



THE SAIGA ANTELOPE (*SAIGA TATARICA*) IN THE QUATERNARY OF UKRAINE: DISTRIBUTION AND MORPHOLOGY

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Abstract

The article analyses the findings of fossils, archaeological sites, and historical literature on the distribution of saigas in Ukraine during the Quaternary period. Most findings of saiga fossils are concentrated in the Crimea and the Northern Black Sea region. However, the northernmost record localities of the species are known from the territory of Rivne Oblast. The oldest finds date back to the Middle Palaeolithic period. The most famous sites of the Middle Palaeolithic period are Illinka Cave (Odesa Oblast) and a number of Crimean sites, such as Aji-Koba, Alimov's Canopy, Zaskelna V, Temna Cave, and Prolom II. Saiga remains were found in the faunal collections of Late Palaeolithic sites, including Anetivka II (Odesa Oblast), Buran Kaya IV, and Suren I in the Crimea. Remains of saiga from the Mesolithic period were discovered in Odesa (Myrne) and Zaporizhzhia oblasts (Kamyanna Mohyla), and in the Crimea (Syuren II, Alimovskiy canopy, Zamil-Koba, etc.). Remains from the Neolithic, Bronze, and Early Iron Ages come from Odesa (Usatove) and Kherson (Mykhailivka) oblasts. The analysis of the history of the saiga's distribution range in Ukraine allows us to determine the probability of the first migrations of the species to the region during the Pleistocene (MIS5–MIS2). The relatively large number of localities where saiga remains have been found suggests that favourable conditions for the species' existence were formed in the territory of modern Ukraine at that time. Xerophytization of steppe phytocoenoses contributed to the saiga's spread throughout history. Until the mid-18th century, the saiga was a common game species, hunted for its meat and horns. The reduction of the species' range and population in Ukraine took place during the 18th century under the pressure of uncontrolled hunting, intensification of agriculture (which led to changes in natural habitats and seasonal migration routes), nomadic cattle breeding (which caused depression of pastures and competition for trophic resources), and, in some cases, climatic disasters associated with excessive snow cover. The final disappearance of the species from the fauna of Ukraine occurred in the first half of the 19th century. The data on morphological parameters of saiga remains from some Pleistocene and Holocene archaeological sites are presented.

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Антилопа сайгак (*Saiga tatarica*) у четвертинному періоді України: поширення та морфологія

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Резюме. Проведено аналіз знахідок викопних решток, археологічних пам'яток, а також історичних літературних джерел щодо поширення сайгака на теренах України впродовж четвертинного періоду. Найбільша концентрація викопних решток сайгака зосереджена в Криму та Північному Причорномор'ї. Проте їх крайня північна локація розташовується на території Рівненської області. Найдавніші знахідки датуються середньопалеолітичним часом. Найбільш відомими місцезнаходженнями середньопалеолітичного часу є Печера Іллінка (Одеська обл.), а також низка пам'яток Криму — Аджі-Коба, Алімівський навіс, Заскельна V, Печера Темна та Пролом II. Рештки сайгака, були виявлені у фауністичних колекціях пам'яток пізнього палеоліту, зокрема Анетівка II (Одеська область), Буран Кая IV, Сюрень I в Криму. Рештки сайгака часів мезоліту були виявлені в Одеській обл. (Мирне), Запорізькій обл. (Кам'яна могила), а також в Криму (Сюрень II, Алімівський навіс, Заміль-Коба та ін.). За часів неоліту, бронзи та раннього залізного віку — в Одеській (Усатове) та Херсонської обл. (Михайлівка). Аналіз історії ареалу сайгака на території України дозволяє визначити вірогідність перших міграцій виду в регіон за часів плейстоцену (MIS5–MIS2). Порівняно велика кількість місцезнаходжень, в яких виявлені рештки сайгаків, дозволяє вважати, що на теренах сучасної України на той час сформувалися сприятливі умови для існування виду. Розповсюдженню сайгака впродовж історичного часу сприяла ксерофітизація степових фітоценозів. До середини XVIII ст. сайгак був звичайним мисливським видом, який здобували заради м'яса та рогів. Скорочення ареалу та чисельності виду на території України відбулося впродовж XVIII ст. під тиском дії безконтрольного полювання, інтенсифікації землеробства (що стало запорукою зміни природних біотопів та шляхів сезонних міграцій), чового скотарства (яке спричинило депресію пасовищ та конкуренцію за трофічні ресурси), а також, в ряді випадків, кліматичних катаклізмів, пов'язаних з надлишком снігового покриву. Остаточне зникнення виду з фауни України відбулося в першій половині XIX ст. Наведені дані морфологічних показників решток сайгаків деяких плейстоценових та голоценових археологічних пам'яток.

Ключові слова: сайгак, географічне поширення, краніологія, четвертинний період, Україна.

Introduction

The saiga antelope (*Saiga tatarica* L., 1766) is a typical inhabitant of steppes and semi-deserts, being adapted to long-term, rapid, and frequent migrations. Habitats of the saiga are characterised by flat relief combined with low-growing and sparse semi-desert vegetation. Saigas avoid mountainous and dissected terrain [Zhirnov 1982]. Another factor that limits the species's distribution is the depth of the snow cover. At snow depth of over 8–10 cm and snow density of 0.27–0.31 g/cm³, these animals move to areas with a thinner snow cover [Zhirnov 1982]. When the depth of the snow is over 25 cm, the animals are unable to move [Heptner *et al.* 1961]. The presence of saigas in a particular locality is a marker of semi-desert and steppe habitats, which cover large plain areas. In addition, saigas are also markers of areas with little snow [Malikov 2018].

According to palaeontological studies, the saiga had a very wide geographic range in the Pleistocene (2.58–0.012 Mya), stretching from Alaska in the east to England in the west, from the New Siberian Islands in the north to the Karatau in the south [Baryshnikov *et al.* 1998]. During the Pleistocene, the saiga was part of the mammoth mammal assemblage, which also included the woolly mammoth (*Mammuthus primigenius* Blumenbach, 1799), the woolly rhinoceros (*Coelodonta antiquitatis* Blumenbach, 1799), the reindeer (*Rangifer tarandus* L., 1758), the cabaloid *Equus latipes* Gromova, 1949, the cave bear (*Ursus spelaeus* Rosenmüller, 1794), and other species. The distribution of the saiga in the Pleistocene was facilitated by the favourable climatic conditions of the tundra-steppe zones and low human impact. In this period, human dispersal was closely related to migrations of herds of herbivores, which is evidenced by osteological materials recovered from archaeological sites and natural localities. The saiga's meat, similarly to that of other ungulates, was

consumed, while its horns were valued as trophies. Therefore, the saiga was an important game for humans during different historical periods, including the Stone Age hunters.

The oldest saiga remains are known from Yakutia and they are dated to 1.2–0.6 Mya (Olyorian complex) [Ratajczak *et al.* 2015]. The species migrated from Yakutia and Central Asia to Europe in the late Middle Pleistocene and during the Eemian interglacial and the Last Glacial Period [Nadachowski *et al.* 2016].

In the Late Pleistocene of Western Europe, fluctuations in temperature during glaciations and the waves of saiga migration from Central Asia to Eastern and Central Europe seem to be interconnected. In the Late Pleistocene, saiga herds migrated from Central Asia during the warm interglacials. During the Last Glacial Period (Dryas), the saiga migrated during cold phases as well. Thus, the species appeared from Yakutia and Central Asia in the territory of Southern Europe. In Europe, the saiga was present in the Late Pleistocene and gradually disappeared during the Holocene [Nadachowski *et al.* 2016].

Late Pleistocene remains of the saiga were recorded in Kazakhstan, on shoals of the rivers Irtysh, Ural, and Nura [Kozhamkulova 1969; Kosintsev 2003], as well as in Uzbekistan [Ishunin, 1985]. The eastern limits of the saiga's distribution in the Pleistocene reached the north-east of Siberia, the Mackenzie River valley in Canada, and Bailey Island. The importance of the saiga as a game hunted by ancient humans is also indicated by cave paintings found in a number of grottos in France [Braun & Zessin 2018].

Pleistocene and Holocene remains of the saiga are also known from the territory of present-day Ukraine. The history of formation of the mammal fauna in the territory of Ukraine is an important research topic and the aim of this study was to clarify the geographic range of the saiga in the territory of Ukraine during the Pleistocene and Holocene, as well as to present measurements of saiga remains from the territory of Ukraine.

Materials and Methods

The main source of information on the saiga's distribution in past geological periods is the data on species composition of the fauna at sites of ancient humans, and, to a lesser extent, natural localities. Our knowledge on geographic range limits of the saiga during past eras depends on the level of studies of archaeological sites and natural record localities of the species.

As of today, most of the materials recovered from archaeological sites have been published. In the mid-20th century, the bulk of data was collected by I. Pidoplichko [Pidoplichko 1956]. In the second half of the 20th century, the taxonomic composition of archaeozoological collections from the Northern Black Sea region and Crimea was studied by V. I. Bibikova [Bibikova 1984]. Her student, A. Starkin identified materials from the sites Anetivka I and Anetivka II (Odesa Oblast) [Bibikova & Starkin 1989]. Recently, palaeontological materials from the Crimea have been studied by B. Ridush and colleagues [Ridush *et al.* 2013; Salavert *et al.* 2014; Ratajczak *et al.* 2015]. The morphology and taphonomy of the saiga from the Buran-Kaya III site were analysed in detail by M. Patou-Mathis [Patou-Mathis 2004]. Hunting techniques and their specifics based on materials from the same locality were reconstructed by F. Lanoe and colleagues [Lanoe *et al.* 2015]. Issues of fauna extinctions in the Pleistocene and Holocene were also studied by P. Putshkov [Putshkov 1994]. This present study is based on the review of all available data on the saiga's distribution in the past. Additionally, morphometric measurements of the species' remains were also taken.

Chronological limits and dating of the mentioned localities were described according to the respective authors. For Pleistocene sites, absolute radiocarbon dating is used. All dates in the text are given as uncalibrated (BP, before present) with the name of the laboratory and laboratory number. Absolute radiocarbon dates and Marine Isotope Stages (MIS) are also used. The absolute dates cover MIS 5 (130–80 ka) and MIS 2 (29–14 ka). The beginning of the Holocene is considered as 11.7 ka.

The measurement scheme for skull and bone dimensions proposed by A. Driesh [Driesh 1976] was used to study the morphometric parameters of saiga remains. All measurements were taken with a calliper with an accuracy of 0.1 mm.

The saiga in the Pleistocene of Ukraine

Most archaeological sites and localities with saiga remains in Ukraine are concentrated in the Northern Black Sea region and the Crimean Peninsula (Table 1). All Pleistocene record localities of the saiga are dated to the Last Glacial Period (LGP).

The earliest locality with saiga remains is the Emine-Bair-Khosar Cave and the Middle Palaeolithic site Prolom II, which are located in the Crimea.

Today, the territory of Crimea is geographically isolated by waters of the Black Sea and the Sea of Azov. However, sea level was much lower in the Pleistocene. The most significant regression of the Black Sea took place 17–16 ka, when its level was –60 m compared to its modern level [Ivanov & Shmuratko 1982]. This opened migratory routes for terrestrial animals. In the Crimea, saiga remains were found both in the northern (lowland) part of the peninsula and in the yaylas (plateaus) and foothills of the Crimean Mountains.

During the Pleistocene, saigas were an important game for Middle and Late Palaeolithic humans. In the Crimea, Middle and Upper Palaeolithic sites are located only in the southern, mountainous part of the peninsula. In the northern, lowland part, such sites have not been found due to the geomorphological features of the area. Palaeolithic sites in the Crimean Mountains are of cave-type and they are located under cliffs or, in rare cases, in the mouths of karst caves. They provided efficient protection from bad weather and predators. Cave sites are multi-layered, which indicates that various groups periodically inhabited them for long periods. In the Crimean Mountains, most Middle and Upper Palaeolithic sites are located in valleys and gullies of the second sub-range. Separate sites are also located on yaylas—plateaus of the first sub-range. These include the Adji-Koba and Karabi-Tamchyn caves, which indicates that Middle and Upper Palaeolithic humans used the open landscape of yaylas, where ungulates also migrated, as pastures during the warm period of the year.

In the Crimea, V. I. Bibikova and N. G. Bilan described the ‘saiga-cervid’ faunal assemblage due to the prevalence of remains of these animals among materials collected at sites of these periods [Bibikova & Bilan 1979]. This faunal assemblage comprises remains of animals of open steppe and semi-desert (saiga, ass), and semi-open forest-steppe habitats (red deer, corsac, and brown bear). Noteworthy is that bones of representatives of closed forest habitats (wild boar, wildcat, and badger) are completely absent.

This composition of remains of large mammals at Middle Palaeolithic sites in the Crimean Mountains clearly indicates cold and dry climate. Although, at the same time, their diversity suggests that Neanderthals used the mosaic landscape of the second sub-range as hunting grounds: steppes of the cuesta’s plateau and forest-steppe habitats of river valleys. Another factor having a substantial impact on the presence and ratio of saiga remains among archaeozoological materials of the Middle Palaeolithic of the Crimean Mountains is the seasonal migrations of the species between winter pastures in the steppe and summer pastures on the yaylas.

Table 1. Pleistocene finds of saiga remains in the territory of Ukraine

Таблиця 1. Плейстоценові знахідки викопних сайгаків на території України

No.	Site	Dating of layers, BP	Location of the site	Author and year of study	References
1	Illinka Cave	Ki-11681, 27 500 ± 210 BP	Illinka, Odesa Raion, Odesa Oblast	T. Grytsay, 1938	[Pidoplichko 1956; Sapozhnikov 2005; Kavcik-Graumann <i>et al.</i> 2016]
2	Lypa	Pleistocene	Lypa, Dubno Raion, Rivne Oblast		[Pidoplichko 1956]
3	Buran-Kaya III	Layer 4 OxA-25670, 10 040 ± 45 BP; Layer 6-1 GrA-53942, 29 640 +170/-160; Layer 6-2 GrA-50460, 29 440 +190/-180; Layer 6-3 GrA-53939,	Aromatne, Bilohirsk Raion, AR Crimea	O. Yanevich, 1990–1995	[Yanevich <i>et al.</i> 2009; Pean <i>et al.</i> 2013]

No.	Site	Dating of layers, BP	Location of the site	Author and year of study	References
		29 040 +180/-170; Layer 6-4, 31 250 +2450/-1880; Layer 6-5 GrA-47318, 32 800 +230/-210			
4	Temna Cave (Kara-Koba)	Middle Palaeolithic	Peredove, Balaklava Raion, AR Crimea	Yu. Kolosov, 1952–1954	[Bibikova 1958]
5	Zaskelna V	Gra > 47 000–28 850 ± 400	Bilohirsk, AR Crimea	Yu. Kolosov, 1969–1985	[Kolosov, Stepanchuk 2002]
6	Emine-Bair-Khosar Cave	Layer Ba2, unit F Poz-41676, 40 510 ± 630; GdA-4617, 32 430 ± 4617	Chatyr-Dag massif, AR Crimea	B. Ridush, K. Stefaniak, 2012–2013	[Ridush <i>et al.</i> 2013]
7	Anetivka II	LE-2424, 18 040 ± 150; LE-4610, 19 088 ± 980; LE-2947, 19 170 ± 120	Anetivka, Voznesensk Raion, Mykolaiv Oblast	V. Stanko, 1978–2007	[Bibikova 1984; Stanko 1996; Hlavenchuk <i>et al.</i> 2014]
8	Adji-Koba	Lower layer GrA-11442, 46 500 ± 500	Pcholyne, Bilohirsk Raion, AR Crimea	G. Bonch-Osmolovskiy, 1932–1933	[Vekilova 1971; Stepanchuk <i>et al.</i> 2004, p. 43, table 2]
9	Zaskelna VI	Layer II Oxa-4131, 30 110 ± 630	Bilohirsk, AR Crimea	Yu. Kolosov, 1969–1985	[Kolosov, Stepanchuk 2002; Chabai <i>et al.</i> 1998]
10	Prolom II	Layer I; Ki-10745, 24 550 ± 300; Ki-10895, 22 800 ± 600	Prolom, Bilohirsk Raion, AR Crimea	Yu. Kolosov, 1981–1997	[Ratajczak <i>et al.</i> 2015; Stepanchuk 1993; Stepanchuk <i>et al.</i> 2004]
11	Kabazi II	Oxa-4771, 35 100 ± 850; Oxa-4770, 31 550 ± 600; Oxa-4858, 32 200 ± 900	Malynivka, Bakhchysarai Raion, AR Crimea	K. Merezkovskiy, 1880–1882	[Vekilova 1971 Stepanchuk <i>et al.</i> 2004]
12	Shaitan-Koba	Middle Palaeolithic	Skalyste, Bakhchysarai Raion, AR Crimea	G. Bonch-Osmolovskiy, 1929–1930	[Kolosov 1972]
13	Kiik-Koba	Middle Palaeolithic	Zuia, AR Crimea	G. Bonch-Osmolovskiy, 1924	[Vekilova 1971]
14	Starosillya	Layer h1, OxA-4134, 35 510 ± 117; Layer h2, OxA-8249, 28 200 ± 440	Bakhchysarai, AR Crimea	O. Formozov, E. Marks, D. Kraynov, 1952–1956, 1993–1995	[Vekilova 1971; Chabai <i>et al.</i> 1998]
15	Siuren I	Layer Fb1, OxA-5115, 29 950 ± 700; Layer Fb2, Lv-2111, 10 520 ± 150; Layer G, Lv-2112, 25 000 ± 60; Layer GA, OxA-5154, 24 500 ± 600; Layer H, OxA-8249, 28 200 ± 440	Tankove, Bakhchysarai Raion, AR Crimea	G. Bonch-Osmolovskiy, 1924–1925	[Vekilova 1971; Kolosov & Stepanchuk 2002; Otte <i>et al.</i> 1996]
16	Krubera Cave	Pleistocene	Karabi-Yayla massif, AR Crimea		[Ratajczak <i>et al.</i> 2015]
17	Barmaky 2	Layer 2, OxA-38249, 15 610 ± 80; OxA-280440, 15 720 ± 80	Rivne	V. Chabai, 2018–2020	[Chabai <i>et al.</i> 2020; Chabai <i>et al.</i> 2022]
18	Vovchyi Grotto	Middle Palaeolithic	Simferopol	K. Merezkovskiy; G. Bonch-Osmolovskiy; O. Bader; 1880, 1924, 1937, 1939–40	[Vekilova 1971]

Such migrations are also indicated by finds of remains in Middle and Upper Palaeolithic cultural layers of Adjikoba (layers 3, 2-3, and 3) and in the Final Palaeolithic Shpan-Koba (layers of block 6) on the yaylas, where the saiga could only be present in summer due to the thick snow cover in winter [Vekilova 1971: 123–125; Yanevich 2021]. The very large number of saiga remains at some Middle Palaeolithic sites in the foothills of eastern Crimea, particularly at Buran-Kaya III (layer B) and Vovchyi Grotto (layer 6), in our opinion, reflects seasonal hunting on saigas during their migration to the largest yaylas of the peninsula—Karabi-Yayla and Subatkan-Yayla [Patou-Mathis 2004; Vekilova 1971: 123].

In the compiled database of sites with saiga remains prevail those of the Middle Palaeolithic associated with Neanderthals. This is mainly related to the higher density of archaeological sites dated to the Middle Palaeolithic compared to sites dated to the Late Palaeolithic.

In the continental part of Ukraine, saiga remains were recorded in the Northern Black Sea region, at the Illinka Cave locality. Large amounts of saiga remains are also known from the Upper Palaeolithic site of Anetivka II. The northernmost record localities of saiga remains include the Upper Palaeolithic site of Barmaky, near the city of Rivne, and the locality near the village of Lypa in Dubno Raion, Rivne Oblast [Pidoplichko 1956; Bibikova 1984]. This allows suggesting that the saiga could have entered far into continental Ukraine.

The saiga in the Final Pleistocene and Holocene of Ukraine

During the final stages of the Pleistocene (Allerød–Dryas III) and early stages of the Holocene (Preboreal), which were characterised by cold climate and the presence of open or semi-open habitats in the Crimean Mountains, the saiga continued to be an important game for ancient human communities. In particular, its remains are found in most archaeozoological collections of Final Palaeolithic and Early Mesolithic cave sites of the Crimean Mountains. The most abundant ones are known from Buran-Kaya III (layer 4) [Lanoe *et al.* 2015], Buran-Kaya Grotto, Siuren II, Alimov's canopy, Zamil-Koba I, Shan-Koba (layers 7-4) [Vekilova 1971: 125], and Shpan-Koba (layers 6-5 and 6-1).

Unlike the Pleistocene, when the saiga and reindeer were the main species hunted by ancient humans at Middle and Upper Palaeolithic sites, in the Middle Holocene (Boreal and Atlantic) due to climate warming and the spread of closed forest habitats in the Crimean Mountains, the main portion of remains belong to red deer, while starting from the Atlantic to wild boar and roe deer. At the same time, saiga remains are represented in large numbers in the Neolithic cultural layer 4 of the Buran-Kaya IV site [Salavert *et al.* 2014]. Considering that the site is located in the zone of deciduous forests, as well as the dominance in archaeological collections of this layer species associated with this type of habitat, the saiga appeared at the site in the Palaeolithic as prey during migration to the yayla [Salavert *et al.* 2014].

In the Northern Black Sea region, the number of sites with saiga remains increased in the Holocene. The saiga was found at such Mesolithic sites as Myrne (Odesa Oblast) and Kamiana Mohyla (Zaporizhzhia Oblast) (Table 2).

The saiga continues to be an important game for ancient humans in the Neolithic, Eneolithic, Bronze and early Iron ages too, which are synchronous with the climatic stages of the Atlantic, Subboreal, and Subatlantic. The saiga's spread in the Subatlantic, starting from 2500 BP, was facilitated by pasture digression as a result of cattle breeding¹.

It is suggested that the xerophitization of steppe phytocoenoses favoured the spread of saigas. During this time, hunting ceases to be the main factor that affects the geographic range and abundance of the species. In Eastern Europe, arable farming develops, a factor which has been associated with the disappearance of saigas in historical times [Mongait 1973]. The extinction of saigas in the territory of Ukraine was also facilitated by overgrazing by cattle.

¹ Merpert, N. 1968. Ancient history of the population of the steppe zone of Eastern Europe: *Abstract of Thesis*. Moscow, 1–30. [Russian]

Table 2. Holocene finds of saiga remains in the territory of Ukraine

Таблиця 2. Голоценові знахідки решток викопного сайгака на території України

No.	Site	Dating of layers, BP	Location of the site	Author and year of study	References
1	Kamiana Mohyla (stratigraphic position of remains is lost)	Ki-4023, 6120 ± 80; Ki-4024, 6180 ± 90; Ki-4025, 6376 ± 60	Myrne, Melitopol Raion, Zaporizhzhia Oblast	V. M. Danylenko, 1947	[Pidoplichko 1956; Bezusko 2006; Kotova 2002]
2	Mount Kyselivka (Zamkova Hora), Kyiv	6th–12th cent. CE	Kyiv	V. Kozlovska, 1938	[Pidoplichko 1956]
3	Didova Khata	4th–3rd cent. BP	Mykolaiv	V. Nikitin, 1968	[Snytko & Grebennikov 2015]
4	Pitukhivka	6th–1st cent. BP	Ostrivka, Ochakiv Raion, Mykolaiv Oblast	M. Ebert, 1910–1911	[Pidoplichko 1956]
5	Olvia	6th–1st cent. BP	Parutyne, Mykolaiv Raion, Mykolaiv Oblast	L. Slavin, 1935–1940, 1946–1948	[Pidoplichko 1956]
6	Mykhailivka	3 ka BP	Mykhailivka, Beryslav Raion, Kherson Oblast	O. Lagodovska, 1952–53	[Pidoplichko 1956]
7	Liubymivka	late 1 ka BP–early 1 ka CE	Liubymivka, Kakhovka Raion, Kherson Oblast	D. Dmitrov, 1952	[Pidoplichko 1956]
8	Buran-Kaya IV	Layer II1B; SacA-24016, 6360 ± 35; SacA-24018, 6610 ± 35; SacA-24017, 6955 ± 40	Aromatne, Bilohirsk Raion, AR Crimea	O. Yanevych, 1994–2013	[Salavert <i>et al.</i> 2014]
9	Alimov's canopy	(layer 1, 2, 3,4); Mesolithic (Shan-Koba and Murzak-Koba cultures)	Ukrainka, Simferopol Raion, AR Crimea	A. Stoliar, 1955–1956	[Vekilova 1971; Stolyar 1961]
10	Myrne	PI Г24, GrA-37336, 8280 ± 45; PIII B1, GrA-37335, 8350 ± 45; PII B5, GrA-37337, 8385 ± 45; PI Д22, GrA-37312, 8475 ± 45	Myrne, Odesa Oblast	V. Stanko, 1969–1976	[Stanko 1982; Biagi, Kiosak 2010]
11	Usatove	2400–2200 BP	Usatove, Odesa Raion, Odesa Oblast	V. Zbenovych, 1960–1970	[Zbenovych 1974]
12	Zapytiv IV	late 3rd–4th cent. CE	Zapytiv, Kamianka-Buzka Raion, Lviv Oblast	V. Shpak, A. Rozlutska, 2008	[Shyshak <i>et al.</i> 2010]
13	Siuren II	Mesolithic (layers of the Shan-Koba and Murzak-Koba cultures)	Tankove, Bakhchysarai Raion, AR Crimea	G. Bonch-Osmolovskiy; Ye. Vekilova, 1924–1925, 1954, 1955	[Vekilova 1971; Kolosov, Stepanchuk 2002]
14	Shpan-Koba	unit 3; 3-2, KIA-3686, 9760 ± 60; 3-2, Ki-5824, 9890 ± 80; 3-4, KIA-3685, 9930 ± 60; 3-5/6, KIA-3684, 9840 ± 50; 3-5/6, KIA-3683, 9940 ± 50	Subatkan-Yayla, top of the Chau-Ketau balka, 44°52'51"N, 34°23'37"E	O. Yanevych, 1988–1989	[Yanevich 2021]



Fig. 1. Pleistocene record localities of remains of *Saiga tatarica* in Ukraine (numbers correspond to the location numbers in Table 1).

Рис. 1. Плейстоценові місцезнаходження решток *Saiga tatarica* в Україні (цифри відповідають номерам місцезнаходжень в табл. 1).



Fig. 2. Holocene record localities of remains of *Saiga tatarica* in Ukraine (numbers correspond to the location numbers in Table 2).

Рис. 2. Голоценові місцезнаходження решток *Saiga tatarica* в Україні (цифри відповідають номерам місцезнаходжень в табл. 2).

The westernmost record locality of saiga remains from the Holocene of Ukraine is the city of Zapytiv in Kamianka-Buzka Raion, Lviv Oblast. The remains were found at the Zapytiv IV site of the Chernyakhiv culture (3rd–4th cent. CE) [Shyshak *et al.* 2010]. One bone was found during the study of Mount Kyselivka (Zamkova Hora) in the city of Kyiv [Pidoplichko 1956]. Considering that the objects found on the hill are dated to the 6th–12th century, it is possible that these remains appeared at the site due to commerce, trade, or gifting.

Historical sources help to trace back changes in the geographic range of the saiga. Notes on the species' distribution can be found in such documents as *Tractatus de duabus Sarmatiis* (Treatise on the Two Sarmatias) by Maciej Miechowita (1517), *Description d'Ukraine* by Guillaume de Beauplan (1660), and *Materials of the Code of Laws of the Russian State* (1649–1676). In particular, Beauplan had the opportunity to taste saiga meat during his stay in the territory of Cossack Ukraine in 1630–1648. He described this experience as follows:

'In the desert plains toward the porouys along the river Nieper, I have met a beast about as tall as a goose [goat?], but its hair very fine and smooth, and soft as sattin, when it has cast its coat, for afterwards it grows harsher, and is of a chestnut colour. This creature has two white shining horns; in the Russian language they call it Sounaky. Its legs and feet are very slender, has no bone in its nose; and when it will goes backward, not being able to graze otherwise. I have eaten of it, and the flesh is as good as kid; the horns which I keep as a rarity, being white, shining, and smooth' [Beauplan 1959: 473].

Data from these and other sources concerning the distribution of important industrial animals in historical times were published by S. Kirikov [Kirikov 1966]. In the Dnipro steppes, hunting on saigas became large-scale [Kirikov 1966], which is evidenced by the hunted saigas delivered to the imperial court in Saint Petersburg in 1753–1762. In the 1760s, in the Crimea and Taurida steppes, saigas were hunted due to the increasing demand for their horns [Kirikov 1966]. According to another author, by the mid-17th century the saigas reached the Siversky Donets River basin near the city of Chuhuiy, the banks of the Samara River, as well as the lands controlled by the Zaporizhzhian Cossacks [Baryshnikov *et al.* 1998]. These data show that in the first half of the 18th century the saiga was a common game species in Ukraine. Overhunting drove the species to become rare in the Dnipro–Bug steppe as early as the 1790s. Harsh, snowy winters (in 1788–1789, 1812–1813, 1825–1826, and 1847–1848) further contributed to the local extinction of the species [Kirikov 1966].

In the 19th century, arable farming developed actively and the number of settled population increases. Natural habitats of the saiga decrease in area, routes of seasonal migration are disrupted, and hunting intensifies. Thus, already at the beginning of the 19th century, in steppes between the Southern Bug and the Dnipro, saigas are present only episodically, while in the first half of the 19th century the species disappears from the territory of Ukraine [Kirikov 1966].

Morphological parameters of saiga remains

Several morphological parameters of saiga remains recovered from Pleistocene (Zaskelna V) and Holocene (Buran-Kaya IV, Pitukhivka, Olvia, and Myrne) archaeological sites were studied. Fragments of saiga remains found at Pleistocene and Holocene sites in Ukraine are shown in Fig. 3. Almost all bones recovered from Mesolithic sites are crushed by humans and thus only a few of them can be measured.

Morphometric parameters of saiga from Zaskelna V

This grotto site is located 7 km north of the city of Bilohirsk (AR Crimea). There are materials in the studied collection from layer IIB, including 16 bone fragments that belong to at least 5 individuals. The morphological parameters of some well-preserved bone fragments are presented in Table 3.

Morphometric parameters of saiga from Buran-Kaya IV

This Neolithic grotto site is located 5 km north of the village of Aromatne in Bilohirsk Raion, AR Crimea. Materials from the layer IIIB were measured. The total number of saiga remains found in this layer is 82 bone fragments that belong to at least 3 individuals. The morphological parameters of some well-preserved bone fragments are presented in Table 3.

Morphological parameters of saiga from Myrne

This Mesolithic site is located in the village of Myrne in Kiliia Raion, Odesa Oblast. At this site, 62 fragments of saiga bones were found that belong to at least 6 individuals. The morphological parameters of some bone fragments are presented in Table 3.



Fig. 3. Fragments of saiga remains: (a) distal part of the tibia from Zaskelna V; (b) distal part of metacarpal from Zaskelna V; (c) first phalanx from Pitukhivka; (d) distal part of the humerus from Pitukhivka; (e) distal part of the humerus from Myrne; (f) distal part of the humerus from Zaskelna V; (g) skull fragment with horns from Pitukhivka; (h) mandible fragment from Myrne; (i-j) horn fragment from Olvia; (k) horn fragment from Pitukhivka; (l) horn fragment from Myrne.

Рис. 3. Фрагменти решток сайгака: (a) дистальна частина великогомілкової кістки з пам'ятки Заскельна V; (b) дистальна частина п'ясткової кістки з Заскельної V; (c) перша фаланга з пам'ятки Пітухівки; (d) дистальна частина плечової кістки з Пітухівки; (e) те саме з Мирного; (f) те саме з Заскельної V; (g) фрагмент черепа з рогами з Пітухівки; (h) фрагмент нижньої щелепи з Мирне; (i-j) фрагмент рогу з Ольвії; (k) те саме з Пітухівки; (l) фрагмент рогу з Мирного.

Table 3. Morphological parameters of remains of saiga limb bones from Pleistocene and Holocene archaeological sites in Ukraine

Табл. 3. Морфологічні показники решток кісток кінцівок сайгака з археологічних плейстоценових та голоценових пам'яток на території України

Site	Humerus			Astragalus					Tibia			Metatarsal	
	n	Bd	Bt	n	Dm	Gli	Di	Glm	n	Bd	Dd	n	Bd
Zaskelna V	2	34.1 ± 1.52	32.1 ± 0.28	3	17.5 ± 1.10	30.3 ± 1.19	16.4 ± 1.05	27.7 ± 0.71	3	26.5 ± 4.08	20.9 ± 1.67	4	25.4 ± 0.94
Buran-Kaya IV	5	30.9 ± 4.00	27.8 ± 4.7	2	15.7 ± 0.58	28.2 ± 1.08	16.7 ± 0.76	26.0 ± 0.06	5	27.9 ± 4.01	21.8 ± 1.30	–	–
Myrne	1	26.4		2	17.9 ± 0.51	30.6 ± 0.68	17.3 ± 0.46	30.2 ± 0.35	–	–	–	–	–
Pitukhivka	1	35.3	29.1	–	–	–	–	–	–	–	–	3	23.8 ± 0.51

Note: Bd, greatest distal breadth; Bt, breadth of the trochlea; Di, greatest lateral depth; Glm, greatest medial length; Gli, greatest lateral length; Dm, greatest medial depth; Dd, greatest distal depth.

Morphometric parameters of saiga from Pitukhivka

This site is a necropolis in a rural area near Olvia, which is located nearby to the village of Ostrovka in Ochakiv Raion, Mykolaiv Oblast. At this site, six fragments of saiga bones were found that belong to at least five individuals. The morphological parameters of some bone fragments are presented in Tables 3–4.

Morphometric parameters of saiga from Olvia

This site is an ancient city located in the village of Parutyne in Mykolaiv Raion, Mykolaiv Oblast. The studied collection of saiga bones comprises 41 fragments that belongs to at least 31 individuals. The morphological parameters of some skull fragments are presented in Table 4.

Comparison of data

Morphometric parameters of saigas from the Pleistocene (Zaskelna V) and Holocene (Buran-Kaya IV, Myrne, and Pitukhivka) were compared and analysed in order to reveal any potential differences. The data from Table 3 were used. Morphometric parameters of saigas from the Pleistocene site were accepted for 100%. The results of comparisons are presented in Table 5.

It was revealed that the characters Dm, Gli, and Glm of the astragalus from the Pleistocene site of Zaskelna V are larger compared to those in saigas from the Holocene site of Kuran-Kaya IV, but are smaller by 0.99–9.02% from those in saigas from the Holocene site of Myrne.

The humerus from the Pleistocene site of Zaskelna V is larger in the character Bt by 9.34% than that from the Holocene site of Pitukhivka and by 13.39% than that from the Holocene site of Buran-Kaya IV. On the other hand, in the character Bd, this bone is larger by 9.38% than that from the Holocene site of Buran-Kaya IV and smaller by 3.51% than that from the Holocene site of Pitukhivka. The tibia from the Pleistocene site of Zaskelna V is smaller in the characters Bd and Dd than that from the Holocene site of Buran-Kaya by 5.28% and 4.3%, respectively. In the character Bd, the metatarsal from the Pleistocene site of Zaskelna V is larger by 6.29% than that from the Holocene site of Myrne.

Discussion

The analysis of the history of the saiga's geographic range in the territory of Ukraine allows suggesting the first migrations of the species to the region during the Pleistocene. The relatively large number of sites at which saiga bones were found indicates that favourable conditions for the species had already formed by that time in the territory of present-day Ukraine.

Table 4. Morphological parameters of saiga horn fragments from Holocene archaeological in Ukraine

Табл. 4. Морфологічні показники фрагментів рогів сайгака з голоценових археологічних пам'яток в Україні

Site	Bone core of the left horn			Bone core of the right horn				
	n	Measurement No. 32*	Measurement No. 40**	Measurement No. 41***	n	Measurement No. 32*	Measurement No. 40**	Measurement No. 41***
Olvia	6	33.7 ± 2.08	29.6 ± 1.59	37.9±1.63	5	32.0 ± 2.53	30.5 ± 0.70	36.9 ± 2.32
Pitukhivka	2	35.1 ± 3.25	29.4 ± 0.10	41.7±090	1	32.0	31.2	38.6

Note: *average greatest breadth between the outer surfaces of the bone core base; **circumference of the bone core base; ***circumference of the horn base.

Table 5. The results of comparison of metric parameters (in %) of saiga limb bone remains from Pleistocene and Holocene archaeological sites in Ukraine

Табл. 5. Результат порівняння морфологічних показників (в %) кісток кінцівок сайгака з плейстоценових та голоценових пам'яток на території України

Site	Humerus		Astragalus				Tibia		Metatarsal
	Bd	Bt	Dm	Gli	Di	Glm	Bd	Dd	Bd
Zaskelna V	100 (2)	100 (2)	100 (3)	100 (3)	100 (3)	100 (3)	100 (3)	100 (3)	100 (4)
Buran-Kaya IV	90.6 (5)	86.6 (5)	89.7 (2)	93.1 (2)	101.8 (2)	93.9 (2)	105.3 (5)	104.3 (5)	n.d.
Myrne	44.4 (1)	n.d.	102.3 (2)	101.0 (2)	105.5 (2)	109.0 (2)	n.d.	n.d.	n.d.
Pitukhivka	103.5 (1)	90.7 (1)	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	93.7 (3)

* Parameters larger than in Pleistocene specimens are given in bold; the number of remains is given in parentheses; n.d.—no data.

The Pleistocene was the period of the saiga's appearance in the territory of Ukraine and later its widest distribution as well. The results of the study of archaeozoological collections allowed for the clarification of the distribution limits of this animal, since the saiga was a game hunted by hunters of the Middle and Late Palaeolithic. The saiga was distributed both in the lowland part of Crimea and in the plateaus (yaylas) of the Crimean Mountains. In the continental part of Ukraine, the largest number of saiga remains was found at sites in Odesa and Mykolaiv oblasts, including Illinka Cave and Anetivka II.

The saiga is one of the few species of the Pleistocene fauna that have survived the dramatic environmental changes at the end of the Dryas period. In the Early Holocene, the saiga was a game species for Mesolithic and Neolithic hunters. In the Holocene, the number of saiga remains increases at sites of the Northern Black Sea region, but this is due to the increase in human population density at this time in the south of Ukraine rather than the expansion of the species' range. In particular, the Northern Black Sea region was populated by ancient hunters–gatherers of the Stone Age, Bronze Age and early Metal Ages, as well as by ancient settlers.

Based on the morphological analysis of remains of saiga limb bones collected from Pleistocene and Holocene sites in Ukraine we can suggest that saigas in the Pleistocene were larger than in the Holocene.

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Declarations

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