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Geographical and stratigraphic distribution of fossil saiga antelope (*Saiga* sp. and *Saiga tatarica borealis*, Bovidae) finds in the Pleistocene of Yakutia (East Siberia, Russia)

Gennady G. Boeskorov*, Alexander D. Stepanov, Albert V. Protopopov & Marina V. Shchelchkova

ABSTRACT. The article presents an analysis of the spatial and temporal distribution of the currently known finds of fossil saiga antelope (*Saiga* sp. and *Saiga tatarica borealis*) in Yakutia (Eastern Siberia, Russia). Saiga remains in the north of Eastern Siberia were first identified by I. Chersky (1876, 1891). Since then, the presence of this species in the Pleistocene of Yakutia has been established over a significant part of its territory. It is assumed that some finds of saiga remains date back to the Early Pleistocene. Nevertheless, the earliest reliable saiga remains in Northeast Asia are dated to the Middle Pleistocene (the Achchygyi Allaikha and Keremesit rivers). An analysis of the finds of saiga remains indicates that this species had a very wide range in the territory of Yakutia during the Late Pleistocene. Saiga inhabited the valleys of Lena, Vilyui, Olenek, Yana, Adycha, Indigirka, and Kolyma rivers (as well as in the interfluves of the latter two rivers). It also lived on Primorsky lowlands and on Bolshoi Lyakhovsky Island. Radiocarbon-dated or related finds indicate a fairly wide distribution of the saiga both during the Karginian interstadial and Sartanian glaciation. By the end of the Pleistocene, with climate changing, expressed in warming and humidization, the depth of snow cover during winter increased in the north of Eastern Siberia, which became an insurmountable factor for saigas. The climate change led to the degradation of the cold steppe zone and its replacement by the tundra and taiga zones. This could led to the regional extinction of saiga antelope in Northeast Asia and Beringia.

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Географическое и стратиграфическое распространение находок ископаемого сайгака (*Saiga* sp. и *Saiga tatarica borealis*, Bovidae) в плейстоцене Якутии (Восточная Сибирь, Россия)

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РЕЗЮМЕ. В статье представлен анализ пространственного и временного распределения известных к настоящему времени находок остатков ископаемого сайгака (*Saiga* sp. и *Saiga tatarica borealis*) на территории Якутии (Восточная Сибирь, Россия). Впервые остатки сайгака на севере Восточной Сибири были идентифицированы И. Черским (1876, 1891). С тех пор присутствие этого вида в плейстоцене Якутии установлено на значительной части ее территории. Предполагается, что некоторые находки остатков сайгака относятся к раннему плейстоцену. Достоверно же самые ранние остатки

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сайгака на Северо-Востоке Азии датируются средним плейстоценом (реки Аччыгый Аллаиха и Керемесит). Анализ находок свидетельствует о том, что этот вид имел весьма широкий ареал на территории Якутии в позднем плейстоцене, обитая в долинах рек Лена, Вилюй, Оленек, Яна, Адыча, Индигирка, Колыма (а также, на междуречьях последних двух рек), на Приморской низменности и на острове Большой Ляховский. Радиоуглеродные датировки и датированные отложения свидетельствуют о достаточно широком распространении сайгака как во время каргинского интерстадиала, так и в период сартанского оледенения. К концу плейстоцена с изменением климата, выразившимся в потеплении и увлажнении, на севере Восточной Сибири увеличилась глубина снежного покрова в зимний период, что стало непреодолимым фактором для сайгака. Изменение климата привело к деградации холодной степной зоны и ее замене на тундровую и таежную зоны, в результате сайгак вымер на территориях Северо-Восточной Азии и Берингии.

КЛЮЧЕВЫЕ СЛОВА: *Saiga* sp., *Saiga tatarica borealis*, плейстоцен, распространение, Якутия, Восточная Сибирь, Россия.

Introduction

At present, the saiga antelope *Saiga tatarica* (Linnaeus, 1766) is a typical representative of the fauna of open landscapes in the arid regions of the central part of Eurasia from the Caspian plains in the west to Mongolia in the east. It occurs in forest-steppes and forb-cereal steppes in the north of the range through the deserts of temperate latitudes in the south (Bannikov, 1963; Zhirnov, 1998).

Several species of extinct *Saiga* from the Pleistocene of Eurasia and Alaska have been named, including *S. borealis* (Chersky, 1876), *S. prisca* (Nehring, 1891), *S. ricei* (Frick, 1937), and *S. binagadensis* (Alekperova, 1953). It was noted that according to some measurements of the skull, the fossil saiga *S. borealis* (including *S. prisca* and *S. ricei*) is an independent species from recent *S. tatarica* (Sher, 1967; Baryshnikov & Tikhonov, 1994). According to a proposed taxonomic scheme, *S. tatarica* is represented by three extinct subspecies: *S. tatarica borealis* Tscherski, 1876 (=*ricei*) (Eastern Siberia and Alaska), *S. tatarica prisca* Nehring, 1891 (Europe and Western Siberia), and *S. tatarica binagadensis* Alekperova, 1953 (Transcaucasia) (Baryshnikov & Krakhmalnaya, 1994a).

Genetic data suggest the existence of a single recent saiga species (*S. tatarica*) with two subspecies: *S. tatarica tatarica* and *S. tatarica mongolica* (Kholodova *et al*., 2006). Based on their analysis of fossil remains and the recent saiga range, Campos *et al*. (2010, 2014) identified one large cluster with most fossil and recent saiga forms, comprising also two samples of *S. borealis* that occurred in most of the distribution area (Northern Urals, Middle Urals, and northeast Yakutia). Recent morphological studies suggest that prehistoric *Saiga* representatives were merely geographical variants of the extant species that was formerly much more widespread. The observed dissimilarities between *S. borealis* and *S. tatarica* correspond most probably to subspecies level and may have resulted from a biogeographical differentiation of saiga populations in the Pleistocene (Ratajczak *et al*., 2016). The latter authors followed subspecies taxonomy of *Saiga* by Kahlke (1991) and Baryshnikov & Krakhmalnaya (1994a) and favored the single species *S. tatarica*, with subspecies *S. tatarica borealis* and *S. tatarica tatarica.* In this paper, we adhere to this opinion and consider the Late Pleistocene saiga from Yakutia as a subspecies *S. tatarica borealis*.

Fossil remains of the species have been found in throughout Eurasia from the territories of modern England and France in the west to Kolyma River Basin and Chukotka (Ayon Island) in the east, as well as in Alaska and the Yukon region (Northwest Territories of Canada). This indicates the existence in the Pleistocene of a vast zone of cold loess steppes or "tundra steppes" (Sher, 1971; Velichko, 1973; Yurtsev, 1981) suitable for habitation of the species.

Despite the significant number of fossil remains of the saiga, the time and place of its origin has not yet been precisely determined. Andrei Sher (Sher, 1986), presumably included *Saiga* sp. in the Olyorian fauna (Eopleistocene–Early Pleistocene, 1.5–0.5 Ma ago). This concept suggested that the oldest finds of representatives of the genus *Saiga* come from the Olyorian fauna of the Primorskaya lowland in the north of Yakutia (Baryshnikov & Krakhmalnaya, 1994b) and from the outcrop of Ulakhan Sullar on the Adycha River (Baryshnikov *et al*., 1998).

Middle Pleistocene finds of saiga remains in Northeast Asia are the bone of *Saiga* sp. found *in situ* at the Achchygyi Allaikha locality (Indigirka River basin) in deposits of the Allaikha Formation of the first half of the Middle Pleistocene (i.e. Tobolskian and Samarovian times, approximately 427–242 thousand years ago, MIS-11–MIS-8) (Kaplina *et al*., 1980) and a tooth originating from the lower unit of the Middle Pleistocene Keremesit Formation (Keremesit River, a tributary of the Kolyma channel of the Indigirka River). The lower unit of the Keremesit Formation belongs to the first half of the Middle Pleistocene (Tobolskian–Samarovian time, MIS-11–MIS-8) (Sher *et al*., 1987; Baryshnikov *et al*., 1998). Middle Pleistocene finds of the saiga were discovered in a large area: the Volga region (Vereshchagin, 1959); Western Siberia: Tobol River near the village Khudyakovo, Tazovian deposits, MIS-6 (Sher, 1967), a number of localities in the West Siberian Plain, MIS-11–MIS-6 (Shpansky, 2019); Northern Kazakhstan, Pri-Irtyshian faunistic complex, MIS-11–MIS-9 (Kozhamkulova, 1968). The fossil saiga from the Eemian Interglacial (MIS-5, early Late Pleistocene) found in

Binagady (Azerbaijan) (Alekperova, 1953). There are quite a lot of finds of saiga remains from the early Late Pleistocene (MIS-5) in Western Siberia (Drozdov *et al*., 2005; Malikov, 2018; Shpansky, 2019).

In Western Europe fossil remains of *Saiga* are known in the Middle Pleistocene MIS-11–MIS-6 (Saalian, Riss), and were described from several localities of that age in France and Germany (Toepfer, 1964; Delpesch & Heintz, 1976; H.D. Kahlke, 1975; R.D. Kahlke, 1990, 2014), where they were identified as *Saiga* sp. or *S. tatarica* ssp. During the Eemian Interglacial, *Saiga* occurred in Central Asia and the Caucasian foothills (Baryshnikov & Krakhmalnaya, 1994b; Baryshnikov & Tikhonov, 1994).

Harington (1981) dated two saiga skulls from Alaska to late Middle Pleistocene, MIS-7–MIS-6 (Illinoian/Saale). Thus, it can be stated that in the second half of the Middle Pleistocene, the saiga already had a huge range from France through almost the entire northern Eurasia to central Alaska. The formation of such a vast range was due to the wide distribution of steppe herbaceous communities in a dry continental climate, as well as the drying of shelf zones in the Bering Strait region with a decrease of the world ocean level (Sher, 1968; Harington, 1981; Kahlke, 1992; Guthrie *et al*., 2001).

Most of the saiga finds in Yakutia date back to the Late Pleistocene (Table 1). The most known of them are: the Bolshoy Lyakhovsky Island, Vilyui River, mouth of the Olenyek River (Chersky, 1891); Svyatoy Nos outcrop (Nikolsky & Basilyan, 2003); Rassokha River, Balyktakh River; Alazeya River; Bolshaya Chukochiya River (Lazarev & Tomskaya, 1987); lower reaches of the Lena River; lower reaches of the Kolyma River, mouth of the Ozhogina River, and Alyeshkina Zaimka outcrop (Sher, 1971; Baryshnikov *et al*., 1998).

In recent decades, new Pleistocene saiga remains have been discovered in Yakutia, and a number of new radiocarbon dates have been obtained (Campos, 2010; our unpublished data). These data have not yet been systematized and analyzed. An analysis of these data may make it possible to outline the range of the saiga in the Pleistocene in more detail and, to a certain extent, to discuss its dynamics over time.

Material and methods

Published materials and unpublished museum and original materials on osteological finds of saiga at various locations in Yakutia were studied. The age of the finds of bones of the studied species was estimated on the basis of radiocarbon dates obtained both directly from the bones and indirectly, from other organic remains (including bones of other animal species) from the layer containing remains of saiga antelope, as well as using archaeological and stratigraphic methods.

In recent decades, new Pleistocene saiga remains have been discovered, represented by fragments of skulls with horn cores of various preservation: MBV No. 207, found in 1992; MBV No. 232, found in 2009, all these remains were found on the Oskhordokh outcrop, Adycha River; AS RS (Y) No 1443, found in 2015, Ulakhan Sullar outcrop, Adycha River; AS RS (Y) No. 6904, found in 1993, Lena River, 3 km below the mouth of the Batamay River; AS RS (Y) No. 1443, found in 2014 and AS RS (Y) No. 2019-US, found in 2019, both from Ulakhan Sullar outcrop, Adycha River; ECY No. 8, Sullar Myran outcrop, Lena River, found in 2008; DPMGI No. 7132, lower reaches of the Bolshaya Chukochya River, 90 km up-stream from the mouth, found in 2015; OS No. 2023/8, Locality "Kyzyl-Elesin", right bank of the Lena River, Khangalassky District, found in 2023.

The information published in recent years on the records of saiga remains in the territory of Yakutia includes finds from the Yana River basin, Batagayka outcrop (2017, Protodyakonov *et al*., 2018) and Yunyugen outcrop (2016, Grigoriev *et al*., 2017); Kyra Sullar outcrop, Adycha River, Ozhogina River and Silyap River (Campos *et al*., 2010).

Radiocarbon analysis of three samples of saiga bones was carried out at the Center for Collective Use "Laboratory of Radiocarbon Dating and Electron Microscopy" of the Institute of Geography, Russian Academy of Sciences (Moscow, Russia) and the Center for Applied Isotope Research at the University of Georgia (USA).

The work uses the stratigraphic division corresponding to the scheme of the International Commission on Stratigraphy (2009) with the position of the lower boundary of the Quaternary at 2.58 million years, as well as the General Stratigraphic Scale of the Interdepartmental Stratigraphic Committee of Russia (2011). The names of the superhorizons and formations (suites) of the Neopleistocene of Yakutia are adopted in accordance with the resolutions of the Interdepartmental Stratigraphic Committee of Russia (1982, 2009).

Institutional and museum abbreviations: DPMGI — Diamond and Precious Metals Geology Institute, Siberian Branch of the Russian Academy of Sciences, Yakutsk; AS RS (Y) — Academy of Sciences of the Republic of Sakha (Yakutia), Yakutsk; ECY — Ecological camp "Yunyuges", Sottintsy village, Ust-Aldansky District, Yakutia; MBV — Museum of the Betenkes village, Betenkes village, Verkhoyansk District, Yakutia; OS — Oyskaya secondary school, Oy village, Khangalassky District, Yakutia.

Radiocarbon dating terminology abbreviations: BP — ^{14}C years before present; IGAN — laboratory code of the Center for Collective Use "Laboratory of Radiocarbon Dating and Electron Microscopy" of the Institute of Geography of the Russian Academy of Sciences, Moscow, and the Center for Applied Isotope Research of the University of Georgia, Athens, USA; KIA — laboratory code of the Leibnitz laboratory, Kiel, Germany; GV — laboratory code of the Center for Collective Use "Cenozoic Geochronology" of the Institute of Archaeology and Ethnography, Siberian Branch of the Russian Academy of Sciences, Novosibirsk; AA — laboratory code of the University of Arizona, Tucson, USA; AAR — laboratory code of the Aarhus AMS Centre, Aarhus University, Denmark.

Results

The analysis of saiga fossil records indicates that this species had a very wide range in the territory of Yakutia during the Late Pleistocene. Saiga inhabited valleys of the Lena, Vilyui, Olenek, Yana, Adycha, Indigirka, Kolyma rivers (as well as in the interfluves of the latter two rivers), it also occured on Primorsky lowlands and on Bolshoi Lyakhovsky Island (which was part of the mainland at that time).

Radiocarbon-dated or related finds indicate a fairly wide distribution of the saiga both during the Karginian interstadial (when this species was recorded in the basins of the Lena, Yana, Kolyma rivers, on the Primorsky lowlands and on the southern coast of Bolshoy Lyakhovsky Island), and during the Sartanian glaciation (basins of the Lena and Kolyma rivers, the interfluve of the Indigirka and Kolyma rivers) (Fig. 1, Table 1).

Finds in the middle reaches of Lena River supplement information about the range of the species during the Late Pleistocene of Eastern Siberia. Judging by previous finds (Chersky, 1891; Sher, 1967; Vangengeim, 1977; Lazarev & Tomskaya, 1987; Baryshnikov *et al*., 1998; Klementiev, 2013; Campos, 2010) and the new finds, it extended from the Baikal region to the Arctic coast.

There are no currently known Holocene finds of saiga remains in Yakutia, and in the Northeast Asia in general. This may be an indication of a regional extinction of this species by the end of the Late Pleistocene.

Until now, there are no finds of saiga in the valley of the Aldan River at Upper Paleolithic human sites and in the sites with the Mammoth fauna (Vangengeim, 1977; Mochanov, 1977; Lazarev, 2008; Boeskorov & Baryshnikov, 2013). It can be assumed that the adjacent elevated and hilly areas were not inhabited by this antelope. There are no finds of saiga in many uplands of Yakutia and Chukotka. Quite numerous remains of the Pleistocene saiga have been found in Yakutia on smaller elevations in river valleys among the Verkhoyansk Mountains (Fig. 1, Table 1).

Modern *S. tatarica* lives in herds of up to 500–1000 or more individuals, and during seasonal concentrations they can gather in large herds of many thousands (Zhirnov, 1998). Finds of saiga remains in the Middle and Upper Paleolithic caves of Western and Eastern Europe are quite numerous (Baryshnikov & Krakhmalnaya, 1994b; Kahlke, 1999). In the north of Eastern Siberia, although saiga remains are quite common, usually they are not numerous, one or two bones even in larger localities. This likely accounts for taphonomic reasons, or it can be assumed that the saiga did not form large herds during the Pleistocene of Yakutia.

Discussion

The place and time of origin of the saiga still remains unclear. A.V. Sher himself, supposedly including the saiga in the Olyorian fauna of the Early Pleistocene (Sher, 1986), nevertheless, he later specified that the

Table 1. Fossil saiga finds in Yakutia.

No. on Fig. 1	Locality or human site	Deposits and/or geologic age, radiocarbon date, years before present	Source
1	Khaiyrgas Cave (south-western Yakutia)	Sartanian glaciation, dates of the enclosing horizon 13700–13200	Kuzmin *et al*., 2017
2	Sullar-Myran outcrop, Middle Lena	Sartanian glaciation, deposits of the Dyolkuminskaya suite (20–12 thousand years ago)	this work
3	Tumara River, 40–45 km upstream of the mouth	Upper Pleistocene deposits	Sher, 1967
4	Near mouth of the Batamay River	Sartanian glaciation, 13180±35 (IGAN-8213)	this work
5	Lena River, 46 km upstream from Sangary settlement	Karginian interstadial, 26070±280 (AA-3894)	Guthrie *et al*., 2001
6	Vilyui River, near the city of Vilyuysk	Late Pleistocene	Chersky, 1876; Sher, 1967
7	Vilyui River, vicinity of the city of Vilyuysk	Late Pleistocene	Sher, 1967
8	Vilyui River, 29 km upstream of the city of Vilyuysk	Upper Pleistocene deposits	Alexeev, 1961; Sher, 1967
9	Markha River, a tributary of the Vilyui River	Pleistocene	Campos *et al*., 2010
10	Buolkalakh River, left tributary of the Olenyok River	Late Pleistocene	Sher, 1967; Baryshnikov & Tikhonov, 1994
11	Mouth of the Olenyok River	Late Pleistocene	Sher, 1967; Baryshnikov & Tikhonov, 1994
12	The delta of the Lena River, the Mogoe channel, above the Khaigalakh settlement	Late Pleistocene	Chersky, 1891; Baryshnikov & Krakhmalnaya, 1994b
13	Bolshoi Lyakhovsky Island (obviously, south coast)	Late Pleistocene	Chersky, 1891; Baryshnikov & Krakhmalnaya, 1994b

Table 1 (*end*)

14	Bolshoi Lyakhovsky Island (south coast, west of Zimovye River mouth, cape shore)	Karginian interstadial, about 34000	Kuznetsova & Tesakov, 2003
		Karginian interstadial, 46790±1180 (KIA-10682)	Sher *et al*., 2005
		Karginian interstadial (?) >52380	this work
		Karginian interstadial (?) >53262	this work
15	Svyatoy Nos outcrop	Late Pleistocene	Nikolsky & Basilyan, 2003
16	Junyugen outcrop, Yana River (Bunge-Toll site)	Karginian interstadial, dating of the bone layer 47600±2300–36300±640	Pitulko *et al*., 2014; Grigoriev *et al*., 2017
17	Batagayka outcrop, Yana River	Late Pleistocene	Protodyakonov *et al*., 2018
18	Ulakhan Sullar outcrop, Adycha River	Karginian interstadial, 42110±280 (IGAN-8214)	this work
		Karginian interstadial (?), >46520 (IGAN-8215)	this work
		Early Pleistocene (?)	Lazarev, 2008
		Early Pleistocene (?)	Baryshnikov *et al*., 1998
19	Kyra Sullar outcrop, Adycha River	Pleistocene	Campos *et al*., 2010
20	Oskhordokh outcrop, Adycha River	Pleistocene	Campos *et al*., 2010; this work
21	Khaptashinskiy Yar (Loc.4118)	Karginian interstadial, 27740±330 (AA-3891)	Campos *et al*., 2010
22	Achchygyi Allaikha outcrop	Deposits of the Allaikhovskaya Formation of the Middle Pleistocene	Kaplina *et al*., 1983
23	Keremesit River outcrop	Deposits of the Keremesit Formation, Middle Pleistocene	Baryshnikov *et al*., 1998
24	Bolshoi Khomus–Yuryakh River outcrop	Pleistocene	Baryshnikov *et al*., 1998; Campos *et al*., 2010
25	Creek Balyktakh, left tributary of the Rassokha River	Deposits of the Karginian age (55000(60000)–25000	Lazarev & Tomskaya, 1987
26	Chukochya River, Loc. N 17, Kolyma Lowland	Late Pleistocene	Lazarev & Tomskaya, 1987
27	Chukochya River, Svyatoi Nos outcrop (Loc. N 21), Kolyma Lowland	Late Pleistocene	Lazarev, 2002
28	Chukochya River, Loc. N 23, Kolyma Lowland	Early Pleistocene (?)	Virina *et al*., 1984; Baryshnikov *et al*., 1998
29	Chukochya River, Loc. N 25, Kolyma Lowland	Late Pleistocene	Lazarev & Tomskaya, 1987
		Early Pleistocene (?)	Baryshnikov *et al*., 1998
30	Chukochya River, Loc. N 34, Kolyma Lowland	Sartanian glaciation, 14495±80 (AAR11391)	Campos *et al*., 2010
31	Chukochya River, lower stream, Kolyma Lowland	Pleistocene	this work
32	Alyoshkina Zaimka outcrop, Kolyma Lowland	Sartanian glaciation, dating of the Aleshkinskaya Formation 15000±200–14980±100	Sher *et al*., 1976
		Sartanian glaciation, 13260±250 (AA-3895)	Campos *et al*., 2010
33	Ozhogina River, Loc. 3660, Kolyma Lowland	Sartanian glaciation, 15460±130 (AA-3892)	Campos *et al*., 2010
34	Silyap River, Kolyma Lowland	Karginian interstadial, 34400±750 (AA-3893)	Campos *et al*., 2010
35	Locality “Kyzyl-Elesin”, right bank of the Lena River, Khangalassky District	Late Pleistocene	this work

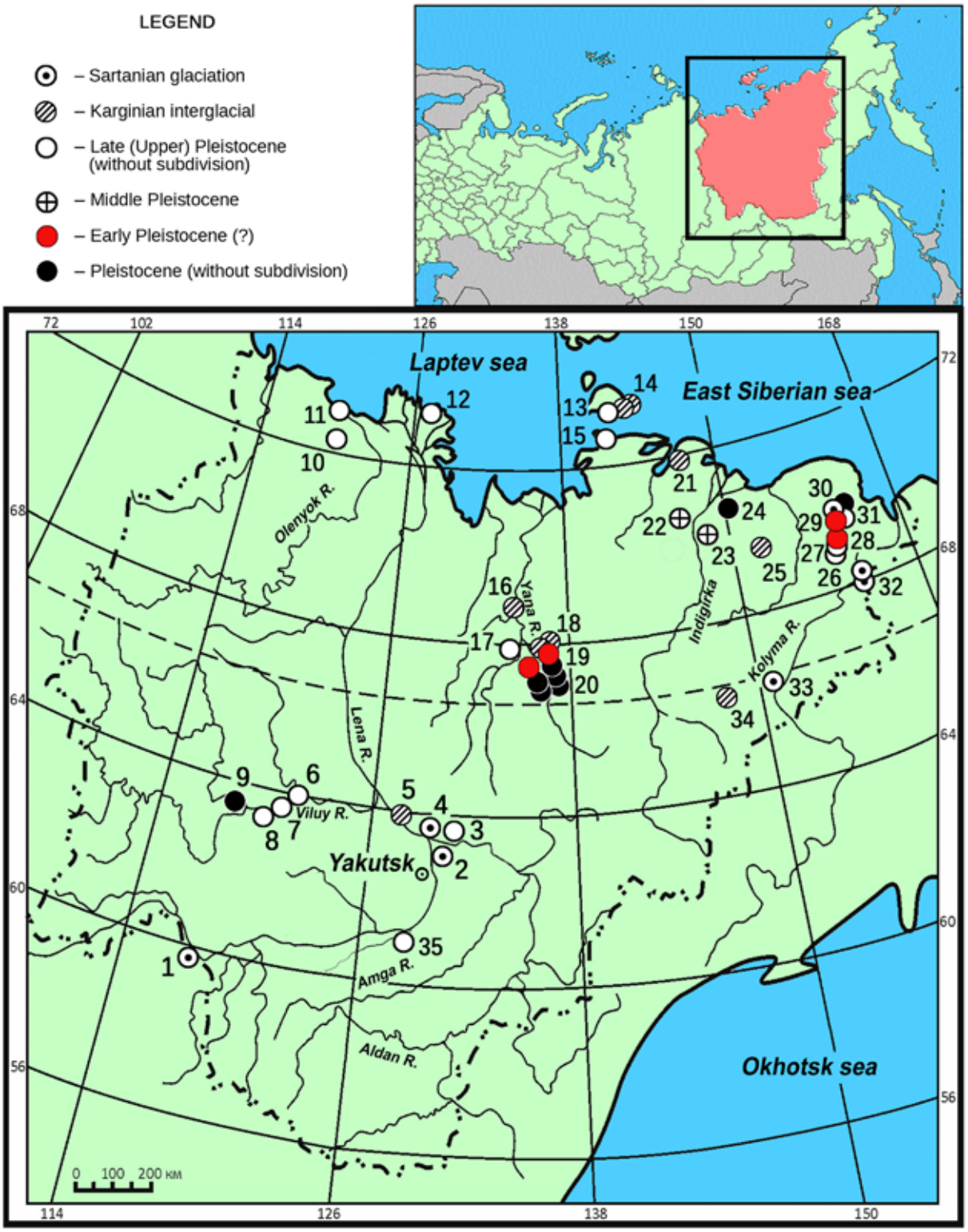

Fig.1. Locations of the *Saiga* sp. and *Saiga tatarica borealis* on the territory of Yakutia (numbers in circles correspond to the location numbers in Table 1). Finds from the Middle Pleistocene and presumably the Early Pleistocene are attributed to *Saiga* sp. (Sher, 1986; Sher *et al*., 1987; Baryshnikov *et al*., 1998).

two finds of *Saiga* sp. remains from the Bolshaya Chukochya River were surface material (not *in situ*), and only by the degree of their preservation can one assume that they belong to the Olyorian Formation (Baryshnikov *et al*., 1998). The finds from the Ulakhan Sullar outcrop were also not found *in situ*, they are surface material, and only by their color and degree of preservation they were attributed by A.V. Sher (Baryshnikov *et al*., 1998) to the Olyorian fauna. Thus, there is still no convincing evidence that the saiga existed in Northern Asia in the Early Pleistocene.

Other specialists did not list the saiga among the representatives of the Olyorian fauna (Vangengeim, 1977; Lazarev & Tomskaya, 1987; Lazarev, 2008; Vereshchagin, 2002).

A.V. Sher himself noted that the most ancient reliable finds of saiga remains in Northeast Asia are the bone of *Saiga* sp. found *in situ* at the Achchygyi Allaikha and Keremesit outcrops (Indigirka River Basin) (MIS-11–MIS-8) (Kaplina *et al*., 1980; Sher *et al*., 1987; Baryshnikov *et al*., 1998). At that time, the saiga was already encountered in Western Europe, Western Siberia, and Kazakhstan (see above), and therefore, we believe, it is not yet very clear where the saiga's place of origin is. However, it is obvious that the fossil saiga was a typical representative of the periglacial fauna, fully adapted to the cold and dry climate of the nonglacial region of Siberia, and we agree with the opinion that the place of origin of the saiga is most likely not in the steppe zone, but in the Arctic zone of Siberia (Baryshnikov *et al*., 1998). Judging by the available radiocarbon dating of saiga remains (or containing deposits) from the territory of Yakutia, it can be stated that the distribution of this species was very similar during the Karginian thermochron and the Sartanian glaciation. This looks somewhat paradoxical, since the Karginian time is considered by many researchers as a much warmer and more humid time in Siberia (with a climate from moderately cold to subarctic), compared with the time of the Sartanian glaciation (the climate was predominantly subarctic-arctic) (Volkova *et al*., 2010). At the same time, in the north of Yakutia, almost the same set of species of large mammals was recorded during the periods of the Karginian thermochron and the Sartanian glaciation (Sher, 1997a; Lazarev, 2008; Boeskorov & Baryshnikov, 2013). Analyzing this paradox, A.V. Sher (1997a) concluded that the "interglacial" vegetation of northeastern Siberia cannot be compared with the modern taiga formation, since it slightly differed from the tundra-steppe vegetation of the cold phases of the Late Pleistocene, representing a light birch forest with an admixture of larch, shrubs and herbaceous associations. Apparently, this circumstance also explains the similarity of the distribution of the saiga in the territory of Yakutia during the Karginian thermochron and the Sartanian glaciation.

The recent saiga is a stenotopic mammal in terms of relief and it inhabits exclusively flat areas throughout its range from region near the Caspian Sea to Mongolia and, as a rule, avoids mountainous and rugged terrain. At the same, saigas can live in hilly terrain in summer if the vegetation there is more lush. Saigas cross smooth hills, knolls, and plateaus every year during their migrations (Bannikov, 1963; Zhirnov, 1998). Saigas can be forced out of the plains into the mountains by high snow levels. For example, during the snowy winter of 1975/76, saigas were noted high in the Zailiyskiy Alatau mountains (2400 m above sea level) (Zhirnov, 1998). Approximately the same picture is revealed by the fossil finds of the saiga: the majority of these finds are confined to flat areas, but there are also Pleistocene finds of saiga in the mountainous regions of Europe, in the Urals, in the uplands of southern Siberia (Baryshnikov & Tikhonov, 1994; Baryshnikov *et al*., 1998; Kahlke, 1999). To reach the Lost Chicken Creek site in Alaska, where the remains of the Late Pleistocene saiga were found, it likely had to travel through extremely rugged terrain, reaching altitudes of about 1500 m above sea level (Harington, 1998). It is possible that the fossil finds of saigas found in high areas are the result of migrations of these mammals or their forced departure from the plains to the mountains. Nevertheless, finds in the Verkhoyansk Mountains area are quite numerous, but they are all located at low altitudes (130–250 m above sea level) and suggest that animals could penetrate into intermountain basins along the river valleys (Fig. 1).

The saiga is a typical representative of the cryoxerotic (tundra-steppe) fauna. Analysis of the morphology and ecology of the modern and fossil saiga shows that it must have lived in a rather dry and cold climate, thin snow cover and even, fairly dense ground (Sher, 1967; Vereshchagin & Baryshnikov, 1980). The saiga has a large specific weight load on the footprint area up to 600–800 g/cm2 (Heptner *et al*., 1961), and therefore the maximum snow depth for it is 40–50 cm (Nasimovich, 1955). The snow deeper than 20 cm hinders saiga moving (Sher, 1967; Vereshchagin & Baryshnikov, 1980). In comparison, the reindeer *Rangifer tarandus* (Linnaeus, 1758), well adapted to movement on snow, has a specific weight load on the footprint area of 140–180 g/cm^2 (Heptner *et al*., 1961; Nasimovich, 1955) and the maximum snow depth for it is 70–80 cm (Nasimovich, 1955).

By the end of the Pleistocene, with climate changing, expressed in warming and humidization, the depth of snow cover during winter increased in the north of Eastern Siberia, which became an insurmountable factor for saigas. The climate change, that led to the degradation of the cold steppe zone and its replacement by the tundra and taiga zones, caused the extinction of the saiga antelope in Northeast Asia and Beringia.

The saiga antelope dispersed from Asia to North America along the Bering Land Bridge in the Pleistocene. Moreover, apparently, such migrations were repeated, they could occur during the period of glaciation, when the sea level dropped and the Bering Land Bridge formed between Eurasia and North America. Already in the Middle Pleistocene, judging by the finds of S. Harington (Harington, 1981), the saiga appeared

in Alaska. During the Late Pleistocene, the saiga also appears to have entered East Beringia, especially during the maximum of the Sartanian glaciation (Sher, 1967; Harington & Cinq-Mars, 1995; Kahlke, 1999).

Saiga remains have been found in at least 11 localities in Alaska and Yukon (Frick, 1937; Guthrie *et al*., 2001; Harington, 1981, 2011; Harington & Cinq-Mars, 1995; Porter, 1988; Zazula *et al*., 2006). Radiocarbon dates indicate that the saiga lived there both during the Middle Wisconsinan (approximately corresponds to the Karginian time of Eastern Siberia) and during the Late Wisconsinan (=Sartanian glaciation), in general, from 37000 to 12200 years ago. There are no Holocene remains of the saiga in North America, that is, it apparently died out there synchronously with Northeast Asia, at the end of the Pleistocene.

At the same time, until now, the single known record of saiga between the Kolyma Lowland and Alaska is the remains of this species on Ayon Island (Western Chukotka) (Agadjanian, 1979). No new finds of *S. tatarica* remains have been published from the territory of Chukotka and, according to the personal communications by archaeologist Dr. S.B. Slobodin and paleogeographer Dr. S.L. Vartanyan, saiga remains were not found here at human sites and localities of Mammoth fauna. In our opinion, this can be explained by the fact that the main routes of saiga migration along the Bering Land Bridge from Asia to America passed through lowlands and were flooded during the rise of the sea level in the Holocene.

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