and woolly rhinos (*Coelodonta antiquitatis*). The youngest dates for bison were obtained from the Koksa River (12,090±120 ka BP, GrA 6615), the Alei River (12,300±450 ka BP, GrA 8087), and the Orda River (9,320±95 ka BP, GrA 4568) [Vasiliev et al., 2007; Rusanov et al., 2010]. The genus *Bos* L. in Western Siberia is represented by *B. primigenius* Boj. Its oldest remains are found in Grigoryevka (Pavlodar Province) [Shpansky, 2009]. A complete skull was found near the village of Kachira on the Irtysh River (Pavlodar Province). Single Late Neopleistocene remains of bovids are found throughout the southern part of the West Siberian Plain (Pavlodar, Kokchetav, and Akmola Province). However, there are no radiocarbon dated bovid remains from

these localities yet. In addition, a bovid skeleton was found in Tuva having an Early Holocene age (9,860±160 ka BP, SB RAS -6336) [Lavrov, Zabelin, 2007].

### Cervidae

Pleistocene deer in the territory of the West Siberian Plain are represented by three subfamilies: Cervinae, Odocoileinae, and Alcinae. The true deer of the Cervini tribe are represented by the extinct genus *Eucladoceros* Falc. and the modern genus *Cervus* L. The only finding of an antlered deer is *Eucladoceros* sp. described by I.A. Vislobokova in Podpusk 1 [Vislobokova, 1996]. B.S. Kozhamkulova [1969] notes the most ancient remains of *Cervus elaphus* in Early Neopleistocene sediments near the village of Lebyazhye (Fig. 5). The Middle Neopleistocene sediments helped to find the remains of *C. elaphus* from Pyatiryzhsk, Moiseyevka and other numerous remains, including skulls and a skeleton fragment from Grigoryevka [Shpansky et al., 2007]. *C. elaphus* is widely distributed and occurs quite often in the Late Neopleistocene. The share of its remains in multi-species localities is from 2 to 5% [Shpansky, 2018a]. Phylogenetic and biogeographic studies have shown that during the Late Pleistocene, the same haplotype of *Cervus elaphus* existed in the territory of the West Siberian Plain [Doan et al., 2022].

Giant deer of the genus *Megaloceros* Brookes are represented by the species *M. giganteus* (Blum.) (Fig. 5). V.V. Shcheglova [1950, 1958] made an attempt to divide giant deer into two subspecies of different age – *Megaloceros giganteus ruffi* (Nehr.) for the Middle Neopleistocene and *M. giganteus giganteus* (Blum.) for the Late Neopleistocene, which was confirmed by data from the south-east of the West Siberian Plain [Shpansky, 2011]. An almost complete skeleton of *M. giganteus giganteus* is found in Dzhambul (Pavlodar Province) [Shpansky, 2014]. Its radiocarbon dating is 43,600±550 ka BP (OxA-20250). The last giant deer in the south of Western Siberia were preserved in the first half of the Holocene. They are found in localities of the Novosibirsk Province – Preobrazhenka 6 (7,865±40 ka BP, GrA-56935) and Sopka 2 (7,925±40 ka BP, GrA-56934) [Plicht et al., 2015]. Several Holocene dates were obtained from Priangarye (from 8,890 to 10,320 radiocarbon years) and the Chernigovskiy quarry in Kemerovo Province (10,055±45 ka BP, OxA-13026). The youngest findings of the giant deer today are an incomplete skeleton from Kamyshlov (Sverdlovsk Province [Shpansky, 2014]), its radiocarbon age is 6,816±35 ka BP (KIA-5669), and a skull from Redut on the Miass River (6,968±33 ka BP, KIA-5668) [Soubrier et al., 2016]. Such young dates indicate the preservation of a refugium in southern Siberia with favorable conditions for *M. giganteus* [Plicht et al., 2015; Shpansky, 2021a].

Quaternary roe deer (Odocoileinae: Capreolini) are represented by a single genus *Capreolus* Gray. The most ancient remains of *Capreolus* sp. were found by I.A. Vislobokova [1973] in the upper part of the Irtysh formation in Podpusk 2 [1996]. *C. capreolus* L. is represented by singular findings in the Upper Neopleistocene sediments in the south-east of Western Siberia (Pre-Altai Plain) and in Kazakhstan. More numerous remains have been found in cave complexes of the Altai Mountains and are associated with the activity of the Paleolithic man [Agadjanian, Shunkov, 2018].

The most ancient finding of the reindeer *Rangifer* sp. is a skull fragment from the sediments of the Mukur formation (the second half of the Paleopleistocene) in Isakovka 4, Omsk Province [Bondarev et al., 2017] (Fig. 5). I.V. Foronova [2001] notes the finding of a reindeer in the Mokhovo quarry at the base of the Kedrovskaya formation (Lower Neopleistocene) in Kuzbass. The remains of *Rangifer tarandus* L. occur quite regularly from the end of the Middle Neopleistocene.

The history of Alcinae in Eurasia, at present, is well studied by P.A. Nikolsky [2010]. The remains of moose in the territory of the West Siberian Plain are represented by two genera – *Cervalces* Scott and *Alces* Gray. The most ancient broad-fronted moose are *Cervalces* sp. found in the upper part of the Irtysh formation near Podpusk [Vislobokova, 1973, 1996, 2008] and *Alces* sp. from the sediments of the Mokhovo formation (Lower Eopleistocene) in the Bachatsky quarry (Kemerovo Province) [Foronova, 2001]. The remains of *Cervalces latifrons* Johnson are rare. I.V. Foronova [2001] notes the remains from the Sagarlyk formation of the Upper Eopleistocene. A.N. Motuzko [1970b] describes a horn fragment found in Early Neopleistocene sediments near the village of Skorodum (Omsk Province). N.E. Bobkovskaya [2002] found a lower jaw in Gornaya Subbota; a skull fragment without antlers was found in the sediments of the Tobolsk horizon at the base of Krivosheinsky Yar and Krasny Yar (Tomsk Province) and is considered to be the youngest finding [Shpansky, 2005a]. According to P.A. Nikolsky [2010], the broad-fronted moose of the Early–Middle Neopleistocene is represented by three species, successively replacing each other – *Cervalces (Latifrons) amplicontus* (between the Eopleistocene and Neopleistocene), *C. (Latifrons) alaskensis* (Early Neopleistocene), and *C. (Latifrons) latifrons* (the beginning of the Middle Neopleistocene). The rare occurrence of remains of the broad-fronted moose, at present, does not allow giving an accurate taxonomic assessment of the available data from Western Siberia. The moose *Alces alces* L. spread from the second half of the Middle Neopleistocene. Their remains reach the greatest number during the Karginian Interglacial and Holocene.

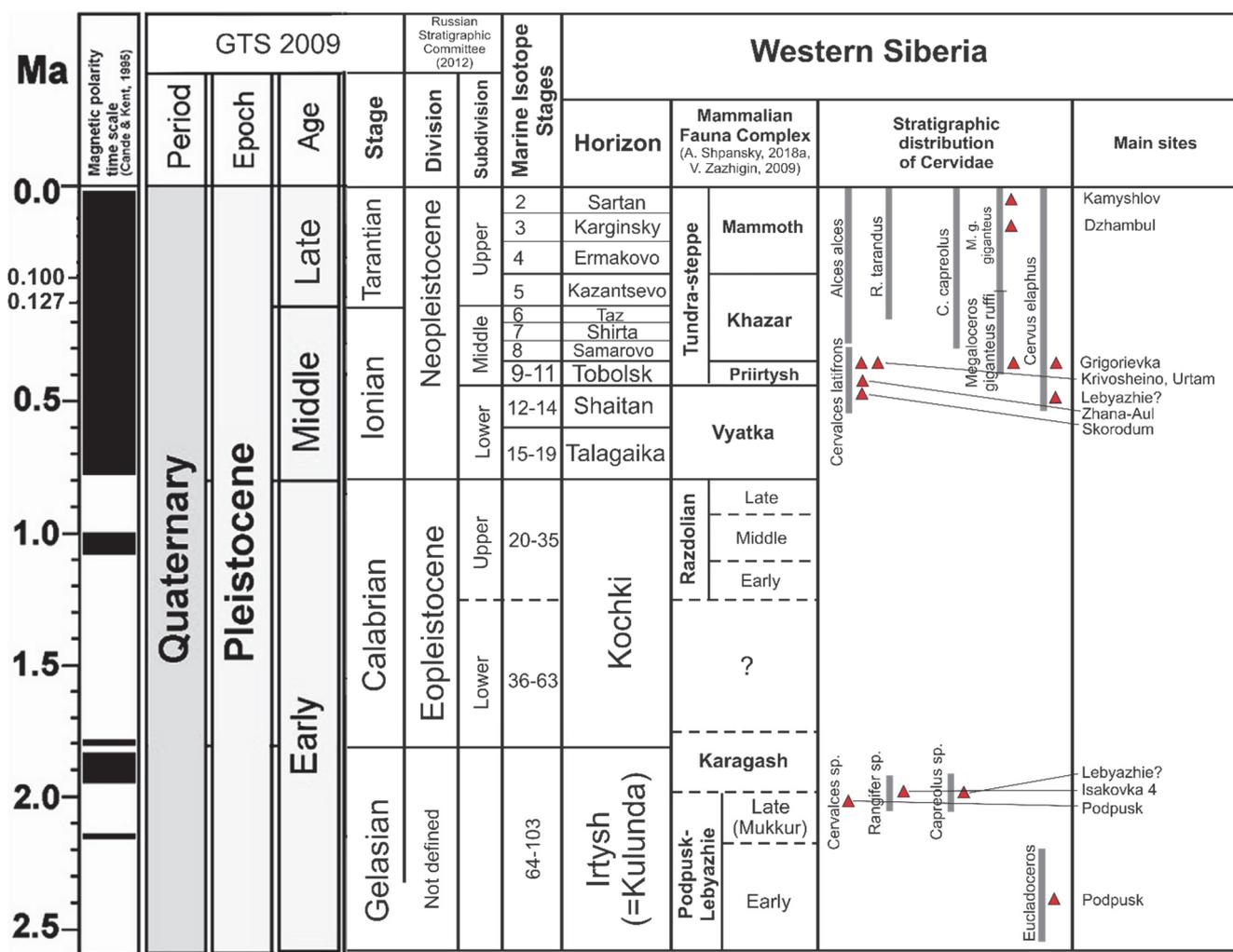


Fig. 5. Scheme of stratigraphic distribution of representatives of the family Cervidae

Рис. 5. Схема стратиграфического распространения представителей семейства Cervidae

### Camelidae

The West Siberian Plain was inhabited by representatives of two genera of camels during the Quaternary period – *Paracamelus* Schlosser and *Camelus* L. (Fig. 6). The first genus is represented by the species *P. gigas* Schlosser, the second one by the species *C. knoblochi* Poljakov.

The findings of the older camel *P. praebactrianus* (Orlov) are reported from Upper Pliocene sediments (Bitekeysky horizon) in Northern Kazakhstan within the Iliysky faunal complex (MN 16) [Kozhamkulova, 1981].

The remains of *P. gigas* are found in gelasium sediments in Podpusk [Kambaritdinov, 1969]. The youngest remains of *P. gigas* come from the sediments of the Karaul formation of the Lower Neopleistocene near the village of Zhana-Aul (Pavlodar Province). Here its remains are found together with other species of the Koshkurgan (=Vyatka for the West Siberian Plain) faunal complex: *E. (Palaeoloxodon) antiquus*, *Equus mosbachensis*, *Elasmotherium sibiricum*, *Cervales*

*latifrons*, *Gazella* sp., and *Praeovibos* sp. [Kambaritdinov, 1969]. One camel bone was found in the blue-gray clays exposed on Lake Maraldy. The accompanying Khazar fauna allows suggesting that this bone was re-sedimented in the second half of the Middle Pleistocene or belongs to the late camel *Camelus knoblochi*.

The most ancient remains of *Camelus knoblochi* come from Grigoryevka (Pavlodar Province) where a forelimb fragment was found together with the remains of representatives of the Irtysk faunal complex: *Elasmotherium sibiricum*, *Mammuthus trogontherii chosaricus*, *Bison priscus*, *Saiga tatarica*, *Megaloceros giganteus ruffi*, etc. [Shpansky et al., 2007; Shpansky, 2018b]. According to B.S. Kozhamkulova [1969, 1981], the Knobloch camel continued to exist in the Late Neopleistocene within the south-western Altai (East Kazakhstan Province). This conclusion is based on the co-occurrence of remains of the camel with the woolly rhino (*Coelodonta antiquitatis*) and a “late type of mammoth” within Zyryanovsk and

near the mouth of the Bukhtarma River. The presence of the camel in the Late Neopleistocene fauna of the Pre-Altai Plain is not excluded. Single finds of the camel, presumably of Late Neopleistocene age, were reported from

near Zarinsk on the Chumysh River [Vasiliev, 2016] and on the Ob River 60 km to the south from Barnaul [Buynovsky, Haveson, 1953], but the young geological age of these remains requires confirmation.

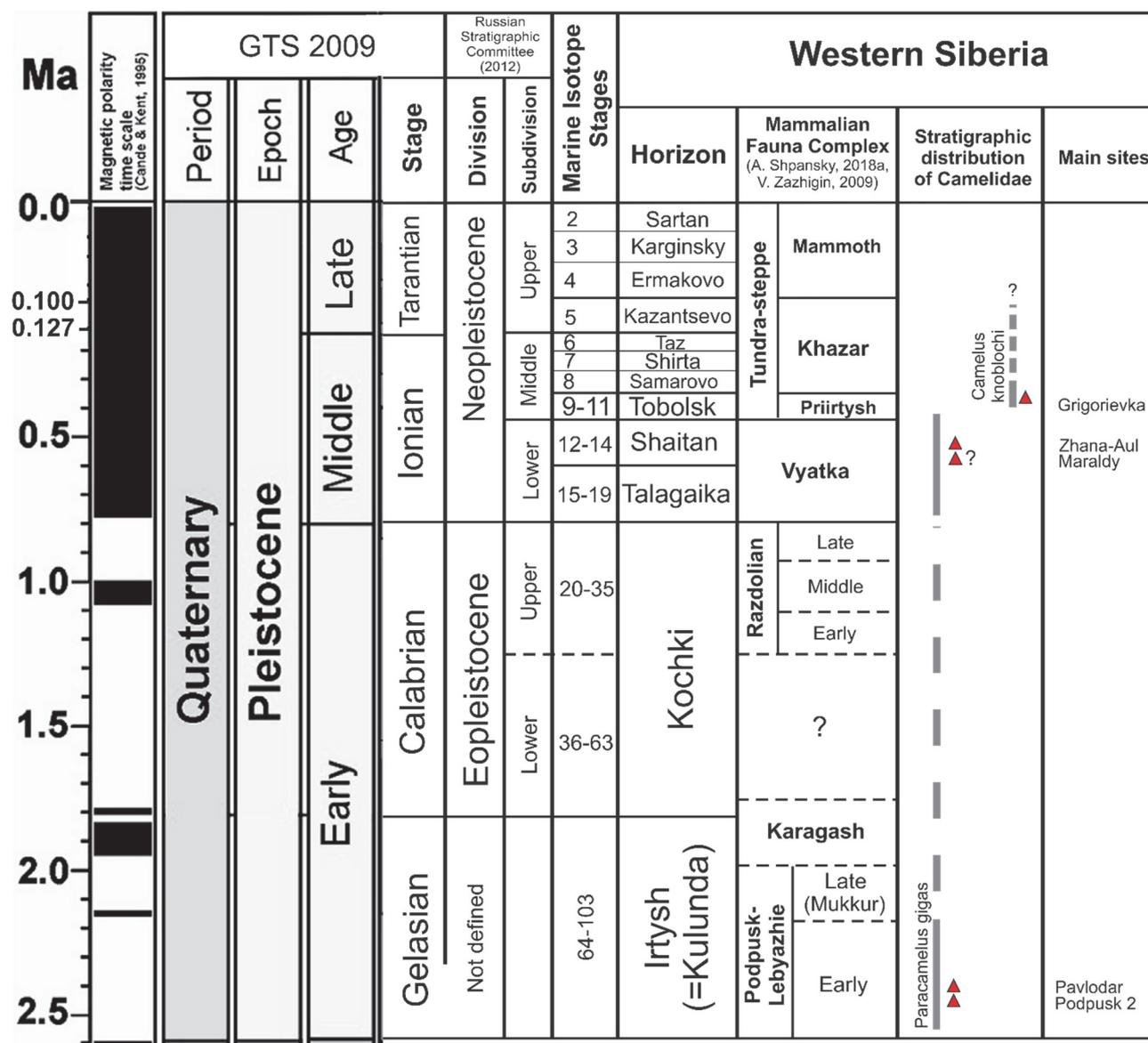


Fig. 6. Scheme of stratigraphic distribution of representatives of the family Camelidae

Рис. 6. Схема стратиграфического распространения представителей семейства Camelidae

### Carnivora

The remains of predatory mammals are of subordinate importance in the biostratigraphy of Quaternary sediments due to their rather rare occurrence. Nevertheless, single findings of representatives of the families Ursidae Fischer, Hyaenidae, Felidae Fischer, and Canidae Fischer are known from the sediments of the Irtysh formation in Podpusk 2 [Motuzko, 1971; Vislobokova, 1996]. Data on the remains of hyenas and lions from Early–Middle Pleistocene sediments show that at this period there was a change

in representatives of these groups. Among hyenas, the change occurred at subspecies level – *Crocota crocuta praspelaea* gives way to *C. c. spelaea*. Among lions, *Panthera fossilis* is replaced by *P. spelaea*. In addition, the appearance of bears *Ursus arctos* and *U. savini rossicus*, as well as the small wolf *Canis cf. lupus*, and the wolverine *Gulo gulo* is noted within the West Siberian Plain. The data emphasizes the significance of the boundary between the Early and Middle Neopleistocene and reflects a certain response of the fauna to landscape and climate changes.

There is a certain restructuring of the fauna. As indicated below, the author provides information on the main findings of carnivoran fossils divided by families.

**Ursidae**

A.N. Motuzko [1970a] notes the finding of an *Ursus* sp. bone from the sediments of the Irtysh formation near the village of Podpusk. A description of this finding has not been published yet. I.V. Foronova [2001] notes the finding of an *Ursus* sp. femur in the sediments of the Mokhovo formation in the Bachatsky quarry (Kuzbass). In the Neopleistocene in the territory of the West Siberian Plain, bears are represented by two species – small cave

(=steppe) *Ursus savini rossicus* Borissiak and brown *U. arctos* L. (Fig. 7), which existed together and are often found together in multi-species localities. The earliest remains of the small cave bear were found in the sediments of the Tobolsk horizon near the village of Kartashovo (Omsk Province) and Moiseyevka 2 (Pavlodar Province). For *U. arctos*, the earliest findings are the remains of very large specimens: the humerus PLHM (Pavlodar Local History Museum, Pavlodar, Republic of Kazakhstan) 9640 (identified by A. Marciszak, University of Wroclaw) from Urlyutyub (Pavlodar Province) and a skeleton from Anastasyevka (Shegarka River, Tomsk Province) [Baryshnikov, 2007].

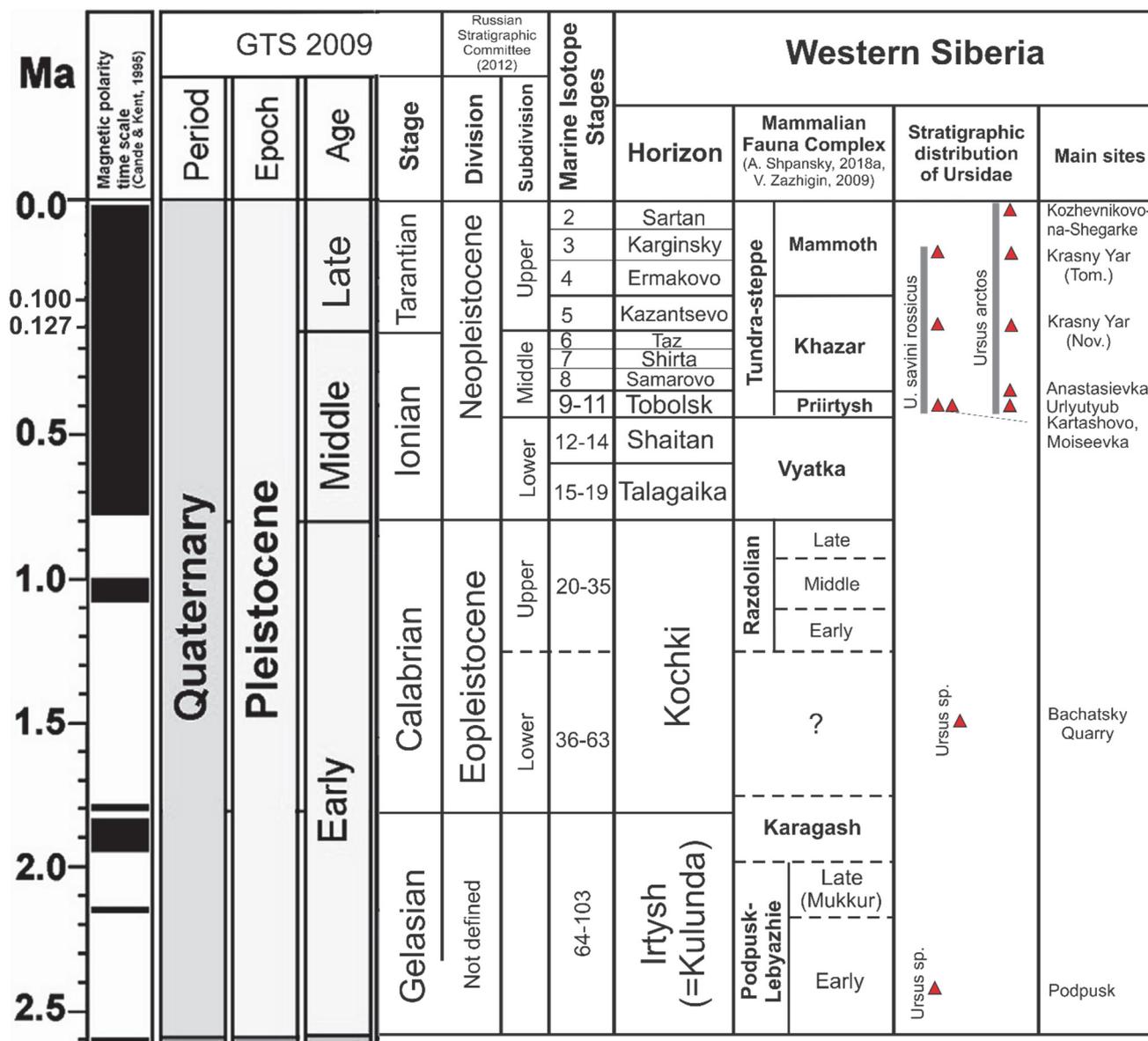


Fig. 7. Scheme of stratigraphic distribution of representatives of the family Ursidae

Рис. 7. Схема стратиграфического распространения представителей семейства Ursidae

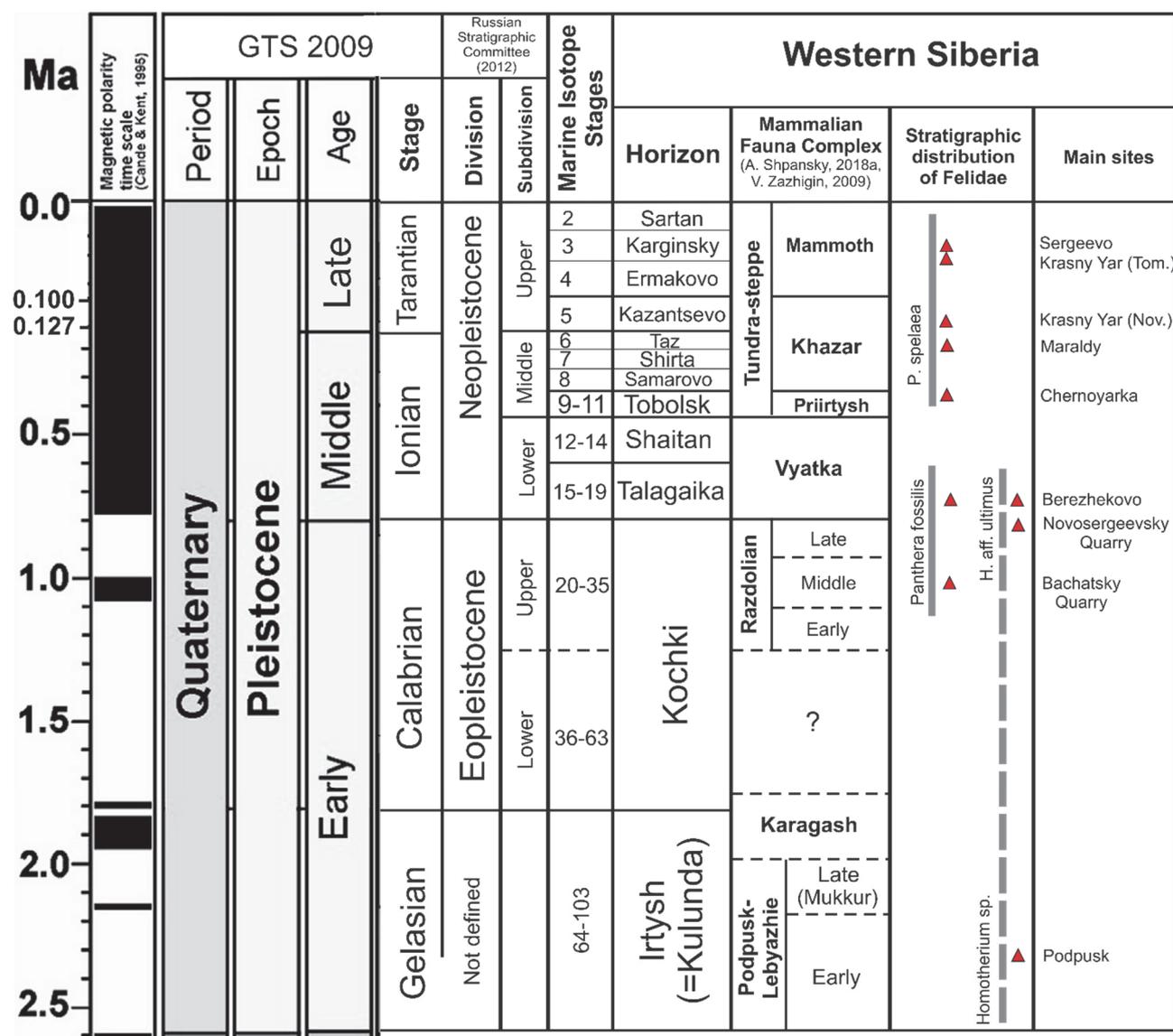


Fig. 8. Scheme of stratigraphic distribution of representatives of the family Felidae

Рис. 8. Схема стратиграфического распространения представителей семейства Felidae

The remains of *U. s. rossicus* from Kurtak on the Yenisei River belong to the second half of the Middle Neopleistocene [Malikov, 2018]. The number of remains of both bear species is close to each other in the multi-species localities of the Late Neopleistocene [Shpansky, Chernous, 2012a]. The extinction of the steppe bear *U. s. rossicus* probably occurred earlier than the ungulates of the mammoth fauna [Shpansky, 2021a].

### Felidae

Cats in the Quaternary sediments of the West Siberian Plain are represented by three subfamilies –Machairodontinae Gill, Felinae Fischer de Waldhem, and Pantherinae Pocock, and three genera – *Homotherium* Fabrini, *Panthera* Oken, and *Felis* L. (Fig. 8). I.A. Vislobokova notes the find-

ing of a late representative of the saber-toothed cats *Homotherium* sp. in the deposits of the Irtysh formation [Vislobokova, 1996]. I.V. Foronova [2001] described the lower jaw of *Homotherium* aff. *ultimus* Teilhard de Chardin from the sediments of the Sergeevskaya formation of the Novosergeevka quarry (Kemerovo Province). The geological age of this finding is estimated to be the end of Late Eopleistocene. Another finding of the lower jaw of *Homotherium* was noted at the site of Berezhekovo of the Kurtak archaeological district (left bank of the Yenisei River, Krasnoyarsk Krai) [Sotnikova, Foronova, 2009]. The age of this finding is estimated as Early Neopleistocene.

Large panthers appear from the end of the Eopleistocene and are represented by two species successively replacing each other. The lower jaws of the large *Panthera*

*(Leo) fossilis* (von Reichenau) are found in the Upper Eopleistocene sediments of the Bachatsky quarry (Kemerovo Province) [Foronova, 2001; Sotnikova, Foronova, 2014] and Early Neopleistocene sediments in the Kurtak archaeological district (Berezhkovo) [Ovodov, Tarasov, 2009]. Resedimented remains of a large panther are also found in Krasny Yar (Tomsk Province). *P. spelaea* Goldf is widely distributed from the Middle Neopleistocene. The earliest findings come from Chernoyarka and Maraldy (Pavlodar Province).

Studies of the last ten years have shown that the youngest 14C dates of *Panthera spelaea* for the territory of the West Siberian Plain are not evenly distributed. North of 54° S, the youngest dates originate from the localities of Sergeyevo (Tomsk Province) 34,280±737 BP

(UBA-38455; 38406-34724 calBP) [Shpansky, Svyatko, 2018; Shpansky, Kuzmin, 2021] and Krasny Yar (Novosibirsk Province) 25,143±825 BP (NSKA-s 559) [Vasiliev et al., 2018]. Several younger dates have been obtained from localities south of this latitude and within the mountainous area (Altai, Pre-Altai Plain, and Mountain Shoria). The youngest dates are marked by finds from the Chik River and south of Novosibirsk – 13,250±242 BP (BINP-NSU-1306) and 18,884±677 BP (NSKA-s 394), as well as from the Chumysh River [Vasiliev et al., 2018]. Thus, the time of extinction of the cave lion within Western Siberia can be assumed to have occurred from north to south [Aidos, 2022]. The final extinction in this area is comparable to the time of its extinction in Central and Eastern Europe, the Urals and Eastern Siberia.

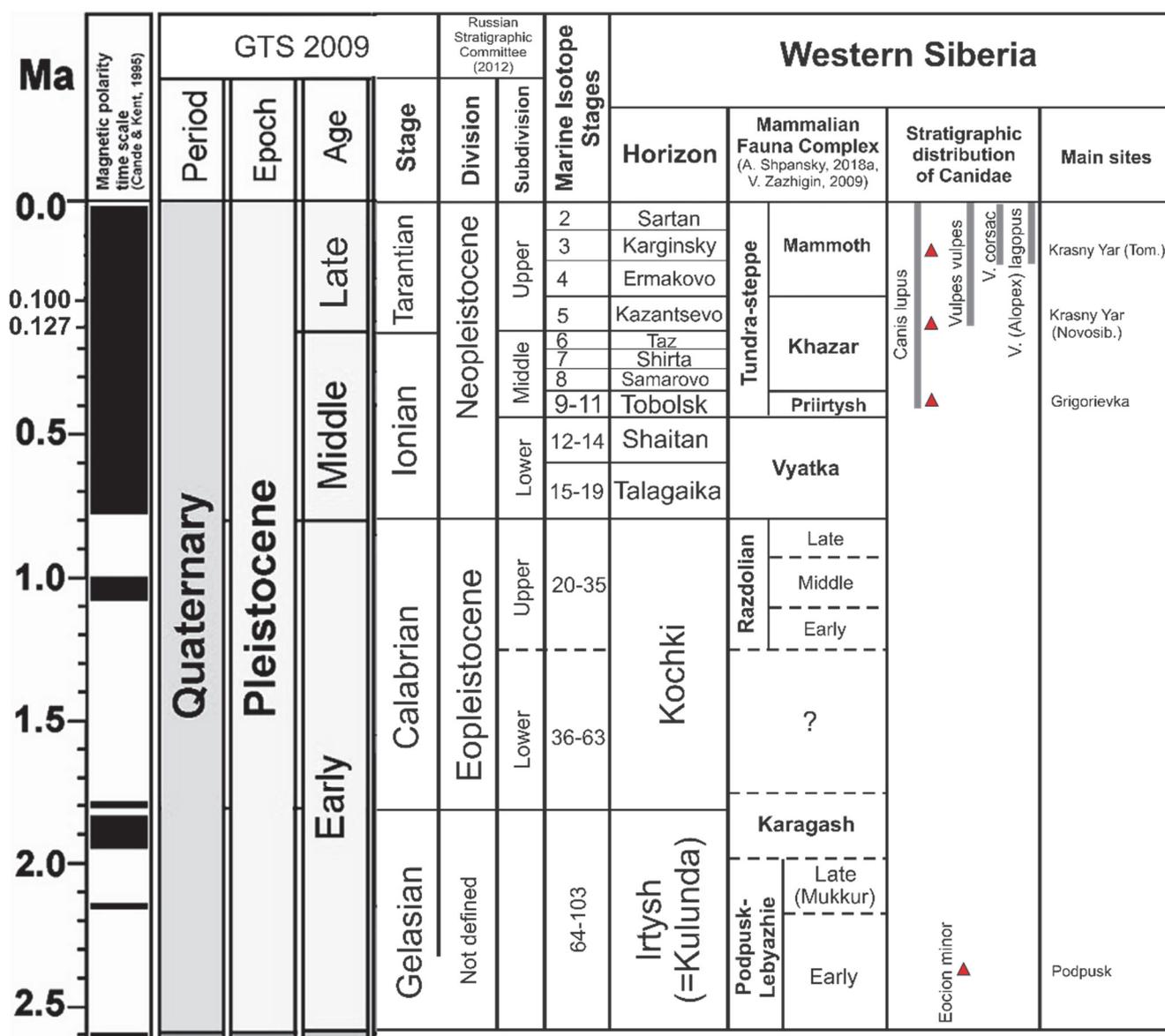


Fig. 9. Scheme of stratigraphic distribution of representatives of the family Canidae

Рис. 9. Схема стратиграфического распространения представителей семейства Canidae

**Canidae**

The most ancient find of a canidae representative in the territory of the West Siberian Plain is the lower jaw of *Eocion minor* (Teilhard et Piveteau) from the Podpusk 2 locality [Vislobokova, 1996; Sotnikova, Rook, 2010]. In later sediments, up to the Middle Neopleistocene, the remains of members of the Canidae family are not known (Fig. 9). The earliest discovery of the small wolf *Canis cf. lupus* L. was found in the Grigoryevka locality [Shpansky, 2018b]. Morphometrical parameters of the lower jaw and teeth showed that the Grigoryevka wolf occupies an intermediate position in the evolutionary line between the small wolf *C.*

*mosbachensis* of the Early Neopleistocene and the typical *C. lupus* of the Late Neopleistocene–Holocene. Small canids such as *Vulpes vulpes* L., *V. corsac* L., and *V. (Alopex) lagopus* L. appear only from the Late Neopleistocene [Kosintsev, Vasiliev, 2009; Shpansky, 2018a].

**Mustelidae**

Mustelidae in the Quaternary sediments of the West Siberian Plain are represented by three species – Schlosser’s wolverine *Gulo schlosseri* Kormos, the modern type wolverine *G. gulo* L., and the Asian badger *Meles leucurus* Hodgson (Fig. 10).

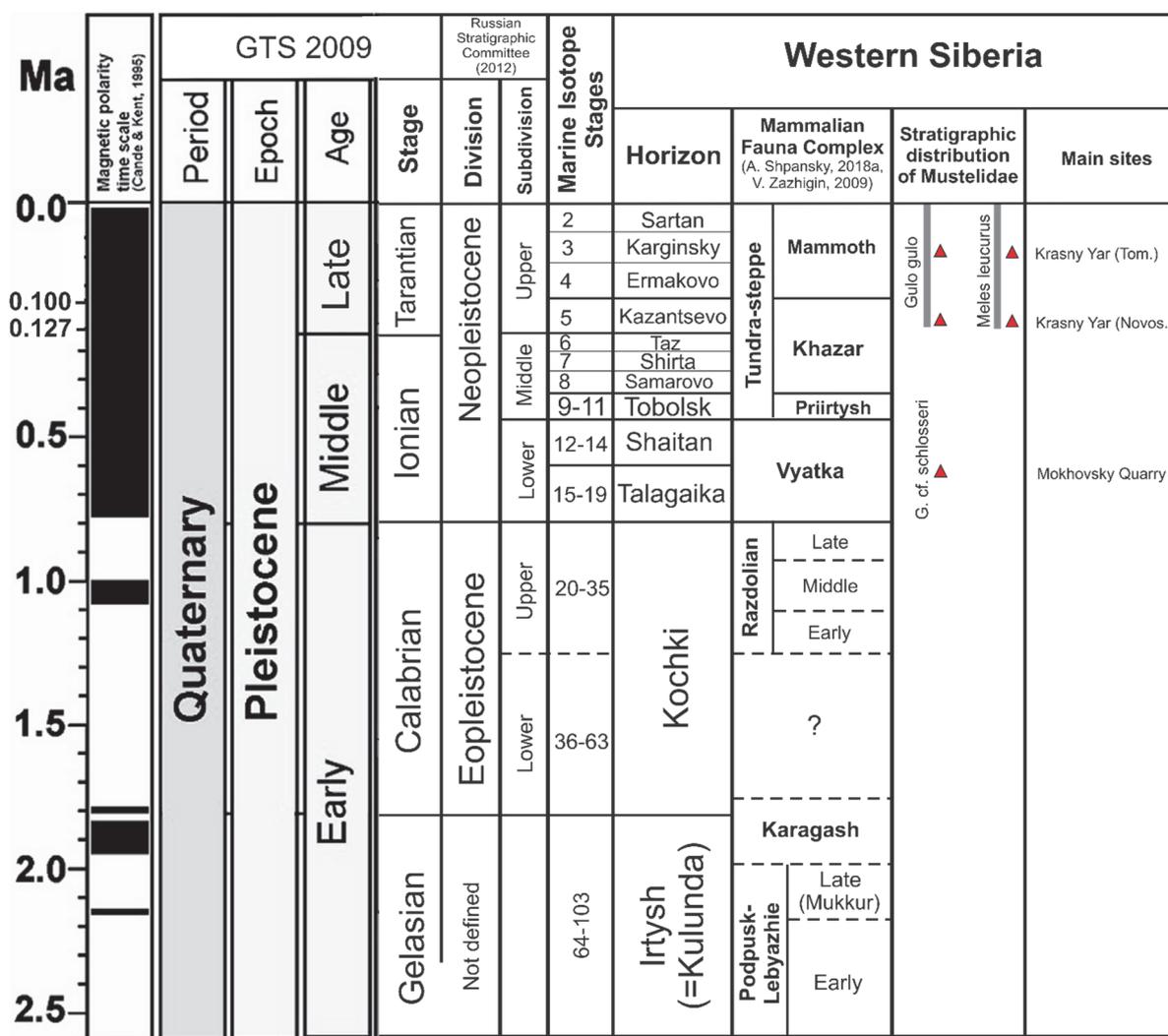


Fig. 10. Scheme of stratigraphic distribution of representatives of the family Mustelidae

Рис. 10. Схема стратиграфического распространения представителей семейства Mustelidae

The remains of these animals are very rare. A lower jaw of *G. cf. schlosseri* is reported by I.V. Foronova [2001] from the Kedrov Formation (Lower Neopleistocene) in the Mokhovskiy quarry of Kuzbass. A craniometric revision of badgers showed that the Asian badger *M. leucurus* currently lives in Western Siberia, rather than

the European *Meles meles* L. [Abramov, 2002; Gasilin, Kosintsev, 2012]. For this reason, it is most likely that the Asian badger was distributed in the territory of the West Siberian Plain in the Late Neopleistocene. Various representatives of the genera *Mustela* L. (ermine, weasel) and *Martes* L. (marten, sable) spread from the Holocene.

For the territory of the West Siberian Plain, the most ancient remains of *G. gulo* come from layer 6 of the Krasny Yar locality (Novosibirsk Province) and belong to the Kazantsevo Interglacial [Kosintsev, Vasiliev, 2009]. I.V. Foronova [2001] dates the lower jaw from the Mokhovskiy quarry to the second half of the Middle Neopleistocene. In multi-species localities of the Late Neopleistocene, the remains of wolverines are found as single specimens [Shpansky, 2018a].

### Hyenidae

The most ancient find of Quaternary hyenas in the territory of the West Siberian Plain is *Pachycrocuta* sp. from the Podpusk 2 locality (Fig. 11) [Vislobokova, 1996]. For the Eopleistocene, remains of hyenas in this area are not

known. The skull of the ancient cave hyena *Crocota crocuta praespelaea* Schutt [Baryshnikov, Vereshchagin, 1996] was described from the Early Neopleistocene deposits in the section between the villages of Zhelezinka and Moiseyevka. The lower jaw PLHM 9641 comes from the Middle Neopleistocene deposits of this section, identified by the author as *C. crocuta spelaea* Goldf. In the Late Neopleistocene, the cave hyena was widespread throughout the south of the West Siberian Plain. Its extinction in this territory occurred quite early; it can be assumed that the last hyenas became extinct in the middle of the Karginskiy Interglacial. Today, the youngest radiocarbon dating of the cave hyena is 43,141±2,371 ka BP (UBA-28335), or 46,691 ka cal BP, obtained from Krasny Yar (Tomsk Province) [Shpansky, Kuzmin, 2021].

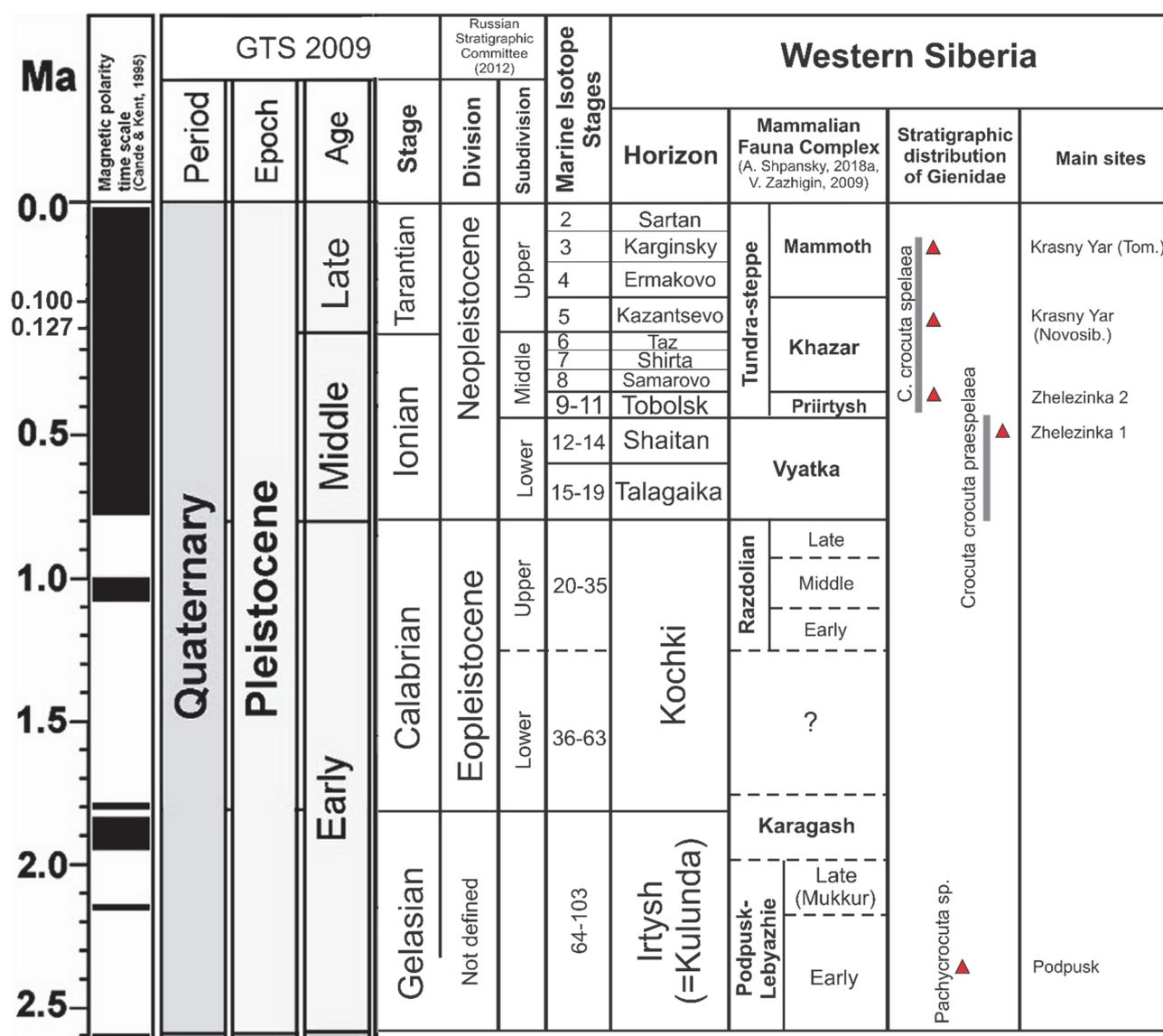


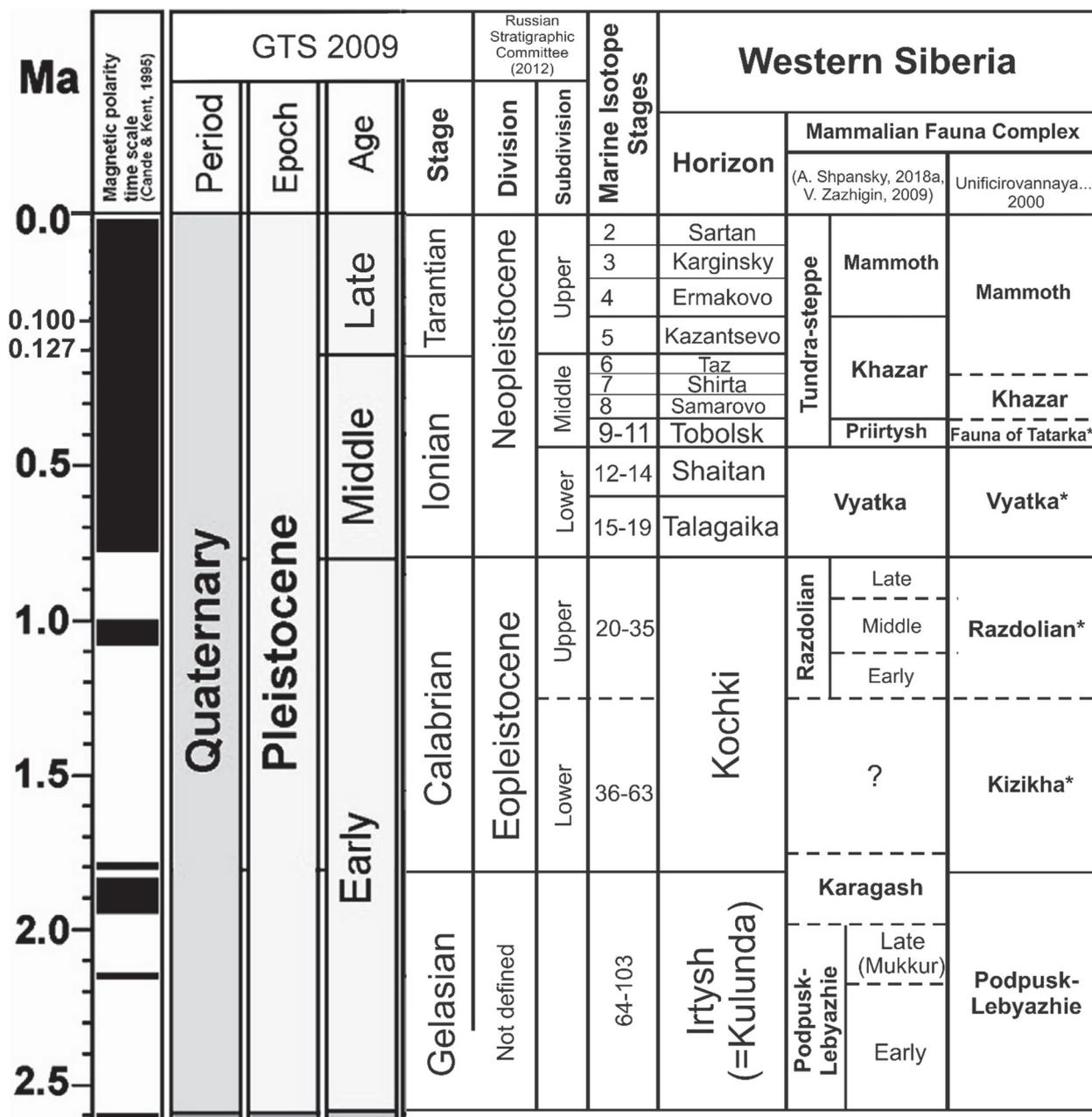
Fig. 11. Scheme of stratigraphic distribution of representatives of the family Hyenidae

Рис. 11. Схема стратиграфического распространения представителей семейства Hyenidae

**Review of species compositions of Quaternary mammalian faunal complexes**

In the Unified Stratigraphic Scheme of Quaternary deposits of the West Siberian Plain [Unificirovannaya...,

2000], the complexes of large and small mammals are presented in parallel. Small-mammal complexes in the scheme are marked for the Eopleistocene (Kizikha and Razdolian) and for the Early Neopleistocene (Vyatka) (Fig. 12).



**Fig. 12. Stratigraphic position of the mammalian faunal complexes of the West Siberian Plain**

\* Complexes established mainly for small mammals [Zazhigin, 2009]. \*\* By E.A. Vangengeim [1977]

**Рис. 12. Стратиграфическое положение фаунистических комплексов млекопитающих Западно-Сибирской равнины**

\* Комплексы, выделенные в основном для мелких млекопитающих [Zazhigin, 2009]. \*\* по Е.А. Vangengeim [1977]

No small-mammal complexes were identified for the Middle and Late Neopleistocene [Zazhigin, 1980]. Later,

V.S. Zazhigin [2009] proposed for the Paleopleistocene (Gelasian) – Podpusk-Lebyazhie (characterizing the first

half of the Paleopleistocene), Mukkur (characterizing the second half of the Paleopleistocene), and Karagash (characterizing the end of the Paleopleistocene and the beginning of the Eopleistocene). For large mammals, the scheme [Unificirovannaya..., 2000] shows the following: a mammoth complex with an interval of distribution from the Taz to the Sartan time and the isolation of mammoths of the early and late types. For the Samarovo Ice Age, the Khazar complex is given. For the Tobolsk age, the species composition of the fauna is not determined. For the Talagaika age, *Archidiskodon cf. trogontherii* and *Equus sp.* are noted. For the Late Eopleistocene, the presence of separate taxa not identified to species – *Palaeoloxodon sp.*, *Equus sp.*, *Ovibovini gen.* – was noted. For the Gelasium, the Podpusk-Lyabyazhie complex (due to a later change in the Neogene–Quaternary boundary) were not included in the scheme [Unificirovannaya..., 2000], similarly to the “Tatarka fauna” proposed by E.A. Vangengeim [1977] for the beginning of the Middle Neopleistocene and the Priirtysh faunistic complex proposed by B.S. Kozhamkulova [1969] for the Middle Neopleistocene. There is a situation when within one zoogeographic province two identical complexes are distinguished – the Priirtysh [Kozhamkulova, 1969] and the “Tatarka fauna” [Vangengeim, 1977] related to the first half of the Middle Neopleistocene and comparable with the Singil complex of Eastern Europe. V.S. Kozhamkulova designated the Pavlodar Priirtyshye as a type locality of the Priirtysh complex, the location near the village of Tatarka, which is also located within this area, but it is a local fauna; the material of this fauna comes from the collection of R.A. Zinova (1966–1967, collection of GIN 895) on modern beaches. This state of the biostratigraphy of the Quaternary of such a vast and important region as the West Siberian Plain cannot satisfy either geologists or paleontologists.

Recently, new data on mammalian biostratigraphy have been obtained for the territory of the West Siberian Plain. In the stratigraphic sequence for the Quaternary, 8 faunal complexes of large and small mammals are distinguished [Zazhigin, 2009; Shpansky, 2018a]: Podpusk-Lebyazhie; Mukkur, Karagash, and Razdolian (=Skorodum fauna of small mammals) complexes are distinguished for small mammals. The Vyatka complex is also distinguished mainly for small mammals; the Priirtysh, Khazar, and Mammoth complexes are distinguished for large mammals.

A close examination of the taxonomic features of mammalian faunal complexes reveals the unequal taxonomic changes underlying the allocation of complexes. These differences are particularly significant between the Podpusk-Lebyazhie, Karagash, Razdolian and younger Neopleistocene complexes. It seems to us more correct to use a differentiated biostratigraphic basis that more fully

reflects both the stages of development of the mammal fauna and the natural environment in the Quaternary period. Similar structured biostratigraphic bases were proposed for the hipparion fauna of southern Eastern Europe [Korotkevich, 1988] and the Pavlodar Priirtysh region [Shpansky, 2008]. For the fauna of large mammals of the Quaternary period, we propose the use of a three-level system of gradation and subordination of temporary groups of mammals, such as supercomplex, complex, and subcomplex.

Supercomplex reflects a major stage in the development of fauna, covering a large time interval with specific paleoecological conditions and illustrating large changes in the taxonomic diversity of mammals (at the level of tribes). In accordance with the stated criteria, the entire Quaternary fauna of Northern Eurasia is one supercomplex. Throughout the entire period, the predominating mammalian taxa were those related mainly to open landscapes with a gradual increase in cold aridization. This stage is connected with the adaptive radiation of odd-toed ungulate horses (Equinae), mammoth elephants (Mammothini), elasmotheriinae and dicerorhinae rhinoceroses (genera *Stephanorhinus*, *Coelodonta*, and *Elasmotherium*), deer, tylopods (*Paracamelus*, *Camelus*), bovids (bison, musk-oxen and others), rodents (Arvicolinae, etc.), and carnivorans (panthera, bears, dogs, etc.).

The identification of Quaternary complexes is based on differences at the level of genera, subgenera, and sometimes species in the phyletic groups of elephants, horses, rhinoceroses, deer, musk-oxen, bears, rodents, and others. According to these characteristics, five complexes can be distinguished for the West Siberian Plain: Podpusk-Lebyazhie, Karagash, Razdolian, Vyatka, and Tundra-steppe.

Subcomplexes are separated at the level of species and subspecies, and the degree of similarity of taxonomic composition between “neighboring” subcomplexes within the same complex is more than 75 %.

The following is a description of the faunal complexes established within the West Siberian Plain, with an emphasis on a more detailed analysis of large-mammal complexes.

The Podpusk-Lebyazhie complex was established by E.A. Vangengeim and V.S. Zazhigin in 1965, later renamed as “Lebyazhinsky” [Vangengeim, Zazhigin, 1969]. Since the main outcrop of the Irtysh formation, including the remains of mammals, is located between the villages of Lebyazhye and Podpusk (series of localities Lebyazhye 1 and 2, Podpusk 1 and 2), E.A. Vangengeim [1977] suggested the name “Podpusk-Lebyazhie complex”. The generic location is an outcrop of the Irtysh formation near the village of Podpusk on the right bank of the Irtysh River (Pavlodar Province). According to I.A. Vislobokova [1996], the oryctocenosis obtained from

the localities of Lebyazhye 2, Podpusk 1 and 2, originating from the lower and upper layers of the Irtysh formation, have a slightly different geological age, but are combined into one complex consisting of two subcomplexes and characterizing the Gelasium. Other locations: the Podpusk-Lebyazhye complex includes the findings of postcranial remains of *Elasmotherium* sp., *Equus (Allohippus) robustus* Pomel [Kozhamkulova, 1969] and *Stephanorhinus etruscus* from the sands of the Moiseevskaya formation at the base of the section between the villages of Moiseevka and Zhelezinka (Moiseevka 1 location) on the right bank of the Irtysh River (Pavlodar Province) [Shpansky, Ilyina, 2020]; the location of the Prorva, located 7 km upstream of the Irtysh River from the village of Podpusk [Gaiduchenko, 1986, 2003]. The species composition of the early subcomplex is as follows: *Ursus* sp., *Homotherium* sp., *Pachycrocuta* sp., *Archidiskodon meridionalis gromovi* Garutt et Alexeeva, *Elasmotherium* sp. (similar to *E. peii*), *Stephanorhinus etruscus* Falconer, *Equus livenzovensis* Bajgusheva, shallow *Equus* sp., *Antilospira* cf. *gracilis* Teilhard et Trassaert, *Gazella (Vetagazella) sinensis* Teilhard et Piveteau, *Eucladoceros* sp., *Paracamelus gigas* Schlosser, and Bovinae gen. indet. M.V. Sotnikova [Sotnikova, Rook, 2010] identified the canid *Canis* sp. as *Eucyon minor* (Teilhard et Piveteau). The author identified the lower jaw PLHM 100/386 and metatarsal PM TSU 36/7 from Moiseevka 1 and Lebyazhye 2 as *S. etruscus* [Shpansky, Ilyina, 2020]. A fragment of a limb bone from Podpusk reported by I.A. Vislobokova [1996] also tends to be attributed to the Etruscan rhinoceros *S. cf. etruscus*. From the Prorva tract, L.L. Gaiduchenko [2003] reports the remains of *Bison (Eobison)* aff. *tamanensis*. V.S. Zazhigin [2009] indicates a significant number of forms of insectivores, duplicitous rodents and true rodents from Podpusk and Lebyazhye: *Hemiechinus* sp., *Petenya* sp., *Beremendia fissidens* Kormos, *Hypolagus* sp., *Ochotona* sp., *Ochotonoides* sp., *Castor* sp., *Allactaga* sp., *Pygerethmus* sp., *Plioscirotopoda* sp., *Stylodipus* sp., *Mimomys reidi* Hinton, *M. ex gr. pliocaenicus* F. Major, *Cromeromys irtyshensis* Zazhigin, *Borsodia petenyii* (Mehely), *Clethrionomys* sp., *Cricetulus* sp., and *Prociophneus* sp.

The late subcomplex of the Podpusk-Lebyazhye complex, obtained from the Podpusk 2 locality, has the following species composition: *Archidiskodon* cf. *meridionalis* Nesti, *Equus* cf. *sussenbornensis*, shallow *Equus* sp., *Cervalces* sp., *Capreolus* sp., and *Gazella* sp. The quality of the preserved material (mainly postcranial remains) could not be determined accurately. A fragment of an elephant tooth from Podpusk 2 has characteristics typical of the southern mammoth – *A. meridionalis meridionalis* Nesti, according to I.A. Vislobokova [1996].

The Mukkur complex was emphasised by V.S. Zazhigin based on small mammals [Zykin et al., 1987]. Generic location: near the village of Novoselovka on the right bank of the Bitek River, 1.5 km above the mouth of

the Kyzyl-Aigir River. Other locations: large mammals were found in the deposits of the Mukkur formation of the Isakovka 4 locality. From the generic location defined by V.S. Zazhigin, numerous remains of small mammals were obtained, which he refers to the later stage of the Podpusk-Lebyazhye complex: Leporinae gen?, *Ochotona* sp., *Ochotonoides* sp., *Citellus (Urocitellus)* sp., Dipodinae gen., *Mimomys* ex gr. *reidi-coelodus*, *Borsodia* ex gr. *petenyii-hungaricus*, *Borsodia* sp., *Cromeromys* sp., and *Clethrionomys* sp. This complex of rodents is comparable with the Villafranchian faunas of Europe. Near the village of Isakovka (Omsk Province) on the right bank of the Irtysh River, in alluvial deposits belonging to the end of the Gelasia (Mukur formation), at the location of Isakovka 4, a fragment of the skull *Rangifer* sp. [Bondarev et al., 2017], Bovini gen. indet and *Equus* sp. were found. A.S. Tesakov identified numerous remains of small mammals in this locality [Tesakov et al., 2016; Zykin et al., 2021]: Soricidae, *Spermophilus* sp., *Prosiophneus* sp., *Sicista* sp., *Plioscirotopoda* sp., *Allophaiomys deucalion*, *Borsodia* ex gr. *fejervaryi-prolaguroides*, *Mimomys* ex gr. *pusillus*, *Lemmus* sp., and *Clethrionomys* sp. Some of the material was re-deposited from the older deposits of Gelasian (Irtysh horizon) and Piacenzo (Seletin horizon). According to A.S. Tesakov, the first appearance of voles of the genus *Allophaiomys* with rootless teeth allows determining the age of this fauna as transitional from the Gelasian to the Eopleistocene. According to paleomagnetic data, the direct magnetization of the deposits of the upper part of the Mukkur and lower part of the Karagash formations corresponds to the Olduvei episode with an astronomically calibrated age of 1.77–1.95 million years [Zykin, 2012; Zykin et al., 2003].

The Karagash complex was identified by V.S. Zazhigin based on small mammals from the same outcrop as the Mukkur Complex near the south-eastern edge of the village of Novoselovka on the right bank of the Bitek River [Zykin et al., 1987]. The Karagash Formation is overlain by the Mukkur Formation with erosion. From the lower Karagash Formation, V.S. Zazhigin identified the following taxa: *Sorex* sp., *Desmana* sp., Leporinae gen?, *Ochotonoides* sp., *Trogotherium* sp., *Plioscirotopoda* sp., *Allactaga* ex gr. *major*, *Citellus* sp., *Allocrietus* sp., *Mimomys* ex gr. *coelodus-pusillus*, M. sp., *Borsodia* ex gr. *prolaguroides* Zazhigin, and *Prosiophneus* sp. The evolutionary level of this fauna is estimated as intermediate between the Mukkur and Razdolian complexes. Remains of root-toothed voles – *M. ex gr. coelodus-pusillus*, *Borsodia* ex gr. *prolaguroides*, and *Cromeromys newtoni* – show more progressive features than voles from the Mukkur Formation [Zazhigin, 1998]. The presence of *B. cf. prolaguroides* and *C. newtoni* allows us to date this fauna to the Eopleistocene. The species *Mimomys* and *Borsodia* (= *Villanyia*, A.S.) are older than Razdolian.

Earlier, a complex of small mammals, characterizing the lower part of the Kochkovskaya Formation of the Eopleistocene and designated as the Kizikha complex [Vangengeim, Zazhigin, 1972; Zazhigin, 1980], was recognized by V.S. Zazhigin [2009] as invalid. Zykin considered that “the previously described fauna of the type locality of this complex is re-deposited from several stratigraphic levels and cannot be considered unified” [Zykin et al., 2003, p. 78]. Later, V.S. Zazhigin [2009, p. 219] writes: “In connection with revision of the Kizikha complex, a large hiatus between the Razdolian complex and the Lower Karagash fauna was formed”. In 2008–2009, radiocarbon dates were obtained from deposits of the type locality of the “Kizikha complex” that showed the Holocene age of the sediments to be 8,460±100 years (SB RAS-7414), 5,240±120 years (SB RAS-7413), and 5,060±125 years (SB RAS-7911) (date order numbers 392 and 395 in the catalog by G.G. Rusanov and L.A. Orlova [2013]). Remains of large mammals from alluvium of the “type locality”, as defined by A.V. Shpansky, are also of Holocene age [Rusanov, 2010]. The ostracod complex identified by I.I. Teterina from these sediments has a mixed composition of Neopleistocene–Holocene age.

The Razdolian complex was identified by V.S. Zazhigin based on small mammals [Vangengeim, Zazhigin, 1965, 1972; Zazhigin, 1980]. The type locality is a 14 m high cliff with an outcrop of the Kochki Formation located on the right bank of the Alei River, 1.5 km south-east of the village of Razdolie (18 km south-west of the Pospelikha railway station) [Adamenko, Zazhigin, 1965]. Other localities of the fauna were noted by A.A. Krukover [Volkova et al., 2002, p. 108]: Makhanovo is located on the right bank of the Aley River near the village of Makhanovo; Gonba-1, Elunino-1, Malinovka-1, Shelabolikha-1, 2, 3 is located on the Priobskaya plain (right bank of the Ob) near the villages of the same name; the locations of the Skorodum fauna are Nettle II, Skorodum II–IV, Skorodum A-S, Romanovo-1, 1c, 3, Nady are located on the right bank of the Irtysh [Krukover, Krivonogov, 1995]. These locations are confined to the thickness of the “diagonal sands”, which are usually mistakenly attributed to the Tobolsk horizon of the Middle Neopleistocene. The complex characterizes the second half of the Eopleistocene.

Species composition: large mammals – *Panthera fossilis*, *Homotherium* aff. *ultimus*, *Archidiskodon* cf. *meridionalis* (Nesti), *Palaeoloxodon namadicus*, *Equus* (*Allochippus*) sp., *Paracamelus* sp., *Ovibovini*? (?*Praeovibos*), and *Bison* sp.; small mammals – *Beremendia* sp., *Sorex* sp., *Crociodura* sp., *Leporinae* gen.?, *Hypolagus* sp., *Lepus* sp., *Lagomvinae* gen., *Ochotona* sp., *O.* cf. *pusilla*, *Citellus* sp., *Sicista* sp., *Allactaga* ex gr. *jaculus*, *Allactagalus* aut *Pygerethmus*, *Plioscirotopoda* sp., *Cricetus* sp., *Cricetulus* sp., *Clethrionomus* sp., *Mimomys pusillus*

Nich., *M. intermedius*, *Borsodia* (*Kulundomys*) *prolaguroides*, *Eolagurus argyropuloi*, *Prolagurus arankae*, *P. pannonicus*, *Allophaiomys pliocaenicus*, *Stenocranium hintoni* Pall., *Ellobius tarchancutensis* Grom. et Ponf., *Ellobius* sp., and *Prosiphneus* sp. V.S. Zazhigin [2009] distinguishes three stages within the complex: the early stage has the characteristic association of *Borsodia* (*Kulundomys*) *prolaguroides*–*Prolagurus pannonicus*–*Allophaiomys pliocaenicus*; the second stage is represented by the association *Prolagurus pannonicus*–*Allophaiomys pliocaenicus*–*Stenocranium hintoni*; the late stage is represented by the association *Prolagurus pannonicus*–*Stenocranium hintoni*–*Microtus* (*Microtus*) ex gr. *oeconomus*. For sections in the middle reaches of the Irtysh River, the Skorodumskaya fauna stands out; it is analogous to the Razdolian fauna of small mammals of southern Western Siberia [Kambaritdinov, 1969]. There are no known multi-species occurrences of large mammals attributed to the Razdolian complex, and remains are represented by scattered single finds. Remains from Moiseevka 2 were classified by E.A. Vangengeim [1977] as the Vyatka complex on the basis of new finds of large-mammal remains, including *Bison schoetensacki*, *Ursus savini rossicus*, and *Mammuthus trogontherii*.

The Vyatka complex is distinguished by V.S. Zazhigin based on small mammals [Vangengeim, Zazhigin, 1972; Zazhigin, 1980]. The type locality (for small mammals) is an outcrop on the left bank of the Ob River, 2 km downstream from the village of Vyatkino (Altai Krai) [Arhipov et al., 1989]. Other localities of large mammals include the following: nearby to the village of Dalneye on the Zhanyspay River (left tributary of the Ishim River) (Akmola Province); Pyatiryzhsk, Moiseevka 2, Zhelezinka 1, and Zhanabet on the right bank of the Irtysh River (Pavlodar Province) [Kozhamkulova, 1969; Shpansky, 2005b; Shpansky et al., 2008]; Ust-Tarka on the Om River (Novosibirsk Province) [Shpansky et al., 2015]; and Skorodum, Gornaya Subbota (Omsk Province) [Motuzko, 1970b]. Species composition: *Crocota crocuta praespelaea*, *Gulo* cf. *schlosseri*, *Mammuthus trogontherii trogontherii* Pohlig, *Elephas* (*Palaeoloxodon*) ex gr. *antiquus*, *Phanagoroloxodon irtyshensis* Shpansky, *Equus* (*Allochippus*) *sanmeniensis*, *E. mosbachensis* Reichenau, *Stephanorhinus kirchbergensis* Jäger, *Elasmotherium sibiricum* Fischer, *Bison schoetensacki* Freud, *Praeovibos priscus*, *Soergelia* sp. (? *elisabetae* Schaub), *Cervalces latifrons* (Johns.), and *Cervus* ex gr. *elaphus*. Small mammals of the complex are very diverse: *Sorex* sp., *Ochotona* ex gr. *pusilla*, *Marmota* sp., *Citellus* sp., *Allactaga* sp., *Alactagalus* sp., *Pygerethmus* sp., *Cricetus* sp., *Cricetulus* sp., *Clethrionomus* sp., *Mimomys pusillus*, *M. intermedius*, *Eolagurus* aff. *simplicidentis* Grom. et Ponf., *Prolagurus posterius* Kreitz., *Lagurus transiens* Jonossy, *Allophaiomys* sp. aut

*Microtus* sp., *M. cf. nivaloides*, *M. ex gr. hintoni-gregaloides*, *M. cf. oconomus* Pall., *Ellobius* sp., and *Myospalax* sp. [Volkova et al., 2002]. Large mammals are represented by isolated discoveries, sometimes skeletons of *Mammuthus trogontherii trogontherii* (Ust-Tarka, Pyatiryzhsk), and therefore it is difficult to identify a type locality for them. Perhaps a more detailed study would suggest an outcrop on the right bank of the Irtysh River between Moiseyevka and Zhelezinka settlements as a type locality. The complex is characterized by a new stage of mammoth elephant development – steppe or trogontherii – *M. trogontherii trogontherii*; appearance and dispersal of caballoid horses of the subgenus *Equus* – *E. mosbachensis*; and the first appearance of *S. kirchbergensis*. Among small mammals, the first appearance of the subgenus *Lagurus* (*L. transiensis*), and the extinction of Eopleistocene relics *Mimomys pusillus*, *M. intermedius*, *Prolagurus posterius* and *Allophaiomys* were noted. The faunal complex of the Early Neopleistocene in Vyatka comprises mainly species typical for the entire Northern Palearctic.

#### Tundra-steppe complex

The largest number of mammal localities has a “young” geological age and include the remains of representatives of the Priirtysh, Khazar, and Mammoth complexes of the Middle and Late Neopleistocene. They have a highly diverse species composition (Table 1), including large multi-species localities such as Grigoryevka (Pavlodar Province), Krasny Yar (Novosibirsk Province), Sergeyevo, Krasny Yar (Tomsk Province), and others. From the Neopleistocene (the Priirtysh subcomplex), remains of *Panthera spelaea*, *Ursus savini rossicus*, *Saiga tatarica*, *Megaloceros giganteus*, *Coelodonta antiquitatis*, and *Bison priscus* appear and are found in large numbers, as well as a line of large caballoid horses and other species that formed the core of the typical fauna of open landscapes, which significantly distinguishes it from the preceding Vyatka fauna, reflecting more mosaic landscapes. *Mammuthus trogontherii chosaricus* becomes a typical representative of mammoth elephants. The differences between the Priirtysh and Khazar faunas are the replacement of the broad-fronted moose *Cervalces latifrons* by the typical *Alces alces* and the appearance of *Rangifer tarandus*. Until recently, the key difference was the extinction of the rhinoceroses *Elasmotherium sibiricum* and *Stephanorhinus kirchbergensis* in the first half of the Middle Neopleistocene. The traditional difference between the Khazar and Mammoth fauna was considered to be the change of *Mammuthus trogontherii chosaricus* to *M. primigenius*, the appearance of *Ovibos moschatus*, *Vulpes (Alopex) lagopus* and the wide distribution of reindeer and arctic fox.

In the present paper, the author proposes to lower the status of the Priirtysh, Khazar, and Mammoth complexes to subcomplexes and to combine them into a single complex called Tundra-steppe (see Fig. 12). This is due to the appear-

ance of radiocarbon dates for the taxa *Elasmotherium sibiricum*, *Mammuthus trogontherii chosaricus*, and *Stephanorhinus kirchbergensis* [Shpansky et al., 2016a; Kosintsev et al., 2019; Kirillova et al., 2021; Shpansky, Kuzmin, 2021], which previously determined the biostratigraphic difference between these faunas. The increased proximity of the Middle–Late Neopleistocene complexes required a lowering of their status. The name “Tundra-steppe” reflects well the main feature of the ecological structure of all these subcomplexes, namely the habitat in new landscapes that developed in the Middle Neopleistocene.

The Priirtysh subcomplex was identified by B.S. Kozhamkulova [1969] from a series of occurrences in the Irtysh River basin and the Ural River. An outcrop of alluvial deposits of the Tobolsk horizon near the settlement of Grigoryevka on the right bank of the Irtysh River (Pavlodar Province), 40 km north of Pavlodar, was proposed as a type locality by A.V. Shpansky [Shpansky et al., 2007; Shpansky, 2018b]. The sediments are mainly represented by diagonally layered sands, pebbles, and gravel of the Zhana-Aul formation and synchronous sediments, sometimes strongly ferruginous to a dark brown color. Other localities of the fauna: series of outcrops of oblique sands on the Irtysh River in Pavlodar Province – Pyatiryzhsk, Yamyshevo, Zhelezinka 2, and Urlyutyub; Kirillovka on the Burluk River (North Kazakhstan Province); Ilyinka on the Chumysh River (Altai Territory); Krivosheino and Urtam on the Ob River (Tomsk Province); Chembakchino and Koshelevo (Khanty-Mansi Autonomous Area); and Khashgort (Yamalo-Nenets Autonomous Area). Species composition: large mammals – *Mammuthus trogontherii chosaricus*, *Elephas (Palaeoloxodon) ex gr. antiquus* (Falc.)\* (Species that do not originate from a type locality are indicated with asterisk (\*)), *Stephanorhinus kirchbergensis* (Jäger)\*, *Elasmotherium sibiricum* Fischer (in the south), *Coelodonta antiquitatis* (Blum.), *Equus ex gr. mosbachensis-germanicus*, *Bison priscus* Boj., *Bos primigenius* Boj., *Saiga tatarica* L., *Cervalces cf. latifrons* (John.)\*, *Cervus elaphus* L., *Megaloceros giganteus ruffi* Nehr., *Camelus knoblochi* Nehring, *Panthera spelaea* Goldf., *Felis manul* Pallas, *Canis cf. lupus* L., *Ursus savini rossicus* Borissiak\*, *U. arctos* L.\*, and *Crocota crocota spelaea* Goldf.\*. Small mammals from the type locality are not known, their list is based on materials from the Tomsk Ob region [Shpansky, 2021a]: *Sorex* sp., *Ochotona* sp., *Lepus* sp., *Citellus* sp., *Clethrionomys* sp., *Dipodidae* gen.(?), *Cricetus* sp., *Eolagurus luteus* Eversm., *Lagurus cf. lagurus* Pall. (*L. transiens* by A. Krukover [Volkova et al., 2002]), *Mimomys ex gr. middendorffii-hyperboreus*, *Microtus ex gr. arvalis-agrestis*, *Dicrostonyx cf. simplicior* Feifar, *Lemmus* sp., *Arvicola aff. mosbachensis*, *Microtus oconomus* Pall., *Microtus (Stenocranius) gregalis* Pall., and *Myospalax* sp.

Species composition of faunal subcomplexes of large mammals of the Middle–Late Neopleistocene of the West Siberian Plain

Видовой состав фаунистических подкомплексов крупных млекопитающих среднего-позднего неоплейстоцена Западно-Сибирской равнины

Priirtysh	Khazar	Mammoth
<i>Mammuthus trogontherii chosaricus</i> <i>Elephas (Palaeoloxodon) ex gr. antiquus</i>	<i>Mammuthus trogontherii chosaricus</i>	<i>Mammuthus trogontherii chosaricus</i>
<i>Stephanorhinus kirchbergensis</i> <i>Elasmotherium sibiricum</i> <i>Coelodonta antiquitatis</i> <i>Equus ex gr. mosbachensis-germanicus</i> <i>Equus sp. (small)</i> <i>Bison priscus</i> <i>Bos primigenius</i> ?	<i>Stephanorhinus kirchbergensis</i> ? <i>Coelodonta antiquitatis</i> <i>Equus ex gr. mosbachensis-germanicus</i> <i>Equus ovodovi</i> <i>Bison priscus</i> <i>Bos primigenius</i> <i>Soergelia cf. elisabetae</i>	<i>Mammuthus primigenius</i> <i>Stephanorhinus kirchbergensis</i> <i>Elasmotherium sibiricum</i> <i>Coelodonta antiquitatis</i> <i>Equus ex gr. gallicus (=ferus)</i> <i>Equus ovodovi</i> <i>Bison priscus</i> <i>Bos primigenius</i>
<i>Saiga tatarica</i> <i>Cervalces cf. latifrons</i>	<i>Saiga tatarica</i> ? <i>Alces alces</i> <i>Rangifer tarandus</i> <i>Cervus elaphus</i> <i>Megaloceros giganteus</i> ? <i>Panthera spelaea</i>	<i>Ovibos moschatus</i> <i>Saiga tatarica</i>  <i>Alces alces</i> <i>Rangifer tarandus</i> <i>Cervus elaphus</i> <i>Megaloceros giganteus giganteus</i> ? <i>Panthera spelaea</i>
<i>Cervus elaphus</i> <i>Megaloceros giganteus ruffi</i> <i>Camelus knoblochi</i> <i>Panthera spelaea</i> <i>Felis manul</i>	<i>Gulo gulo</i> <i>Canis lupus</i> <i>Ursus savini rossicus</i> <i>Ursus arctos</i> <i>Crocota crocuta spelaea</i>	<i>Gulo gulo</i> <i>Canis lupus</i> <i>Ursus savini rossicus</i> <i>Ursus arctos</i> <i>Crocota crocuta spelaea</i> <i>Vulpes (Alopex) lagopus</i> <i>Vulpes vulpes</i> <i>Meles leucurus</i>
?	<i>Castor fiber</i>	<i>Castor fiber</i>

A distinctive feature of the Priirtysh complex is the appearance and wide distribution in Western Siberia of a number of new taxa (giant deer, saiga, woolly rhinoceros, “cave” predators, etc.), which become the basis for the entire Middle and Late Neopleistocene fauna [Shpansky et al., 2007; Shpansky, 2011, 2018b; Shpansky, Chernous, 2012b;]. At the same time, representatives of more ancient faunas are still present, such as the elasmotherium and broad-brow elk, and the Merka rhinoceros reaches its maximum distribution [Shpansky, 2017]. A transitional form between the steppe elephant (*M. trogontherii*) and the typical mammoth (*M. primigenius*) is formed in the phylogenetic lineage of mammoth elephants, which has obtained subspecies status under the name Khazar elephant – *M. trogontherii chosaricus* Dubrovo.

The Khazar subcomplex was first identified by V.I. Gromova [1932] on the basis of numerous finds of remains of large mammals near the village of Nikolskoe in the Lower Volga Region under the name “Volga fauna”. Later, V.I. Gromov [1948] renamed the fauna as

“Khazar complex”. A type locality for the subcomplex within the West Siberian Plain is not currently identified. Known localities of the fauna are as follows: Kartashovo, Kachesovo, Demianskoe, Bobrovka, and Semeika (Khanty-Mansiysk Autonomous District); Krasny Yar (lower ossiferous level; Novosibirsk Province); and Tarkarka (Omsk Province). Cumulative species composition from different localities: large mammals – *Mammuthus trogontherii chosaricus*, *Coelodonta antiquitatis*, *Stephanorhinus kirchbergensis*, *Equus ex gr. mosbachensis-germanicus*, *Equus ovodovi* Aizenman et Vasiliev, *Soergelia cf. elisabetae*, *Bison priscus*, *Cervus elaphus*, *Megaloceros giganteus*, *Alces alces*, *Rangifer tarandus*, *Castor fiber*, *Panthera spelaea*, *Ursus savini rossicus*, *U. arctos*, *Canis lupus*, *Crocota crocuta spelaea*, and *Gulo gulo*; small mammals – *Sorex sp.*, *Ochotona sp.*, *Lepus sp.*, *Spermophilus sp.*, *Clethrionomus sp.*, *Eolagurus luteus*, *Lagurus lagurus*, *Mimomys (Stenocranium) gregalis*, *Microtus oeconomus*, *M. ex gr. middendorffii-hyperboreus*, *M. ex gr. arvalis-agrestis*, *Dicrostonyx cf. guiljelmi-henseli*, *Lemmus obensis*, *Arvicola kalmankensis* Zazhigin, and *Myospalax sp.*

The upper boundary of the Khazar subcomplex is drawn by the author at the level of the upper boundary of the Kazantsevo horizon [Shpansky, 2018a], thereby extending the age interval of the subcomplex from the Samarovo to Kazantsevo time for the West Siberian Plain. This proposal is based on the finding of three dominant representatives of the Khazar fauna in the Kazantsevo deposits – *Mammuthus trogontherii chosaricus*, *Stephanorhinus kirchbergensis*, and *Equus ex gr. mosbachensis-germanicus* [Kosintsev, Vasiliev, 2009; Shpansky, 2018a]. For south-eastern West Siberia, the Khazar subcomplex includes several specific species (soergelia and Ovodov's horse), noted for the Kazantsevo time.

The Mammoth subcomplex was zoned off and named "Upper Paleolithic complex" by V.I. Gromov [1948]. For Siberia, as the basis of the complex, V.I. Gromov used the remains of mammals from Paleolithic sites of the Yenisei Valley. But such localities, due to the activity of Paleolithic man, always have a distorted and selective species composition. Geographically, these monuments are located on the border of the West Siberian Zoogeographic Province, and their geological age correlates with LGM (MIS 2). For the entire time of the existence of this complex, it is hardly possible to single out one locality as an exemplary one. This is associated with a sufficiently high degree of study of the complex, the use of the radiocarbon method for direct age determination of skeletal remains, and the revealed heterogeneity of the complex over time. The greatest diversity of mammoth fauna is noted for an earlier time interval corresponding to MIS 3. Within the West Siberian Plain, for the Karginsky Interglacial, the author suggests the fossil soil exposed on the right bank of the Chulym River near the village of Sergeevo (Tomsk Province) as an exemplary locality. The coordinates of the position most repleted with remains are 57°15'15" N, 86°05' E [Shpansky, 2021b]. All remains of this locality are embedded in their original location. Direct radiocarbon age determination of bones from stratum 4 is determined to be 32–35 ka [Shpansky, Kuzmin, 2021; Kuzmin, Shpansky, 2023]. There are many localities of the Mammoth subcomplex in Western Siberia. According to radiocarbon data, the vast majority is of Karginsky Interglacial or Sartan Glacial. Most of the localities are known for single finds of individual representatives of the fauna, including Prichulymsky, Dzhambul, Kulachye, and Vladimirskaaya mine. Sometimes these finds can be fragments of skeletons. There is a number of large multi-species localities, such as Krasny Yar, Sergeyevo (Tomsk Province); Chik River, Taradanovo, Krasny Yar (upper bonebed) (Novosibirsk Province); and Baigara (Tyumen Province). Some localities have "superimposed archeology" – Shestakovo, Volchya Griva, and Lugovskoye. The species composition of the subcomplex is as follows: large mammals – *Mammuthus primigenius* (Blum.),

*Mammuthus trogontherii chosaricus*, *Coelodonta antiquitatis* (Blum.), *Elasmotherium sibiricum*, *Stephanorhinus kirchbergensis*, *Equus ex gr. gallicus* Prat., *Equus ovodovi* Eisenmann et Vasiliev, *Bison priscus* Boj., *Bos primigenius* Boj., *Saiga tatarica* L., *Gazella subgutturosa* (Guldenstaedt), *Ovibos moschatus* Zimm., *Alces alces* L., *Cervus elaphus* L., *Megaloceros giganteus giganteus* (Blum.), *Rangifer tarandus* L., *Canis lupus* L., *Vulpes (Alopex) lagopus* L., *Vulpes vulpes* L., *Vulpes corsac* L., *Panthera spelaea* Goldf., *Ursus savini rossicus* Boris-siak, *Ursus arctos* L., *Crocota spelaea* Goldf., *Gulo gulo* L., *Meles leucurus* Hodgson; rodents and hares – *Lepus timidus* L., *Castor fiber* L., *Marmota bobac* L., *Spermophilus citellus* L., *Lemmus sibiricus* Kerr, *Dicrostonyx guillemi* Sanford, *Microtus gregalis* Pallas, *M. oeconomus* Pallas, and *Lagurus lagurus* Pallas. The structure of the mammoth subcomplex in Western Siberia is generally identical to that of Eastern Europe and most part of Western Europe. This similarity is even more significant than for the Khazar subcomplex. B.S. Kozhamkulova [1981] notes the continued existence of *Camelus knoblochi*, *Bos primigenius*, and *E. hemionus* Pallas, but no radiocarbon age determination of these findings has been performed. The mammals *Ovis ammon*, *Camelus knoblochi*, and *Hystrix brachyuran vinogradovi* Argyropulo have been recorded for the Altai territory [Vasiliev, 2016; Kuzmin et al., 2017]. South of Novosibirsk, in the Minusinsk basin and the Pre-Altai Plain, finds of *Ovis ammon* (Taradanovo), *Cuon alpinus* (Chumysh and Krasny Yar) are noted [Vasiliev et al., 2018], which may reflect the ecotone zone between the West Siberian and Altai-Sayan zoogeographic provinces.

Modern (Holocene) fauna of the West Siberian Plain. The Holocene localities of mammalian remains were analyzed by M.M. Devyashin [2013]. The vast majority of the 214 sites are represented by archeological sites, such as settlements and ritual complexes. Wild animals are represented by preserved elements of the mammoth fauna: *Castor fiber*, *Lepus timidus*, *Canis lupus*, *Vulpes vulpes*, *Vulpes (Alopex) lagopus*, *Gulo gulo*, *Meles leucurus*, *Ursus arctos*, *Alces alces*, *Cervus elaphus*, *Rangifer tarandus*, *Saiga tatarica*, and *Equus hemionus*. *Megaloceros giganteus* is preserved in the early Holocene [Stuart et al., 2004; Plicht et al., 2015]. Due to the wide distribution of forests, the number of forest-dwelling species has increased, primarily of martens (*Martes zibeline*, *Mustela sibirica*, and *Lutra lutra*) as well as *Lynx lynx*, *Sus scrofa*, and *Capreolus pygargus*. Remains of *Marmota* sp. and *Vulpes corsac* are quite numerous; isolated finds of *Gazella subgutturosa* and *Ovis ammon* are also known. The widespread distribution of *Equus ferus* and *Bos primigenius* is questionable due to their morphometric proximity to domestic animals.

## Conclusions

The generalized data on the stratigraphic distribution of individual taxa of large mammals from the localities of the West Siberian Plain demonstrate a number of features. Taxonomic diversity over time is unevenly represented due to the extremely small localities of large mammal remains in the Eopleistocene sediments of Western Siberia, and, therefore, reflects an insufficient degree of study. The revealed species diversity reaches its maximum for the Middle Neopleistocene and Late Neopleistocene and is minimal for the Eopleistocene. At present, the lower boundary of the Quaternary coincides with the appearance in Western Siberia of the key Quaternary phylogenetic lines of elephants and horses *Archidiskodon–Mammuthus* and *Equus*. The species composition of the Paleopleistocene and Eopleistocene fauna reflects the ancient stage of development with elephants with thick-tooth enamel of the genus *Archidiskodon*, archaic horses of the Stenon type, early rhinos of the genera *Elasmotherium* (the form from the Podpusk-Lebyazhie complex is similar to *E. peii*) and *Stephanorhinus*, early antelopes and deer *Antilospira* cf. *gracilis*, *Gazella (Vetagazella) sinensis*, *Eucladoceros* sp., and the giant camel *Paracamelus gigas*. This fauna reflects fairly warm and humid habitat conditions, mosaic landscapes from arid steppes to broad-leaved forests, and a mixed species and ecological composition.

The boundary between the Eopleistocene and Neopleistocene is marked by a change at the generic level in the phylogenetic line of elephants from *Archidiskodon* to *Mammuthus*, the extinction of *Homotherium*, the appearance of the line of *E. mosbachensis–E. gallicus*, the origination of *Stephanorhinus kirchbergensis*, the widespread dispersal of *Elasmotherium sibiricum*, the first appearance of the subgenus *Bison* and its short-horned form *B. schoetensacki*. In addition, more ancient forms still occurred, such as *E. (Allochippus) sanmeniensis*, *Praeovibos priscus*, and others. In general, the composition of the Early Neopleistocene fauna near the Vyatka River is transitional, reflecting changes in landscape and climatic conditions towards significant aridization and reduction of forest areas.

The boundary between the Early and Middle Neopleistocene is characterized by a change at the generic level in the musk-oxen *Praeovibos–Ovibos*; the appearance of new genera, namely *Megaloceros*, *Saiga*, *Bos*, *Camelus*, *Coelodonta*, and, probably, *Canis*, as well as new species such as *Ursus arctos* and *U. savini*, *Panthera spelaea*, *Bison*, and others. Since the Middle Neopleistocene, the tundra-steppe area of the fauna has been established, with dominating both in species diversity and in the number of forms that tend to inhabit open landscapes. This time corresponds to a significant aridization of the climate, the maximum distribution of permafrost and eolian deposits.

Thus, fauna revolutions occurred at the primary turns of the Pleistocene, such as Gelasian–Eopleistocene (=Calabrian), Early–Middle Neopleistocene (=Early Middle–Late Middle Pleistocene), and Late Neopleistocene–Holocene. But those revolutions were the same at the turn of the Middle–Late Neopleistocene. New data on the time of key taxa extinction of the Middle Pleistocene within Western Siberia raise a very serious question. Why did the mammal fauna not react to sufficiently significant changes in the landscape and climatic conditions during the Middle–Late Neopleistocene, and if it did react, how did this reaction manifest itself? Moreover, there is the issue of causes that led to extinction and the dynamics of the ecological structure revolution in the mammalian fauna from the end of the Pleistocene to the beginning of the Holocene (45–7 thousand years ago). In this regard, it is even more acute now.

The extinction of the dominant mammoth fauna taxa within Western Siberia occurred differently for different species and for the same species within the territory. The process began in the second half of Karginisky interstadial (about 40–45 thousand years). The extinction was not accompanied by vicariate species substitution, as in previous epochs, which led to the destruction of the paleoecological structure of the fauna that had existed for about 7 million years (since the beginning of the Hipparion fauna).

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**Information about the author:**

**Shpansky A.V.**, Dr. Sci. (Geol-Miner.), Professor of the Department of Palaeontology and Historical Geology, Faculty of Geology and Geography, National Research Tomsk State University, Tomsk, Russia.

E-mail: andreyspansky@yandex.ru

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**Информация об авторе:**

**Шпанский А.В.**, доктор геолого-минералогических наук, профессор кафедры палеонтологии и исторической геологии, геолого-географический факультет, Национальный исследовательский Томский государственный университет, Томск, Россия.

E-mail: andreyspansky@yandex.ru

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