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Quaternary skulls of the saiga antelope from Eastern Europe and Siberia: *Saiga borealis* versus *Saiga tatarica* – One species or two?



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ABSTRACT

During the Pleistocene, the saiga antelope, a nomadic, non-territorial, herding species, inhabited vast areas of Eurasia and North America; its distribution was at its maximum extent in the last glaciation. Now, it is restricted to a few isolated populations in Central Asia. Two main forms of saiga were recognised: *Saiga borealis* and *S. tatarica*. The former became extinct at the beginning of Holocene, the latter has survived since the Pleistocene to the present. They are regarded either as two species or as two subspecies of *S. tatarica*. Our comparison of skull and horn measurements of many Eurasian specimens, including literature data, revealed significant differences between these taxa. *S. borealis* was larger than *S. tatarica* in terms of some cranial measurements, whereas *S. tatarica* was characterised by a greater diameter of horncore base. However, the distinction involved only a few metric features and the ranges of all the analysed measurements overlapped at least partially, indicating that the two taxa may not be true species. Our analyses also showed that the skull of *S. tatarica* had become smaller since the Pleistocene in terms of several measurements, which was probably associated with the climate and palaeogeographical changes at the end of the last glaciation and a decrease in the population size. We found significant differences between the various geographical subgroups of *S. borealis* and *S. tatarica* only in some measurements. The observed dissimilarities between *S. borealis* and *S. tatarica* correspond most probably to subspecies level and may have resulted from a biogeographical differentiation of the saiga populations in the Pleistocene.

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1. Introduction

The saiga antelope *Saiga tatarica* L., 1766 is a steppe-dwelling species, capable of long, fast and frequent migrations. At the same time, it is sensitive to rapid changes in environmental conditions and does not tolerate thick snow cover. During the Quaternary, especially in the Last Glacial (MIS 2 and MIS 1), it became very widespread (Bannikov, 1963; Ratajczak et al., 2014; Nadachowski et al., 2014).

The origin of the species has not been unequivocally resolved; it is thought to be related to the Tibetan antelope (*Panolops hodgsonii*

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Abel, 1926) (Kahlke, 1999). However, it is not related to sheep and goats (Caprini) but is a sister group of the gazelles and belongs to the tribe Antilopini (Groves and Leslie, 2011). The earliest occurrence of *Saiga* sp. was recorded in the Olyorian Complex in Yakutia (Kolyma River) (1.2–0.6 Ma) (Sher, 1968; R.D. Kahlke, 2014). It reached Europe in the late Middle Pleistocene (Saalian), and was described from several localities of that age (H.D. Kahlke, 1975; R.D. Kahlke, 1990, 1991, 1992, 2014; Baryshnikov and Tikhonov, 1994), where it was identified as *Saiga* sp. or *Saiga tatarica* ssp. During the Eemian Interglacial, it occurred in Central Asia and the Caucasian foothills. The locality of that age is Binagady (environs of Baku, Azerbaijan), from where Alekperova described *Saiga binagadensis* Alekperova, 1953, later regarded as a subspecies of the extant *Saiga tatarica*: *S. t. binagadensis* Alekperova, 1953 (Alekperova, 1955; Baryshnikov and Tikhonov, 1994).

The saiga reached the maximum extent of its distribution in the Last Glacial. During MIS 3, it reached Eastern Beringia where its remains were found and described as *Saiga ricei* Frick, 1937. The southernmost distribution fringe was northern China. In the north, within the region of Beringia, it extended to the Arctic Ocean and Northern Urals (Chow et al., 1959; Sher, 1968; H.D. Kahlke, 1975; Vereshchagin and Baryshnikov, 1982; Currant, 1986; R. D. Kahlke, 1990, 1991, 1999; Bachura and Kosintsev, 2007). The saiga was also reported from the Lower Volga and Lower Don Rivers' regions (Vereshchagin and Kolbutov, 1957; Vereshchagin and Kuzmina, 1977; Kosintsev, 2007; Kosintsev and Bachura, 2013). A detailed description of its distribution in Eurasia was provided by Markova et al. (1995, 2010). In Europe its range extended from northern Spain (where its presence may be associated with human activities) and the British Isles in the west to Greece and the Balkans in the south. It was especially abundant at the steppe sites of Ukraine and in the Crimean Mountains. The mountain ranges (Alps and Pyrenees), compact forest areas and deserts, as well as regions with thick snow cover in winter, were the barriers to its spread during the Last Glaciation (H. D. Kahlke, 1975; Vereshchagin and Baryshnikov, 1982; Delpech, 1983; Musil, 1986; R.D. Kahlke, 1990, 1991, 1999; Baryshnikov et al., 1990; Baryshnikov and Tikhonov, 1994; Shpansky, 1998; Aaris-Sørensen et al., 1999; Ridush et al., 2013; R.D. Kahlke, 2014). In Poland, it was recorded from several sites in the Krakow-Częstochowska Upland (Kiernik, 1912; Kowalski, 1959; Lasota-Moskalewska, 1993; Baryshnikov and Tikhonov 1994; Stefaniak et al., 2009; Nadachowski et al., 2014). It probably migrated into Central and Western Europe in large herds, but the migrations were relatively short-lasting. The literature data and dating suggest that its migrations took place at the end of the Last Glacial (MIS 2 and MIS 1) (Nadachowski et al., 2014).

Several species of fossil saiga have been described from the Pleistocene: *Saiga borealis* Tschersky, 1876 from Yakutia; *Saiga prisca* Nehring, 1891 based on a right mandible with P₂–M₃ from Šipka Cave (Moravia, Czech Republic); *Saiga ricei* Frick, 1937 from Alaska, and *Saiga binagadensis* Alekperova, 1953 from the Transcaucasia (Azerbaijan) (Tschersky, 1876; Nehring, 1891; Frick, 1937; Alekperova, 1955).

Sher (1968) assumed the existence of two *Saiga* species: the extant *S. tatarica*, and *S. ricei* including *S. borealis*, which occurred in Alaska and Eastern Asia and became extinct at the beginning of the Holocene. However, R.D. Kahlke (1991) defined only one species, *S. tatarica*, with two subspecies: the extinct *S. tatarica borealis* from north-eastern Siberia and North America, including *S. ricei* and occurring in the Last Glacial till the beginning of Holocene, and the extant *S. tatarica tatarica*, which also includes the fossil saiga from the Crimean Palaeolithic. *S. prisca* from Europe is a junior synonym of *S. tatarica borealis*. In R.D. Kahlke's opinion, the following trends can be recognised in the evolution of saiga: increasingly massive horns, decreasing angle of divergence of the horns and decreasing

distance between their bases. Another, smaller, extant subspecies is *S. tatarica mongolica*. R.D. Kahlke (1991) distinguished two morphotypes of fossil saiga: one, more ancestral, included the Middle Pleistocene and Last Glacial forms ("Bottrop type"), with more divergent horns, and another, more advanced, from the last glacial ("Pahren type") included most skulls from the Last Glacial of Europe, with less divergent horns. However, apart from mentioning the measurements of German specimens, he provided no detailed analysis (H.D. Kahlke, 1975; R.D. Kahlke, 1990, 1991, 1992).

In their revision of fossil saiga antelope, Baryshnikov and Tikhonov (1994) analysed 13 measurements of skull and horns of fossil and recent saiga from Alaska and Eurasia. In their opinion two species of saiga occurred: a larger and more massive *S. borealis* Tschersky, 1876 with three subspecies: *S. borealis borealis* Tschersky, 1876, from Eastern Siberia and Alaska, *S. borealis prisca* Nehring, 1891, from Europe, the Urals and Western Siberia, and *S. borealis mongolica* Bannikov, 1946 which survived till the present day. *S. ricei* was included into *S. borealis borealis*. According to these authors, the recent, smaller and more delicately built *S. tatarica* occurred in steppe and semi-desert areas south of the range of *S. borealis*.

Baryshnikov and Krakhmalnaya (1994a,b) also failed to solve the taxonomic status of the saiga, admitting either the existence of two distinct species, or one species with several subspecies of different distribution in space and time. A new subspecies – *Saiga ricei krasnojaraica* Shpansky, 1998 – was described from the locality Krasnyi Yar (Tomsk region), based on few remains (Shpansky, 1998).

Genetic data suggest existence of one recent saiga species (*Saiga tatarica*), with two subspecies: *S. tatarica tatarica* and *S. tatarica mongolica* (Kholodova et al., 2006). Based on their analysis of fossil remains and recent saiga, Campos et al. (2010) identified two distinct clades. One, larger, with most fossil and recent saiga, comprising also two *Saiga borealis* samples, occurred in most of the distribution area. The other, smaller, was limited to the Northern Urals and became extinct at the end of the Pleistocene. In the later partial revision, aimed at correcting misidentification of some of the samples that turned out to be reindeer remains, Campos et al. (2014) confirmed their earlier suggestions.

R.D. Kahlke (2014) mentioned two species of saiga but stated that genetic data failed to confirm it. The saiga's extinction was a result of climate changes: warming, disappearance of steppe and other open habitats, and forest (taiga) expansion (Campos et al., 2010; Kuhn and Mooers, 2010; R.D. Kahlke, 2014). The objective of this study was to check if distinguishing two species of saiga *Saiga borealis* and *Saiga tatarica* was justified and to determine their geographical differentiation based on the morphometric analysis of earlier data and of new specimens from Eurasia.

2. Material and methods

2.1. Localities

Skull and horn remains of saiga from Eurasia were analysed; the results were compared with the literature data from the late Middle Pleistocene, last glacial, Holocene and recent saiga from North America and Eurasia (Table A.1–4). The distribution of excavation sites with saiga skulls which were newly studied in this paper are shown in Fig. 1.

In Poland, saiga skulls were found in the caves Jasna Strzegowska, Maszycka and Stupianka from the Kraków-Częstochowa Upland. Horn fragments originated from Ukrainian sites: Ol'viya (Mykolaiv region) and Myrne near Odessa. Their age was estimated as the Holocene (Late Mesolithic and Iron Age). From Crimea, we examined relatively well-preserved skulls from Emine-Bair-Khosar

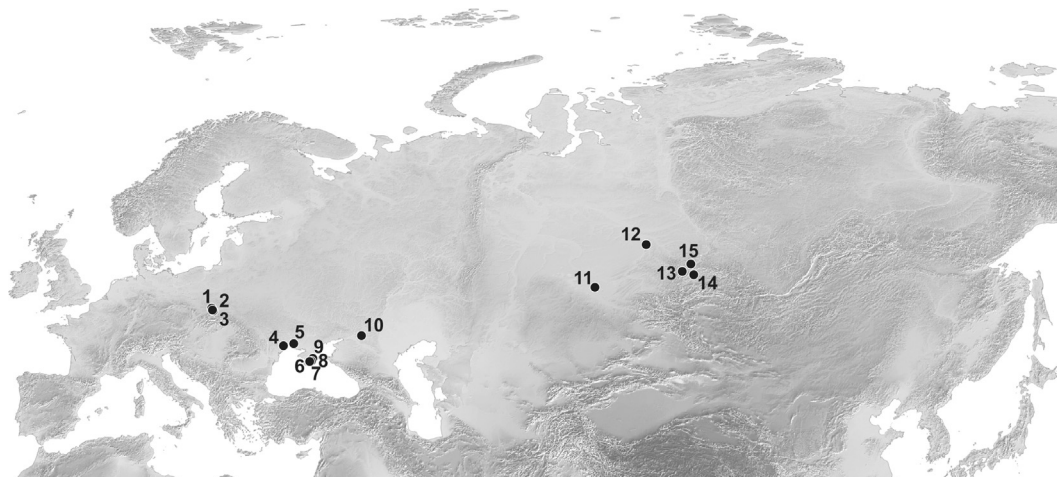


Fig. 1. Distribution of excavation sites with saiga skulls which were newly studied in this paper. 1. Maszycka Cave; 2. Stupianka Cave; 3. Jasna Strzegowska Cave; 4. Mirne; 5. Ol'viya; 6. Emine-Bair-Khosar Cave; 7. Krubera Cave; 8. Prolom II; 9. Zaskalnaya IX; 10. Romanovskaya Village; 11. Grigorievka; 12. Krasnyi Yar; 13. Aydorakh River; 14. Mokhovo; 15. Novoselovo.

Cave, Krubera Cave, Zaskalnaya IX and Prolom II. All of them originated from the end of the Last Glacial. From Siberia, we analysed saiga remains from the Middle Pleistocene (Grigorievka) and Last Glaciation (Krasnyi Yar, Novoselovo and Aydorakh) localities.

The saiga remains from Maszycka Cave are kept in the collection of the Archaeological Museum in Kraków, the skulls from caves Jasna Strzegowska and Stupianka in the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków.

The fossil saiga material from Ol'viya and Mirne (Ukraine), and from the Crimea caves Krubera and Emine-Bair-Khosar (partly), as well as the specimen from Romanovskaya Village (Russian Federation), is housed in the Academician V. A. Topachevsky Palaeontological Museum of the National Museum of Natural History, National Academy of Sciences of Ukraine (NMNHP, Kiev). Another part of the saiga material from the Emine-Bair-Khosar is stored in the Palaeontological Collections of the Natural Museum of 'Yurii Fedkovych' Chernivtsi National University (PC CHNU, Chernivtsi). The material from Prolom II and Zaskalnaya IX is stored in the Department of the Stone Age Archaeology, Institute of Archaeology NAS of Ukraine (SAA IA NASU, Kyiv).

The material from Siberia, Grigorievka site, is kept at the Museum of Nature of the Pavlodar State Pedagogical University (Pavlodar, Kazakhstan) (MG PGPI); the skulls from Novoselovo and Mokhovo are part of the collection of the Zoological Museum of the Khakass State University, Abakan (ZM KHSU), whereas the remains from Krasnyi Yar are at the Palaeontology Museum of the Tomsk State University (PM TSU).

2.1.1. Poland

Jasna Strzegowska Cave (50°24'N, 19°41'E), Krakow-Częstochowska Upland; end of Middle Pleistocene–Holocene, Saalian – Holocene, MIS 6–1 (Sawicki, 1949, 1953; Mirosław-Grabowska and Cyrek, 2009; Stefaniak et al., 2009, 2014).

Maszycka Cave (50°09'N, 19°53'E), Krakow-Częstochowska Upland; Upper Pleistocene – Holocene, Middle Vistulian – Holocene, MIS 3–1 (Kowalski, 1951; Kozłowski et al., 1993, 2012; Lasota-Moskałewska, 1993; Bobak et al., 2013).

Stupianka Cave (50°13'N, 19°47'E), Krakow-Częstochowska Upland; Late Vistulian, MIS 1 (Kowalski, 1951; Szelerewicz-Górny, 1986).

In Poland saiga remains were found also in other sites in the Kraków-Wieluń Jura: Mamutowa Cave, Biśnik Cave, Cave IV on Mt. Birów, Deszczowa Cave; Stajnia Cave, Komarowa Cave

(Nadachowski et al., 2009; Stefaniak et al., 2009; Ratajczak et al., 2014).

2.1.2. Ukraine

Mirne (Myrne, Mirnoe) (46°28'N, 30°22'E), Kilia district, Odessa region; Late Mesolithic; 7–8 cal ka BP (Bibikova, 1982; Stanko, 1982; Smytyna, 2007; Biadzhi et al., 2008).

Ol'viya (Olvia, Olviya) (46°41'N, 31°54'E), Ochakiv district, Mykolaiv region; Holocene; VI century BC–IV century AD, Iron Age (Bibikova, 1958; Zhuravlev, 1996, 2002, 2009).

2.1.3. Crimea

Emine-Bair-Khosar Cave (44°48'N, 34°17'E), Chatyrdag Yayla, Main Ridge of Crimean Mountains; Upper Pleistocene – Holocene, MIS 4–1 (Bachynsky and Dublyansky, 1966; Vremir and Ridush, 2002, 2005, 2006; Vremir, 2004; Bondar and Ridush, 2009; Stankovic et al., 2011; van Asperen et al., 2012; Ridush et al., 2013; Gąsiorowski et al., 2014; Ratajczak et al., 2014).

Krubera Cave (44°52'N, 34°31'E), Karabi Yayla, Main Ridge of Crimean Mountains (Bachynsky and Dublyansky, 1962, 1963).

Zaskalnaya IX (Zaskelna IX in Ukrainian) (45°07'N, 34°37'E), Bilogirsk district; Palaeolithic (Koloso et al., 1993).

Prolom II (45°06'N, 34°42'E), Bilogirsk district, Palaeolithic; ca. 135–60 ka BP (Koloso et al., 1993; Koloso and Stepanchuk, 1989, 2000; Stepanchuk, 1993; Enloe et al., 2000).

Remains of *Saiga* sp. are known from many other cave sites in Crimea (Bachynsky and Dublyansky, 1962, 1963, 1966; Baryshnikov et al., 1990; and others). Besides the Crimean sites, Pleistocene saiga remains were reported only from a few sites in Ukraine: Anetovka II (MIS 1) (Bibikova and Starkin, 1985; Stanko et al., 1989), and from loess sediments near Lypa Village, in the Rivne region (Pidoplichko, 1956). During the Holocene, *S. tatarica* inhabited the steppe areas in Ukraine up to the beginning of the 19th century (Sokur, 1961).

2.1.4. Russian Federation

Romanovskaya Village (47°32'N, 41°58'E), Don River.

Krasnyi Yar (57°07' N, 084°22' E), Ob' River, Tomsk region; Late Pleistocene, Karginian Horizon; MIS 3 (Shpansky, 2006; Shpansky et al., 2015).

Novoselovo (55°05' N, 091°00' E), Krasnoyarsk reservoir, Yenisey River, Krasnoyarsk region; Late Pleistocene, Sartanian Horizon, MIS 2 (Abramova, 1979; Kuzmin et al., 2011; Malikov, 2013).

Mokhovo (53°57' N, 091°26' E), Krasnoyarsk Reservoir, Yenisey River, Khakass Republic; Late Pleistocene, Sartanian Horizon MIS 2 (Malikov, 2014).

Aydorakh (54°17' N, 089°44' E), Aydorah (Aydar) River, Kuznetsk Alatau, Khakassia; Late Pleistocene, Sartanian Horizon (?), MIS 2 (Sher, 1968; Baryshnikov and Tikhonov, 1994; Sekretarev et al., 1999).

2.1.5. Kazakhstan

Grigorievka (52°37'N, 76°44'E), Irtys River, Pavlodar region; Middle Pleistocene, Tobolsk Horizon; MIS 9-11 (Shpansky et al., 2007; Ilyina and Shpansky, 2014).

2.2. Material

2.2.1. General characteristics

The material analysed in this study included larger and smaller fragments of saiga antelope skulls and horns from various sites of Eurasia. They were compared with the remains described in the literature (end of Middle Pleistocene, last glacial, Holocene) and recent saiga from Eurasia and North America (Tables A.1–4). We considered in total 526 measurements obtained from 82 specimens. In statistical analyses, the data were divided into several groups within each of the two saiga species (*S. borealis* and *S. tatarica*) according to the taxonomic affiliation of specimens, their geological age (Pleistocene and Recent) and geographical location of the sites (Eastern Europe, Western-Central Siberia, Eastern Siberia and North America in the case of *S. borealis*, and Western Europe, Poland, Eastern Europe, Azerbaijan and North America for *S. tatarica*). The quality of the material varied and some specimens from museum collections were poorly preserved. Therefore, not all measurements were possible for each specimen.

2.2.2. List of the studied remains

2.2.2.1. Saiga tatarica. Localities: Jasna Strzegowska Cave; skull (MF/261) (Fig. 13A–B; Table A.1). Maszycka Cave: skull with no inventory number (Fig. 13 E; Table A.1). Stupianka Cave: skull

fragment (MF/285) (Fig. 13 C–D; Table A.1). Ol'viya: right horncore (no. 8-6443) and fragment of left horncore without apical part (no. 8-6449) (Fig. 14I–J; Table A.1). Mirne: skull fragment (54-1005) (Table A.1). Emine-Bair-Khosar Cave: skulls (EBH Bc 292; EBH Bc 454) (Fig. 13 G–H; Table A.2); female skull (EBH Ba2 2054); juvenile skulls (EBH Ba2 1081; EBH Bc 1011) (Fig. 13 F; Table A.2); skull with no inventory number; skull fragments: left horncores (EBH Ba2 3301, EBH Ba2 3726, EBH Bc 445); right horncores (EBH Bb 636 and no inventory number) (Table A.2). Kruberka Cave: skull with no inventory number (Table A.2); horncore with no inventory number (Table A.2). Zaskalnaya IX: skull fragment (No 1) (Fig. 14 A; Table A.2). Prolom II: left horncore (Table A.2). Romanovskaya: skull (7-121) (Fig. 14 B; Table A.3).

2.2.2.2. Saiga borealis. Localities: Grigorievka: skull fragment (MP PGPI 1188) (Fig. 14 C; Table A.3); right horncore (MP PGPI 693). Krasnyi Yar: skull (PM TSU 5/805) (Fig. 14 D–E; Table A.3); skull fragments: occipital bone (PM TSU 5/804); three left and one right horncore (PM TSU 5/260, 5/936, 5/3506, 5/5143). Novoselovo, Mokhovo, Aydorakh River: skull fragment (ZM KHSU 6458); right horncore (ZM KHSU 6194) (Fig. 14 G; Table A.4); fragment of left horncore base (ZM KHSU 6349) (Fig. 14 H; Table A.4).

2.3. Methods

The skulls and horns were measured with slide calliper to the nearest 0.01 mm, following Sher (1968), Baryshnikov and Tikhonov (1994) and von den Driesch (1976). The diagram of measurements is shown in Fig. 2. For convenience, we denoted the measurements by m with a corresponding number in the text. When present, measurements for antero-posterior (m4) and latero-medial (m8) diameters of the horncore base from the left and right side were averaged. The measurements are presented in Tables A.1–4. All the liner measurements (m1 to m15) are expressed in mm and angles in degrees (m16 and m17).

Statistical analyses: basic and Mantel tests were performed in R package 3.1.1.; Principal Component Analysis (PCA) and

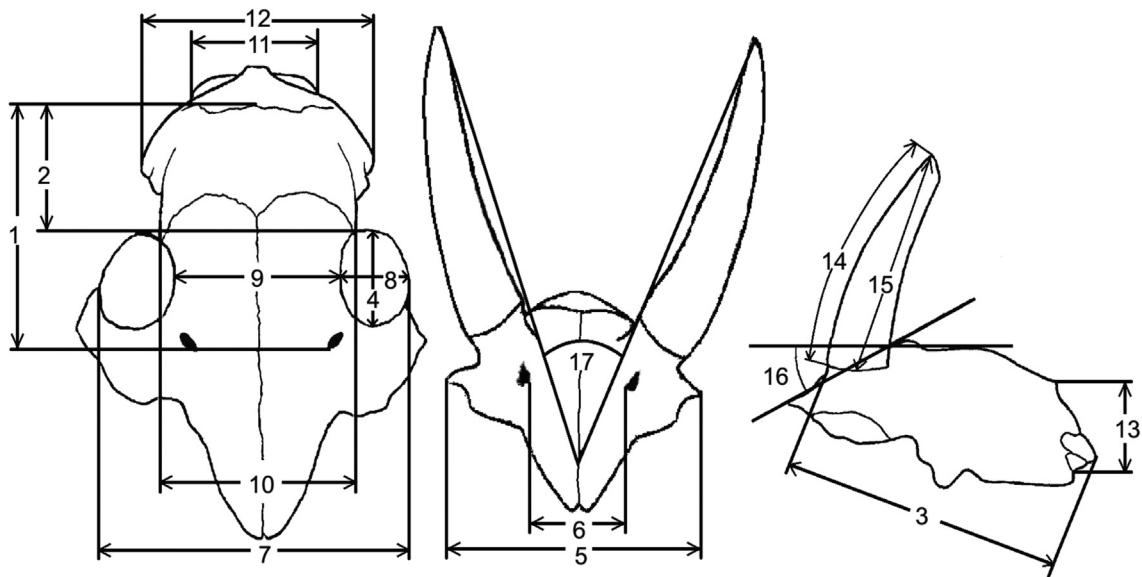


Fig. 2. Scheme of saiga antelope skull measurements: 1. Upper neurocranium length: akrocranium – supraorbitale, 2. Length behind horns: akrocranium – hind surface of horncore bases, 3. Cranial length: akrocranium – bregma, 4. Diameter of horncore base (DAP), 5. Greatest breadth across orbits: ectorbitale – ectorbitale, 6. Width between supraorbital foramina, 7. Width between horns, 8. Latero – medial diameter of horncore base (DT), 9. Minimum distance between inner margins of horn processes, 10. Least breadth of parietal, 11. Greatest mastoid breadth otion – otion, 12. Greatest breadth of occipital condyles, 13. Height of occiput: akrocranium – basion, 14. Full curved length of horncore, 15. Straight length of horncore, 16. Frontal angle, 17. Angle of divergence of horncores (after Sher, 1968; Baryshnikov and Tikhonov, 1994; von den Driesch, 1976).

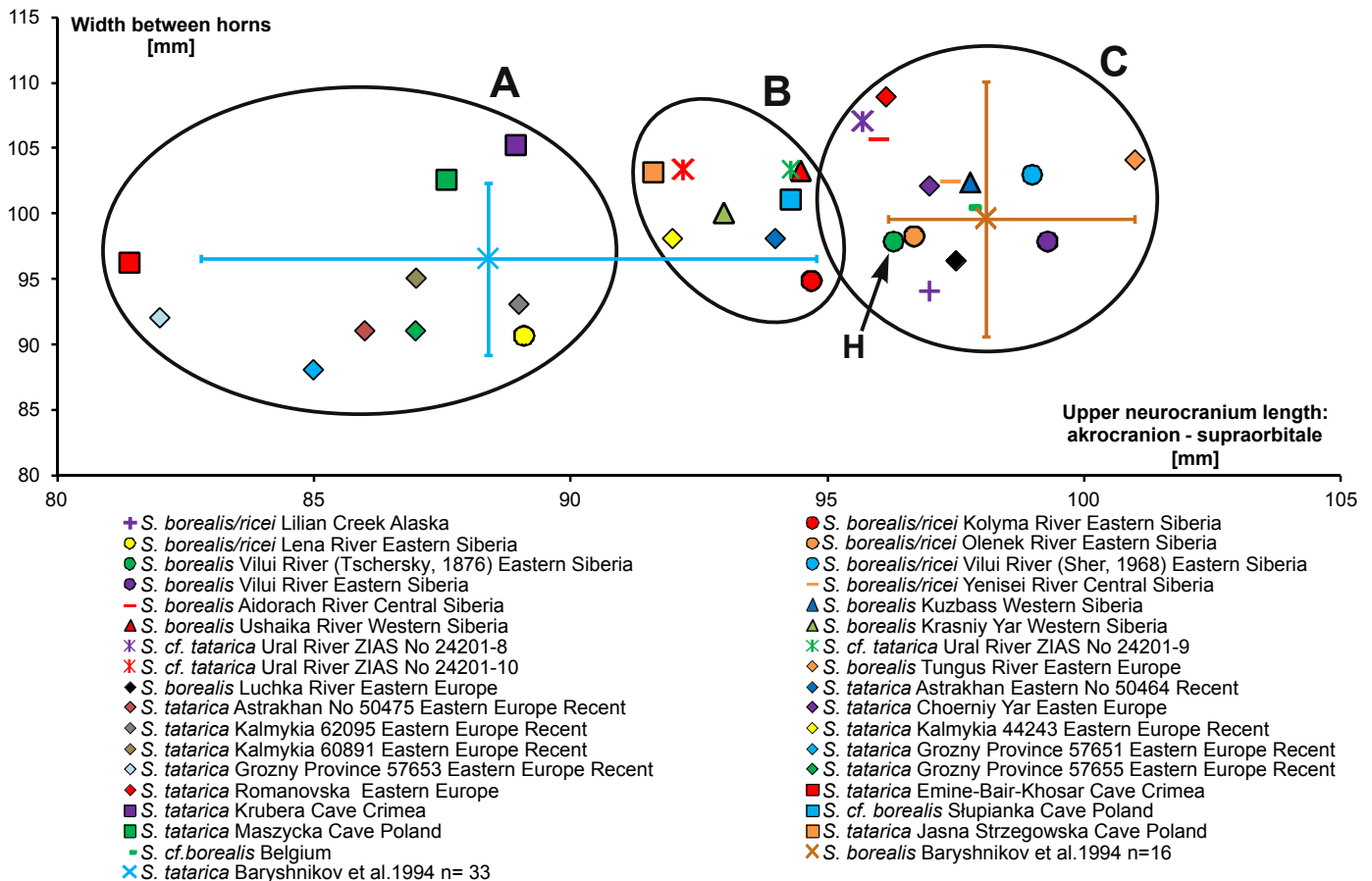


Fig. 3. Variation in the ratio of width between horns to upper neurocranium length in saiga antelope *Saiga borealis* Tschersky, 1876 and *Saiga tatarica* L., 1766. The range of variation of *S. tatarica* reported by Baryshnikov and Tikhonov (1994) is marked with black line, and the range for *S. borealis* from the same publication is marked with grey line. The ovals encircle groups of points for: recent *S. tatarica* and *S. borealis/riciei* from the Lena River, Maszycka Cave and Emine-Bair-Khosar (A), the upper range of variation of *S. tatarica* (B), *S. borealis* (C). Holotype of *S. borealis* (Tschersky, 1876) indicated with arrow.

Discriminant Function Analysis (DFA) including Canonical analysis (CA) were done using *Statistica* software. The statistical tests were performed only on groups containing at least three samples using particular skull measurements as variables. To check if the analysed variables fulfilled the criteria of normal distribution, we applied the Shapiro–Wilk test. The homogeneity of variance across the studied groups was verified with the Lévene test. When the assumption about normality of distribution was fulfilled, the unpaired t-Student test was applied; otherwise, its non-parametric counterpart – unpaired Wilcoxon–Mann–Whitney test was used to compare two groups. In the case of more than two groups' comparison, we used the parametric one-way Analysis of Variance (ANOVA) with moderately conserved Tukey HSD post-hoc test because the assumptions about normality of distribution and variance homogeneity were fulfilled. When many hypotheses were tested, we applied the Benjamini-Hochberg method for p-value correction to control the false discovery rate. Differences were considered significant when $p < 0.05$.

Significance of correlation between two matrices describing pairwise differences between skull measurements of particular specimens and the geographical distance between the sites was estimated with the Mantel test using `mantel.rtest` function from `ade4` package in R and assuming 1000 permutations. The differences in skull measurements were expressed as absolute values. The geographical distances were calculated as orthodromic distances based on geographical latitudes and longitudes of the sites

assuming the mean earth radius 6371 km. In the case of distances from Eurasian to North American (Alaska and Canada) sites, we calculated the distance across the Bering Strait. In the PCA analysis, correlation matrix was used to calculate principal components.

3. Results

3.1. Description and comparison of saiga antelope skulls and horncores

Our comparison of ratio of upper neurocranium length to width between horns shows that the neurocranium length given by Baryshnikov and Tikhonov (1994) for *S. borealis* is somewhat larger, and the width between horns is slightly greater (Fig. 3). Three groups of points can be distinguished in the plot. Two of them are close to each other and include the variation range for *S. borealis* and the upper range of variation of *S. tatarica*. The remaining specimens are within the lower range of variation of *S. tatarica* and include recent *S. tatarica* and *S. borealis/riciei* from the Lena River, Maszycka Cave and Emine-Bair-Khosar. The specimens from the delta of Lena, Kolyma and Ushaiki are within the range of variation of *S. tatarica*, while the skulls identified as *S. borealis* from Alaska and Eastern Siberia (including the holotype described by Tschersky, 1876) to the Urals and Volga River are mostly within the range of variation of *S. borealis*. The skulls from Lilian Creek (Alaska), Kolyma River and Krasnyi Yar have smaller measurements than the other

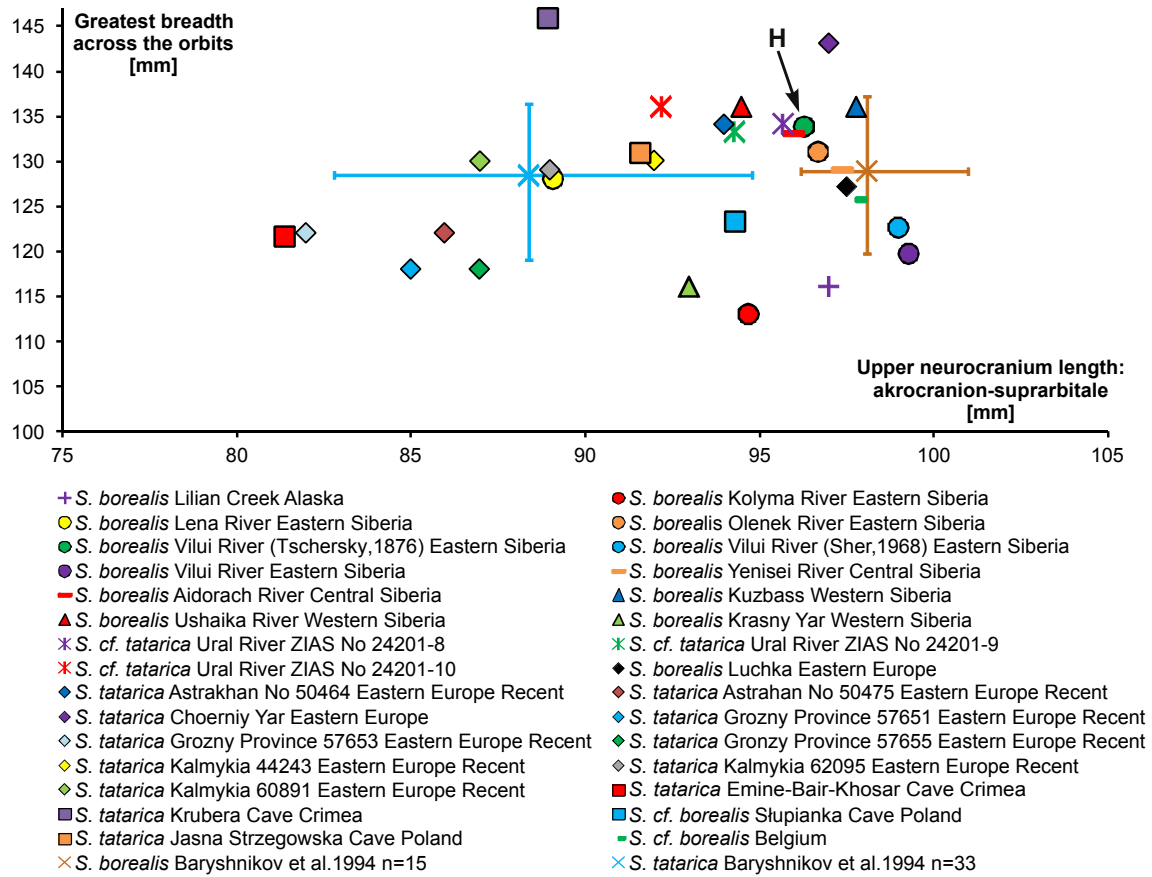


Fig. 4. Variation in the ratio of greatest breadth across orbits to upper neurocranium length in saiga antelope *Saiga borealis* Tschersky, 1876 and *Saiga tatarica* L., 1766. Holotype of *S. borealis* (Tschersky, 1876) indicated with arrow.

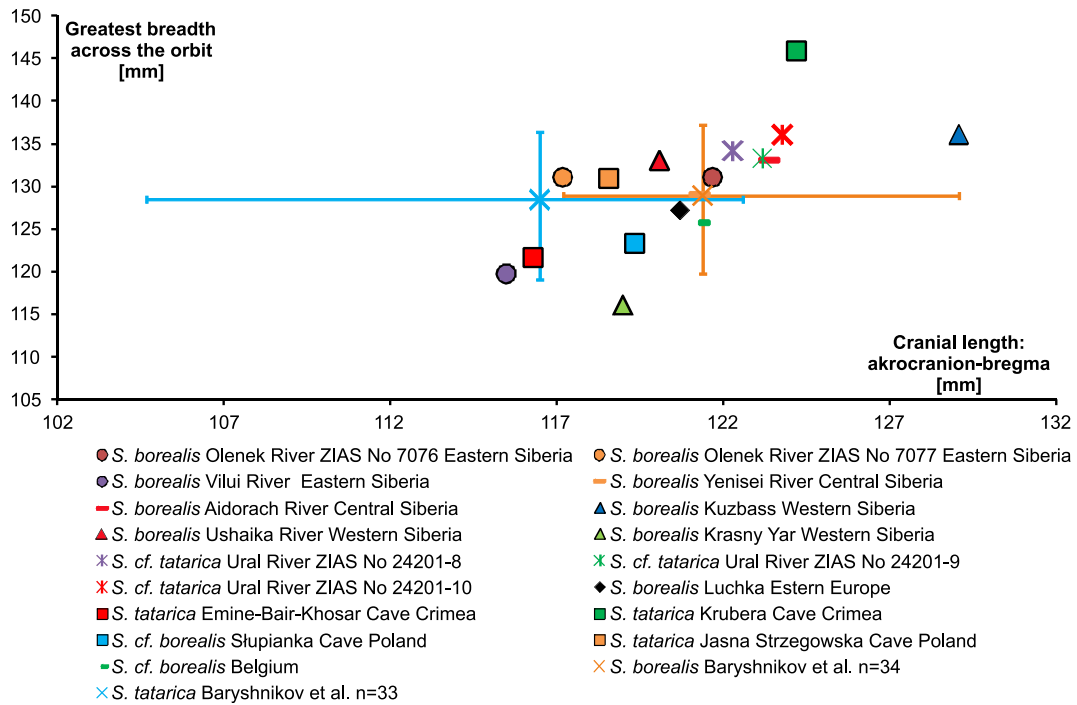


Fig. 5. Variation of the ratio of greatest breadth across orbits to cranial length acrocranium-bregma in saiga antelope *Saiga borealis* Tschersky, 1876 and *Saiga tatarica* L., 1766.

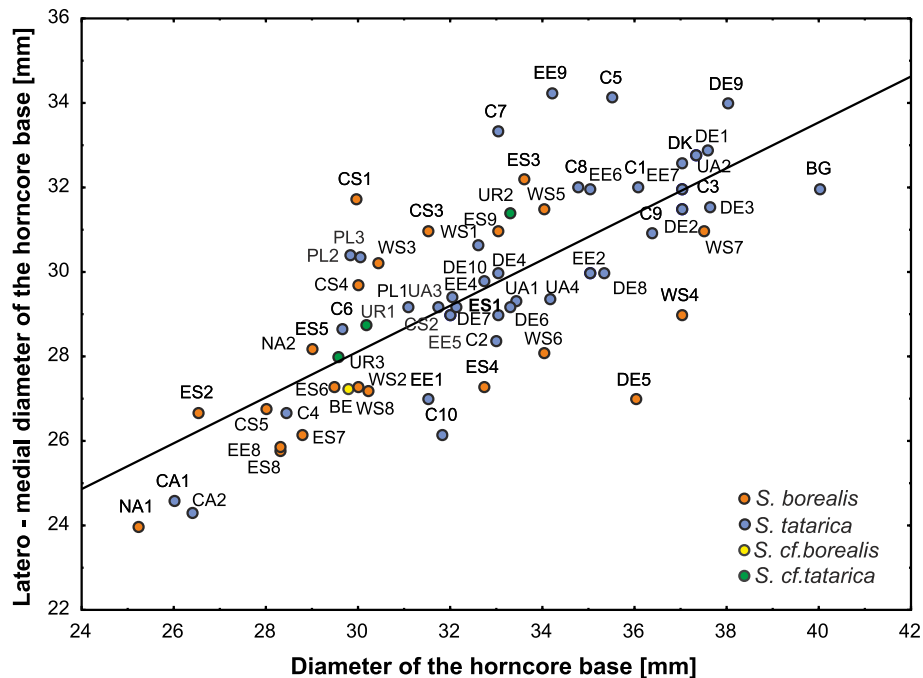


Fig. 6. Relationship between greater latero-medial and anterior-diameters of horncore base in saiga antelope *Saiga borealis* Tschersky, 1876 and *Saiga tatarica* L., 1766. **BE** *S. cf. borealis* Belgium, **BG** *S. tatarica* Durankulak Cave Bulgaria, **C1** *S. tatarica* EBH Ba2 3301 Crimea, **C2** *S. tatarica* EBH Ba2 3726 Crimea, **C3** *S. tatarica* EBH Bb 636 Crimea, **C4** *S. tatarica* EBH Bc 292 Crimea, **C5** *S. tatarica* EBH Bc 454 Crimea, **C6** *S. tatarica* EBH Bc 445 Crimea, **C7** *S. tatarica* EBH Crimea, **C8** *S. tatarica* Zaskalnaya IX Crimea, **C9–C10** *S. tatarica* Krubera Cave Crimea, **CA1** *S. tatarica* Bluefish Cave Canada, **CA2** *S. tatarica* Baillie Islands Canada, **CS1** *S. borealis* Aydorakh River Central Siberia, **CS2** *S. borealis* Yenisei River Central Siberia, **CS3** *S. borealis* ZM KHSU 6458 Central Siberia, **CS4** *S. borealis* ZM KHSU 6194 Central Siberia, **CS5** *S. borealis* ZM KHSU 6349 Central Siberia, **DE1** *S. tatarica* Pahren Germany, **DE2** *S. tatarica* Bernburg Germany, **DE3** *S. tatarica* Königsee Germany, **DE4** *S. tatarica* Garsitz Germany, **DE5–DE8** *S. tatarica* Kniegrotte Germany, **DE9** *S. tatarica* Zeuchfeld Germany, **DE10** *S. tatarica* Bottrop Germany, **DK** *S. tatarica* Boltinggaards Skov Denmark, **EE1** *S. tatarica* *S. borealis* Tungus River Eastern Europe, **EE2** *S. tatarica* Astrakhan Eastern Europe, **EE3** *S. tatarica* Grozny Province 57651 Eastern Europe, **EE4** *S. tatarica* Grozny Province 57653 Eastern Europe, **EE5** *S. tatarica* Grozny Province 57655 Eastern Europe, **EE6** *S. tatarica* Kalmykia Eastern Europe, **EE7** *S. tatarica* Chernyi Yar Eastern Europe, **EE8** *S. borealis* Luchka Eastern Europe, **EE9** *S. tatarica* Romanovskaya Eastern Europe, **ES1** *S. borealis* Viluy River (Tschersky, 1876) Eastern Siberia, **ES2** *S. borealis* Viluy River Eastern Siberia, **ES3** *S. borealis* Viluy River (Sher, 1968) Eastern Siberia, **ES4** *S. borealis* Viluy River Eastern Siberia, **ES5** *S. borealis* Olenek River ZIAS No 7076 Eastern Siberia, **ES6** *S. borealis* Olenek River ZIAS No 7077 Eastern Siberia, **ES7** *S. borealis* Lena River Eastern Siberia, **ES8** *S. borealis* Kolyma River Eastern Siberia, **ES9** *S. borealis* Tumara River Eastern Siberia, **NA1** *S. borealis* Lilian Creek Alaska, **NA2** *S. borealis* Gold Hill Alaska, **PL1** *S. tatarica* Maszycka Cave Poland, **PL2** *S. tatarica* Jasna Strzegowska Cave Poland, **PL3** *S. tatarica* Stupianka Cave Poland, **UA1** *S. tatarica* Mirne Ukraine, **UA2** *S. tatarica* Sarepta Ukraine, **UA3** *S. tatarica* Ol'viya 8-6443 Ukraine, **UA4** *S. tatarica* Ol'viya 8-6449 Ukraine, **UR1** *S. tatarica* No 24201-8 Ural River, **UR2** *S. tatarica* No 24201-9 Ural River, **UR3** *S. tatarica* No 24201-10 Ural River, **WS1** *S. borealis* Tura River Western Siberia, **WS2** *S. borealis* Ushaika River Western Siberia, **WS3** *S. borealis* Kuzbass Western Siberia, **WS4** *S. borealis* Grigorievka Western Siberia, **WS5** *S. borealis* Krasnyi Yar 5/805 Western Siberia, **WS6** *S. borealis* Krasnyi Yar 5/260 Western Siberia, **WS7** *S. borealis* Krasnyi Yar 5/936 Western Siberia, **WS8** *S. borealis* Krasnyi Yar 5/5143 Western Siberia. Holotype of *S. borealis* (Tschersky, 1876), **ES1** bolded.

specimens of *S. borealis*. The specimen determined as *S. cf. tatarica* from the Ural River (ZIAS No 24201-8), skulls of *S. tatarica* from Chernyi Yar and the specimen from Romanovskaya Village (No 50475) are within the range of *S. borealis* but not *S. tatarica*. The longest neurocranium belongs to the skull from the Tungus River from the Middle Pleistocene. The skulls from the Polish caves Jasna Strzegowska and Stupianka are within the variation range of *S. tatarica*, whereas the specimen from Emine-Bair-Khosar is distinctly smaller than the remaining ones. The skull from Stupianka has the longest neurocranium among them. Considering European specimens, the skull from Belgium is the largest: it is close to the mean values of *S. borealis* and is larger than *S. tatarica*.

Comparison of the ratio of upper neurocranium length to the greatest breadth across orbits shows two groups of points (Fig. 4). The ranges given by Baryshnikov and Tikhonov (1994) for *S. borealis* and *S. tatarica* differ for the first measurement. At a similar greatest breadth across orbits, the neurocranium is longer in *S. borealis* than in *S. tatarica*. The holotype of *S. borealis* described by Tschersky (1876) from Eastern Siberia is within the range given by Baryshnikov and Tikhonov (1994), whereas the specimens from Alaska, Kolyma, Krasnyi Yar and Lena, determined also as *S. borealis*, are smaller than the other representatives of the species. The specimen from the Lena River is close to the average values for *S. tatarica*. Among the forms identified as *S. cf. tatarica*, the specimen

from the Ural River (ZIAS No 24201-8) is obviously within the variation range of *S. borealis*, like the fossil skull from Belgium. It is also clearly seen that the skulls from Poland are within the upper range of variation of *S. tatarica*, and the skull from Stupianka has the longest neurocranium. The specimen from Emine-Bair-Khosar is small and comparable to the recent *S. tatarica*. The skull from Krubera Cave in Crimea was the widest across the orbits, whereas the narrowest is the skull from Kolyma River (Fig. 4).

Fig. 5 shows the greatest breadth across orbits plotted against the length of skull akrocranium – bregma. As in Fig. 4, according to Baryshnikov and Tikhonov (1994), *S. tatarica* and *S. borealis* have a similar skull breadth but the length is somewhat larger in *S. borealis*. There are no distinct groups of points in the plot. Skulls identified as *S. borealis* from the Viluy River in Eastern Siberia, Krasnyi Yar in Western Siberia, *S. tatarica* from Emine-Bair-Khosar and the skull from Stupianka in Poland have the smallest breadth across orbits. The remaining specimens, identified as *S. borealis* or *S. tatarica* have similar measurements. The skull from Kuzbas shows the maximum dimensions.

The smallest horncores at the base are from skulls found in North America and the largest in Durankulak Cave Bulgaria and Zeuchfeld Germany (Fig. 6). The greatest latero-medial diameter has skulls from Romanovskaya, specimen Bc 454 and unnumbered specimen from Emine-Bair-Khosar. The specimens from Bottrop in

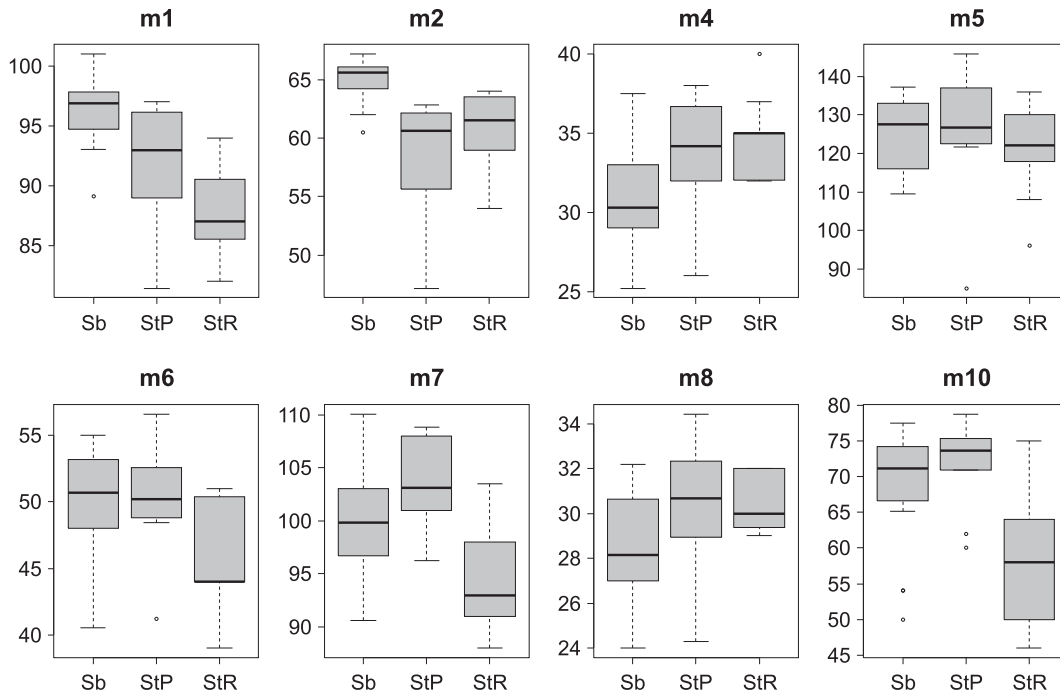


Fig. 7. Box-plots of selected discriminative cranial measurements for *S. borealis* (Sb) and *S. tatarica* from Pleistocene (StP) and recent times (StR). For measurements scheme see Fig. 5. The thick line indicates median, the grey box shows quartile range and the whiskers denote the range without outliers.

Germany, most probably originating from the end of the Middle Pleistocene or the Eemian Interglacial, and some specimens from Kniegrotte were in the middle of the graph, among most of the fossil horncores from Ukraine and modern specimens of *S. tatarica*. The forms from Siberia determined as *S. borealis* and those from the Urals were both above and below the regression line, whereas the holotype of *S. borealis* (Tschersky, 1876) from Eastern Siberia was very close to the regression line and in the middle of the plot.

Except for the smallest specimens from North America, there is no distinct geographical grouping of samples.

3.2. Statistical comparison of skulls of *S. borealis* and *S. tatarica*

In order to assess potential differences between the two saiga antelope taxa, *S. borealis* and *S. tatarica*, we carried out statistical

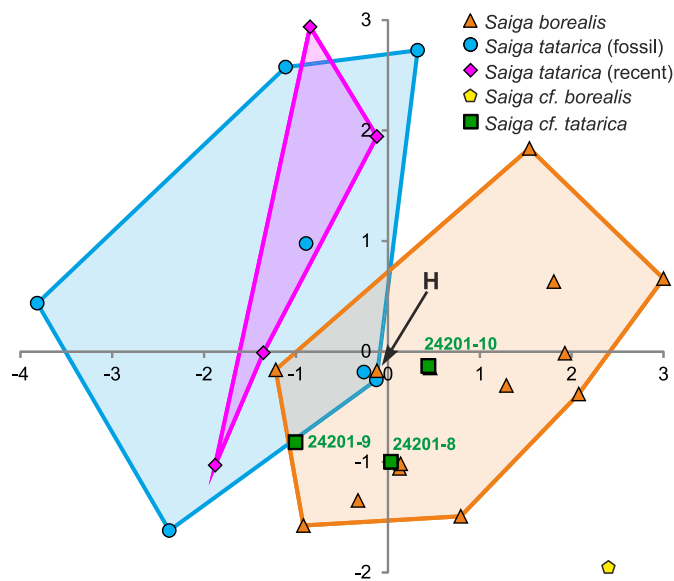


Fig. 8. The plot of the two factor coordinates from Principal Component Analysis for saiga antelope specimens for which all five significantly differentiating measurements (m1, m2, m4, m7 and m8) were available. X axis represents the first factor and Y axis the second factor. Holotype of *S. borealis* (Tschersky, 1876) is indicated with arrow.

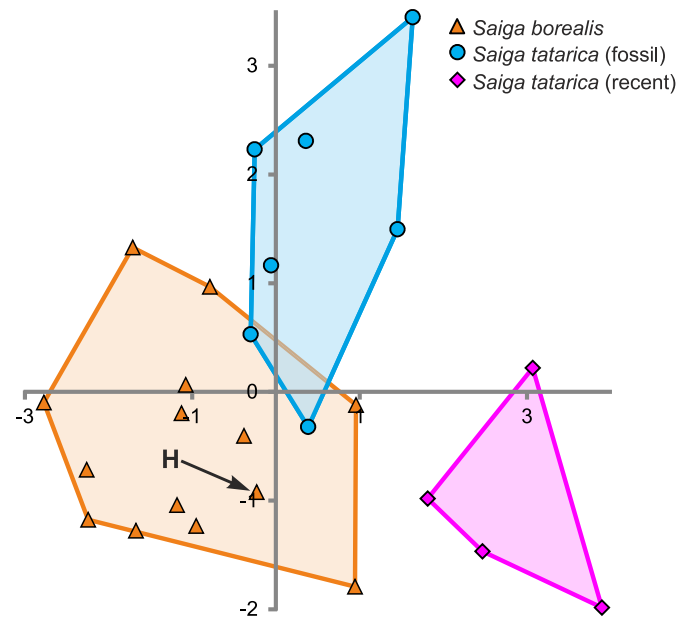


Fig. 9. The plot of two discriminant functions from Discriminant Function Analysis with Canonical Analysis for saiga antelope specimens for which all five significantly differentiating measurements (m1, m2, m4, m7 and m8) were available. X axis represents the first function and Y axis the second function. Holotype of *S. borealis* (Tschersky, 1876) is indicated with arrow.

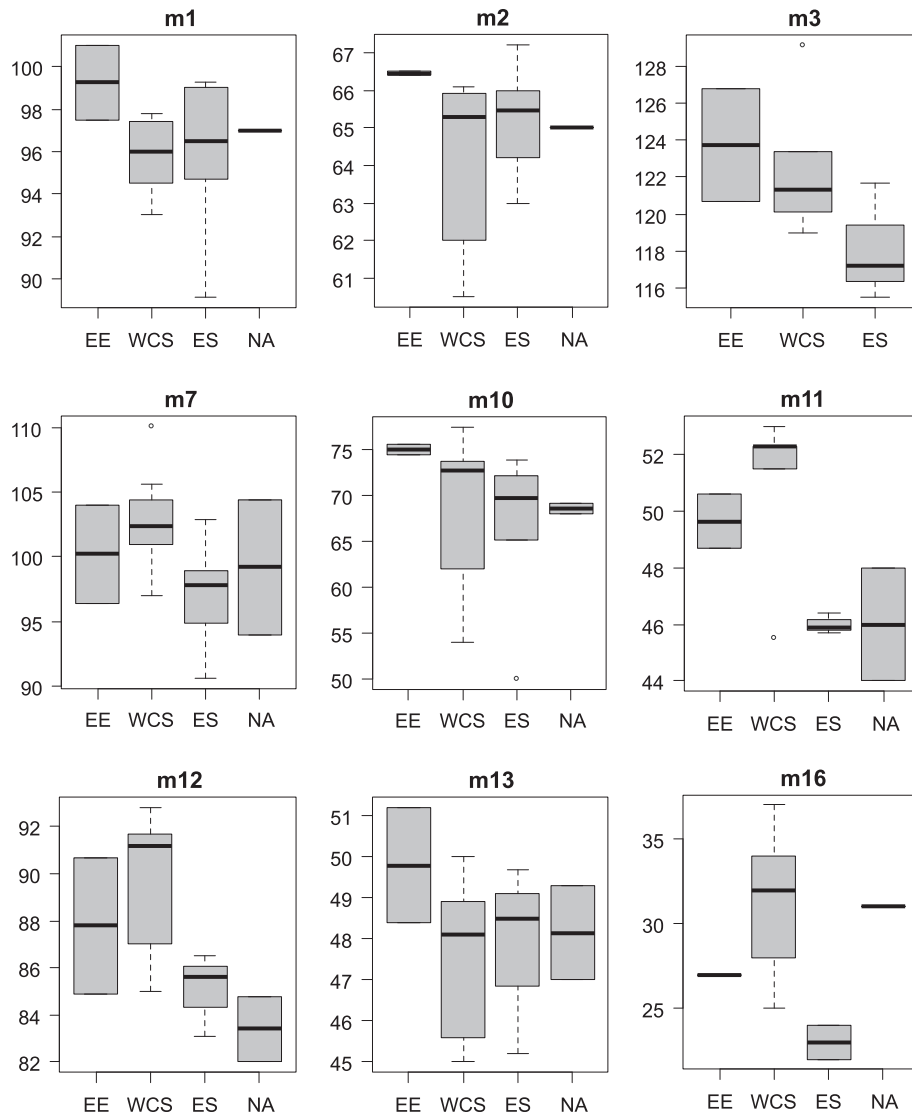


Fig. 10. Box-plots of selected cranial measurements for *S. borealis* geographical groups: Eastern Europe (EE) from Middle Pleistocene, Western-Central Siberia (WCS) from MIS 3-2, Eastern Siberia (ES) from MIS 3-2 and North America (NA) from MIS 3. For schema of measurements, see Fig. 5. The thick line indicates median, the grey box shows quartile range and the whiskers denote the range without outliers.

analyses for thirteen measurements, for which we gathered enough data. Summary statistics for the two *Saiga* and p-value (p) of the performed pairwise tests are presented in Table A.5. *S. borealis* has a significantly larger upper neurocranium length (m1) and length behind horns (m2) compared to *S. tatarica*. On the other hand, *S. tatarica* is characterised by significantly greater antero-posterior (m4) and latero-medial (m8) diameters of the horncore base. In *S. borealis* also the distance between supraorbital foramina (m6), least breadth of parietal (m10), greatest mastoid breadth (m12) and height of occiput (m13) are slightly larger than in *S. tatarica* but the differences are not statistically significant (Table A.5).

Since the *S. tatarica* set includes both Pleistocene and recent specimens, whereas in the *S. borealis* there are only Pleistocene samples, the observed differences might be influenced by the presence of recent skulls in the former set. Therefore, we considered the Pleistocene *S. tatarica* as a separate set (Fig. 7) and compared it with *S. borealis*. The analysis also showed significant and similar differences as in the full sets' studies in the length behind horns (m2) as well as in the antero-posterior (m4) and latero-medial (m8) diameters of horncore base (p-values 0.025, 0.025 and 0.031, respectively). *S. borealis* was still characterised by a

larger upper neurocranium length (m1) too, but the difference was not statistically significant ($p = 0.264$). In contrast to the previous results, in *S. tatarica* the minimum distance between outer margins of horn processes (m7) was larger than in *S. borealis*, but the significance ($p = 0.049$) was very close to the assumed p-value threshold of 0.05. However, the observed general agreement in comparisons with and without the recent samples does not exclude the possibility of some temporal trends and differences between fossil and recent samples (see below: section Temporal and spatial differentiation of saiga).

Principal Component Analysis was carried out for the saiga specimens for which all five significant variables (m1, m2, m4, m7 and m8) were available. The first two factor coordinates explained in total 81% of variance (45% and 36%, respectively). The first component is most correlated with latero-medial diameter of horncore base (-0.915), diameter of horncore base (-0.875) and length behind horns (0.644), whereas the second one with the upper neurocranium length (-0.882) and width between horns (-0.779). A quite clear separation of *S. borealis* and *S. tatarica* in two groups is visible in the plot of the two coordinates (Fig. 8). The holotype of *S. borealis* (Tschersky, 1876) is located within the

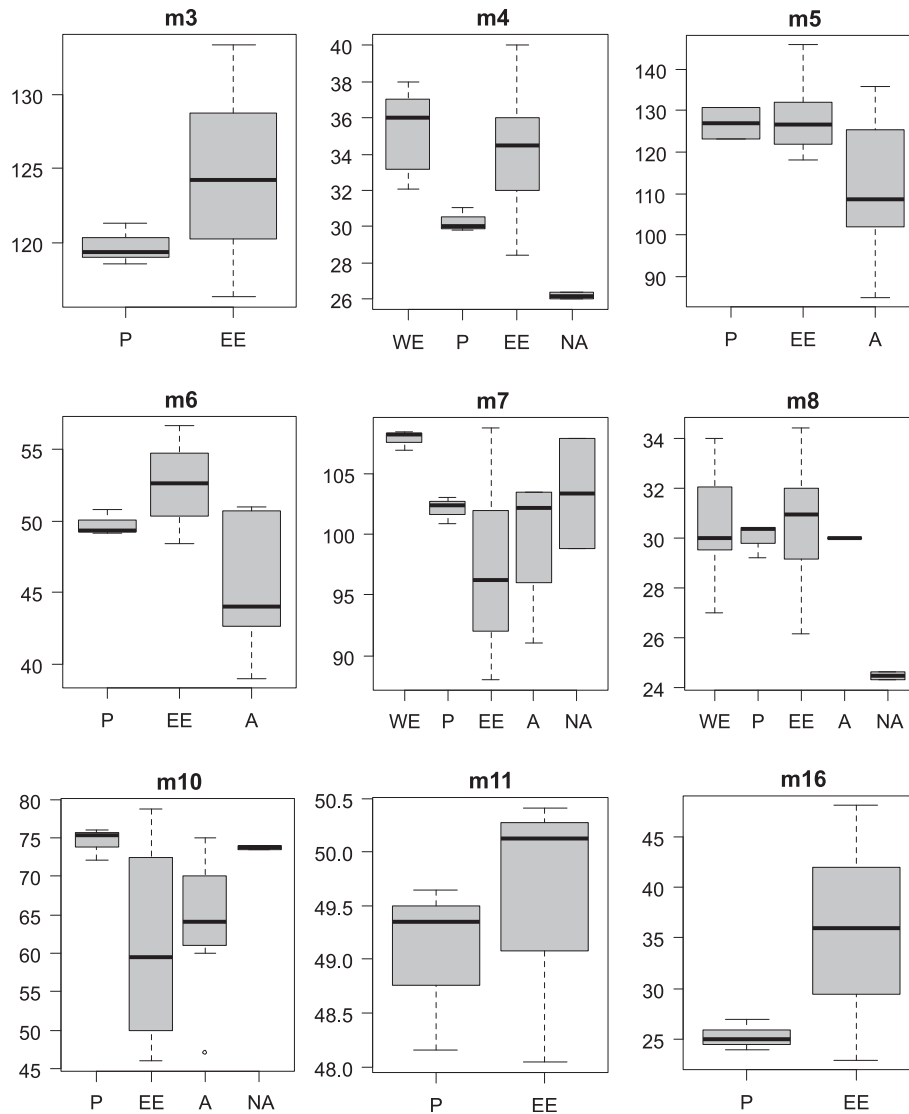


Fig. 11. Box-plots of selected cranial measurements for *S. tatarica* geographical groups: Western Europe (WE), Poland (P), Eastern Europe (EE), Azerbaijan (A) and North America (NA). All samples from Western Europe, Poland and North America were fossil. Eastern Europe was represented by fossil samples for measurements m3, m6, m11 and m16, whereas Azerbaijan by recent samples for m8. The rest measurements for Eastern Europe and Azerbaijan were taken from both fossil and recent specimens. For schema of measurements, see Fig. 5. The thick line indicates median, the grey box shows quartile range and the whiskers denote the range without outliers.

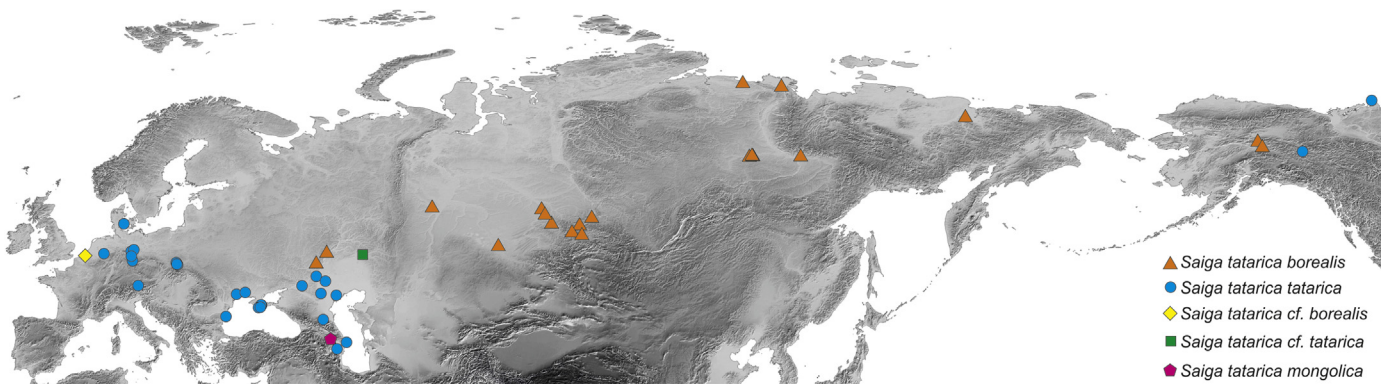


Fig. 12. Geographic distribution of saiga antelope samples used in statistical studies.

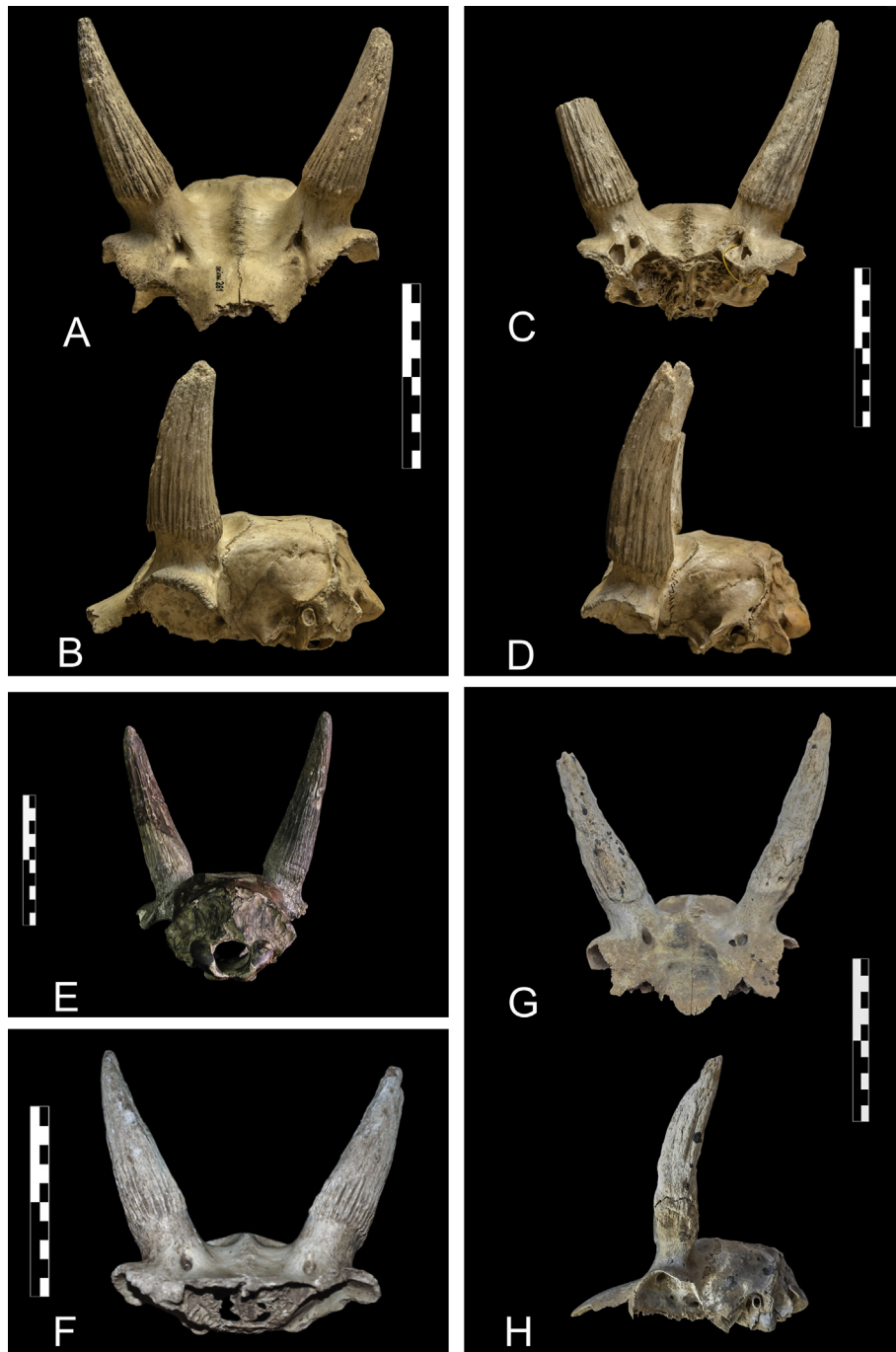


Fig. 13. *S. tatarica*. A. Anterior view of skull Jasna Strzegowska Cave No 261; B. Lateral view of skull Jasna Strzegowska Cave No 261; C. Anterior view of skull Stupianka Cave MF/285; D. Lateral view of skull Stupianka Cave MF/285; E. Posterior view of skull Maszycka Cave no number; F. Anterior view of skull EBH Bc 454; G. Anterior view of skull EBH Bc 292; H. Lateral view of skull EBH Bc 292.

polygon of *S. borealis* and at the border of *S. tatarica* polygon. One sample of *S. borealis* from Krasny Yar in the Tomsk region (PM TSU 5/805) and two specimens of *S. tatarica* from the Polish caves, Stupianka (IASE Z-206/38) and Jasna Strzegowska (No 261), are located in the polygon circumscribed for the other saiga taxon.

The same data set was subject to Discriminant Function Analysis with Canonical Analysis. The discrimination between *S. borealis* and *S. tatarica* appeared highly significant with two discriminant functions (root) proposed ($p = 0.00004$ and 0.0049 , respectively). The first one explained 66% of variance. The distribution of the two canonical roots presented in Fig. 9 shows only a slight overlap of

two Pleistocene saiga sets. According to the standardized function coefficients, the upper neurocranium length (-0.806), the lateromedial diameter of horncore base (0.747) and the width between horns (-0.627) had the greatest contribution to the first discriminant function, whereas the second function was the most associated with the width between horns (1.016) and also with the length behind horns (-0.571) – Table A.6. The factor structure coefficients indicated that the upper neurocranium length (-0.627) is most correlated with the first discriminant function, whereas the width between horns (0.649) and the length behind horns (-0.611) are correlated with the second function – Table A.6. The obtained



Fig. 14. *S. tatarica*. A. Anterior view of skull Zaskalnaya IX; *S. tatarica*. B. Posterior view of skull Romanovskaya; *S. borealis*. C. Anterior view of skull Grigorievka; *S. borealis*. D. Anterior view of skull Krasniy Yar No PM TSU 5/805; *S. borealis*. E. Lateral view of skull Krasniy Yar No PM TSU 5/805; *S. borealis*. F. Anterior view of skull Novoselovo (ZM KHSU 6458; G. Novoselovo No ZM KHSU 6194; *S. borealis*. H. Mokhovo No ZM KHSU 6349; *Saiga tatarica*. I. Horncore Ol'viya No 8-6443; J. Horncore Ol'viya No 8-6449.

function properly classified 92% of the saiga samples. Similar to PCA results, the discriminant function misclassified *S. tatarica* from Stupianka Cave (MF/285) and Chernyi Yar, Astrakhan (AMZ KP 47410) to *S. borealis* set with high 0.67 and 0.79 posterior probabilities, respectively.

3.3. Comparison of other saiga antelopes with *S. borealis* and *S. tatarica*

One of studied specimens was assigned to *S. mongolica*. The comparison of its four available measurements with those of *S. borealis* and *S. tatarica* indicates its closer relationship with the

latter form. The greatest breadth across orbits of *S. mongolica* (106 mm) is within the range of *S. tatarica* (85–145.8 mm) and below the range of *S. borealis* (109.5–137.2 mm). Although the width between supraorbital foramina (44 mm) and the least breadth of parietal (65 mm) of *S. mongolica* are within the range of both *S. borealis* and *S. tatarica*, these measurements are closer to the means for *S. tatarica* (48.6 mm and 64.4 mm, respectively) than to those for *S. borealis* (50.3 mm and 68.4 mm, respectively). Interestingly, *S. mongolica* is characterised by a small width between horns (77 mm), which is much below the minimum values for *S. borealis* and *S. tatarica* (90.6 mm and 88 mm, respectively).

Comparison of skulls which were tentatively identified as *S. cf. borealis* (ZIAS no5 from Belgium) and *S. cf. tatarica* (ZIAS No 24201-10, 24201-8 and 24201-9 from Ural River) with the data for *S. borealis* and *S. tatarica* allow their more precise classification. In respect of most measurements, they are more similar to *S. borealis*. For example, the upper neurocranium length of ZIAS no5, 24201-8 and 24201-9 (97.8–94.3 mm) is much closer to the mean for *S. borealis* (96.4 mm) than to *S. tatarica* (89.3 mm). For *S. cf. borealis* this measurement (97.8 mm) is within the range of *S. borealis* (89.1–101 mm) and outside the range of *S. tatarica* (81.4–97 mm). All four skulls have relatively large least breadth of parietal (72.3–77.2 mm), which is more similar to the mean of *S. borealis* (68.4 mm) than to *S. tatarica* (64.4 mm). The length behind horns in the three skulls of *S. cf. tatarica* (62.5–64.2 mm) also corresponds well to the mean of *S. borealis* (64.9 mm) but not to *S. tatarica* (59.3 mm). However, the value of this measurement is extremely large in the specimen from Belgium (86.2 mm) and exceeds the maximum values for both *S. borealis* and *S. tatarica* (67.2 and 64 mm, respectively). In three skulls (ZIAS no5, 24201-10 and 24201-8) the antero-posterior diameter of horncore base (29.6–30.2 mm) and the latero-medial diameter of horncore base (27.3–28.8 mm) are more similar to the mean of *S. borealis* (31 and 28.5 mm, respectively). One exception is cranium 24201-9, whose diameters (33.3 and 31.4 mm, respectively) correspond to the mean of *S. tatarica* (33.8 and 30.3 mm, respectively).

In agreement with these results, PCA analysis (Fig. 8) places skulls ZIAS No 24201-10 and 24201-8 within the set of *S. borealis*, whereas skull 24201-9 is not clearly assigned to any saiga antelope group. The large skull of *S. cf. borealis* is distinctly separated from the others but still closer to *S. borealis* than to *S. tatarica*. Consequently, discriminant analysis assigns these four skulls (ZIAS no5, 24201-10, 24201-8 and 24201-9) with high and moderate posterior probability (0.999, 0.655, 0.646 and 0.603, respectively) to the group of *S. borealis*.

3.4. Temporal and spatial variation of saiga antelope

The collected data enabled us also to assess the statistical significance of potential differences between the Pleistocene and recent skulls of *S. tatarica*. The fossil skulls were generally larger in terms of five of the eight analysed measurements (Table A.7, Fig. 7), i.e. upper neurocranium length (m1), greatest breadth across orbits (m5), width between supraorbital foramina (m6), width between horns (m7) and least breadth of parietal (m10). However, only the last two proved to be statistically significant. The Pleistocene skulls showed only slightly smaller length behind horns (m2) than the recent crania. In PCA analysis, recent specimens did not form a distinct cluster from the fossil samples (Fig. 8). However, the fossil and recent specimens formed clear separated sets in DFA analysis (Fig. 9).

We also compared the saiga antelope groups according to their geographical distribution (Figs. 10 and 11). To exclude the influence of species factor, we analysed the geographical context separately for *S. borealis* and *S. tatarica*. In the case of *S. borealis*, the skulls from Eastern Europe were the largest in respect of the upper neurocranium length (m1), length behind horns (m2), least breadth of parietal (m10) and height of occiput (m13) – Table A.8, Fig. 10.

However, only the Siberian samples were numerous enough to allow statistical assessment of potential differences. The Western-Central Siberian skulls were on average larger than those from Eastern Siberia with respect to nine out of the thirteen analysed measurements. The greatest differences were observed for the

width between horns (m7), greatest mastoid breadth (m12) and frontal angle (m16). The differences were statistically significant in terms of nominal p-values (0.0088, 0.0488 and 0.0189, respectively), but after the correction for multiple testing they became larger than the 0.05 threshold (0.1145, 0.2113 and 0.1231, respectively). The North American specimens were generally smaller with respect to their antero-posterior diameter of horncore base (m4), maximum width of skull along posterior orbital margins (m5), latero-medial diameter of horncore base (m8) and greatest mastoid breadth (m12), and comparable to the other groups for the rest of the measurements.

We observed some differences between the geographical groups of *S. tatarica* (Table A.9, Fig. 11). However, the small number of samples precluded statistical assessment of the differences in many cases. In the two skulls from North America, the antero-posterior (m4) and latero-medial diameter of horncore base (m8) were below the minimum values of the other groups. In turn, for the Azerbaijan skulls the maximum width along posterior orbital margins (m5) and the width between supraorbital foramina (m6) were smaller compared to the skulls from Poland and Eastern Europe. The skulls of *S. tatarica* from Poland were generally smaller than those from Europe in terms of some measurements. The most distinct differences in comparison to the Eastern European skulls were recorded for the maximum width of skull along posterior orbital margins (m3), width between supraorbital foramina (m6) and angle of deviation of parietal plane from frontal plane (m16). The Polish skulls had also a shorter minimum distance between outer margins of horn processes (m7) than the Western European skulls and a smaller antero-posterior diameter of horncore base (m4) compared to the two European groups. However, the differences proved significant only for the last measurement (p-values 0.0363 and 0.0094 for comparison with Eastern and Western Europe, respectively). The Western European saiga showed also a statistically significantly greater minimum distance between outer margins of horn processes than the Eastern European saiga ($p = 0.0276$). The Polish and North America skulls were on average larger in terms of the least breadth of parietal (m10) than the Eastern European and Azerbaijan skulls.

To further assess the relationship between the skull measurements and the geographical location including all samples, we compared the matrix of pairwise differences in skull measurements between particular specimens with the geographic distances between their sites using the Mantel test. As in the above analyses, we considered *S. borealis* and *S. tatarica* data separately, and also the whole set. None of the thirteen measurements of *S. borealis* proved to be significant after the correction of p-value. The correlation coefficient 0.184 between the differences in latero-medial diameter of horncore base and the geographical distance was significant with the nominal p-value 0.037, but after correction, it became much larger: 0.344. However, a significant positive correlation was found for *S. tatarica* crania in the case of antero-posterior diameter of horncore base (correlation coefficient $r = 0.502$, $p = 0.0130$) and latero-medial diameter of horncore base ($r = 0.485$, $p = 0.013$). We observed a relatively high positive correlation also for the cranial length (0.394) and frontal angle (0.578) but they became insignificant after the p-value correction (nominal and corrected p-values were 0.032, 0.039 and 0.127, 0.127, respectively). For the whole set, including all the saiga antelope data, we found significant correlations for antero-posterior ($r = 0.311$, $p = 0.006$) and latero-medial diameter of horncore base ($r = 0.297$, $p = 0.006$). The greatest breadth of occipital condyles showed significant correlation ($r = 0.235$) before correction for multiple testing ($p = 0.022$) but not after it ($p = 0.095$).

4. Discussion

Analysing the craniometrical parameters, we observed significant geographical differences in the skull size among the Quaternary saiga antelope from Beringia, Eastern, Central and Western Siberia and Europe. The specimens from Alaska, the Kolyma and the Lena River (Eastern Siberia) were smaller than the forms identified as *S. borealis* from Central and Western Siberia. Among the forms identified as *S. tatarica* the largest were some of the specimens from the Urals and the specimen from the Don River in Romanovskaya Village kept at the Museum in Kiev; they were within the range of variation of *S. borealis*. The largest of the analysed skulls from Europe were the skull from Belgium (Leopold Canal) and from Słupianka in Poland, whereas the smallest were the specimen from Emine-Bair-Khosar in Crimea and recent skulls of *S. tatarica* from Central Asia and Eastern Europe.

Analysis of single measurements shows no significant differences between the two species but reveals geographical differences. The fossil saiga from the Eemian Interglacial (MIS 5e) of Binagady (Azerbaijan) and the recent *S. tatarica* from central Asia are smaller than those from Europe, Urals and Siberia. This confirms the suggestions of Baryshnikov and Tikhonov (1994) on the closeness of the Azerbaijan saiga and the recent forms from this area. The most massive skulls are of some specimens from Eastern Siberia, Central Siberia and some from Western Siberia, as well as the single specimen from Belgium, of undetermined geological age. Among the specimens from Poland, the one from Słupianka has a relatively long skull, while the specimen from Maszycka Cave shows a short neurocranium and low occiput. The skull from Jasna Strzegowska Cave is wider than the other skulls from Poland. Except for the smaller-sized North American forms, the horn measurements show no distinct geographical variation related to the geological age. The few Middle Pleistocene specimens (Griгорievka, Bottrop) have typical horncore measurements (Fig. 4). Unfortunately, the poor state of preservation of the skulls precludes other comparisons.

Our comparisons of the skull sets of *S. borealis* and *S. tatarica* revealed significant dissimilarities in several measurements. In addition, the multivariate and discriminant analyses differentiated these taxa well. The most striking differences involved the upper neurocranium length (m1) and the length behind horns (m2), which were significantly greater in *S. borealis* than in *S. tatarica*. This is compatible with the studies of saiga skulls carried out by Baryshnikov and Tikhonov (1994). Overall, our and their results show the same trends in the skull measurements, albeit with some exceptions. In contrast to Baryshnikov and Tikhonov (1994), we did not find statistically significant differences in the maximum width of skull along posterior orbital margins (m3), width between supraorbital foramina (m6), minimum distance between outer margins of horn processes (m7), least breadth of parietal (m10), greatest mastoid breadth (m12) and height of occiput (m13). On the other hand, we observed a significant difference in the antero-posterior diameter of horncore base (m4) which was larger in *S. tatarica* than in *S. borealis*. Similarly, *S. tatarica* showed a significantly greater latero-medial diameter of horncore base (m8) in our data set, while Baryshnikov and Tikhonov (1994) found an opposite trend. The discrepancies may result from the different size of the studied samples and the different statistical approaches, i.e. the tests used and the correction for multiple testing, which reduces the number of false positives.

The results may be also influenced by the various skulls' sets. We analysed 32 Pleistocene specimens of *S. tatarica*, whereas Baryshnikov and Tikhonov (1994) focused on recent skulls of this

taxon. Since, as we noticed for *S. tatarica*, the Pleistocene skulls were generally larger than the recent ones with respect to five of eight analysed measurements, the excess of these measurements would enhance the differences between the usually larger skulls of *S. borealis* and smaller skulls of *S. tatarica*, whereas their scarcity would diminish the difference. The view is supported by the fact that the exclusion of recent samples decreased the averaged values of most measurements in the *S. tatarica* set and made the difference in the larger upper neurocranium length (m1) statistically insignificant. However, the observed general dissimilarity between these taxa was still visible when only the fossil specimens were included, which indicates that these two saiga represented different forms even in the Pleistocene. Our results demonstrated also that *S. tatarica* had become even smaller since the Pleistocene. The change can be related to the climate warming and the palaeogeographical transformations at the end of the last glaciation, and it can follow Bergmann's rule assuming that populations and species in colder environments are characterised by a larger size than those in warmer conditions. When at the end of the Pleistocene and at the beginning of the Holocene, the saiga population became fragmented, the observed differences may have arisen. Such fragmented, isolated populations may have been more sensitive to environmental changes and the pressure from humans, who contributed to their extinction in the northern Urals, North America, Eastern Asia and Europe. Finally, the distribution range of saiga became limited to the South Eastern Europe and Central Asia.

Detailed comparisons of *S. mongolica* with the analysed sets showed that it was much more similar to *S. tatarica* than to *S. borealis*. This is in agreement with the genetic studies, which indicated a close relationship between *S. mongolica* and *S. tatarica*, supporting the status of *S. t. mongolica* as a subspecies rather than a separate species (Kholodova et al., 2006). Moreover, our studies made it possible to assign the large skull ZIAS no5 from Belgium, provisionally called *S. cf. borealis*, to *S. borealis*. Interestingly, the three crania from the Ural River described as *S. cf. tatarica* (ZIAS No 24201-10, 24201-9 and 24201-8) can be also quite reliably classified as *S. borealis*. Our analyses also showed that the skull from Słupianka, described as *S. tatarica* like the remaining skulls from Poland, resembles *S. borealis*, in agreement with Baryshnikov and Tikhonov (1994).

Analysing the craniometrical parameters we observed differences between the various geographical subgroups of both *S. borealis* and *S. tatarica*. However, the small size of the samples precluded assessment of statistical significance of all the differences. In the case of *S. borealis*, the Eastern European specimens were the largest in the whole set, whereas the Western-Central Siberian skulls were on average larger than the Eastern Siberian ones. The North America skulls assigned to either *S. borealis* or to *S. tatarica* were generally the smallest with respect to several measurements, compared to the other geographical sets. This may be associated with a decrease in the founder population size during the migration across Beringia to America, and a predominance of smaller forms resulting from selection or genetic drift. The Azerbaijan and Polish skulls of *S. tatarica* showed smaller measurements than the European crania. The observed differences between these local populations could also result from a decrease in their size as well as from an influence of local environmental conditions and isolation by compact forests, deserts and areas with thick snow cover. The Caucasus and Carpathian Mountains could also restrict the migration of populations of saiga antelope from Azerbaijan and Poland, respectively.

The migrations of saiga were the most intensive during MIS 2 and MIS 1 when it colonised Central Europe at least three or four

times and Western Europe at least twice (Nadachowski et al., 2014). In MIS2, it happened during relatively mild periods, GI-2 (ca. 23.5–23.3 cal ka BP) and GS-2b (ca. 19.0 to 16.0 cal ka BP), whereas in MIS1 during cold phases, GI-1d (ca. 14.0 cal ka BP) and GI-1c₂ (13.5 cal ka BP). The GS-2b period is represented in our studied set by the skull of *S. tatarica* from the Jasna Strzegowska cave, GI-1d by *S. borealis* from the Słupianka cave. It indicates that both saiga forms showed an expansive character.

The observed differences between *S. borealis* and *S. tatarica* most probably correspond to subspecies level. Although multivariate and discriminant analyses managed to separate the two sets, there are only a few metric features to discriminate between the taxa in a significant way. Moreover, the ranges of all the analysed measurements at least partially overlap, which indicates that the two taxa do not represent true species. In agreement with that, the analyses of ancient DNA including two specimens of *S. borealis* placed them within modern and some of the ancient *S. tatarica* samples (Campos et al., 2010, 2014). Therefore, following Kahlke's (1991) view on taxonomic division of *Saiga*, we are in favour of distinguishing only one species, *S. tatarica*, with subspecies *S. tatarica borealis* and *S. tatarica tatarica*.

The great geographical and individual (and probably also sex-related) variation of both taxa suggests that the observed dissimilarities could result from a biogeographical differentiation of saiga populations. We found statistically significant correlations between the differences in skull measurements and the geographical distances between the sites in the whole set. In fact, the studied samples of *S. tatarica borealis* are widely distributed across the whole Siberia, overlapping the East European distribution range of *S. tatarica tatarica* whose samples were collected also from Western and Central Europe (Fig. 12). Remains of both saiga antelopes are also present in north-western North America. Most probably, assuming the view of Baryshnikov and Tikhonov (1994) and Baryshnikov and Krakhmalnaya (1994a,b), *S. tatarica borealis* was the older form, which at the end of the Middle Pleistocene in Eastern Europe and Central Asia gave origin to *S. tatarica tatarica*. Relict populations close to *S. tatarica borealis* may have survived in Asian refuges. The final solution of the problem can be provided by analyses of ancient DNA including more samples classified as *S. tatarica borealis* from its wide distribution range.

5. Conclusions

The taxonomic position of two main saiga antelope forms is still controversial. Some regard them as separate species, *S.*

borealis and *S. tatarica*, whereas others recognise only one species with two subspecies, *S. tatarica borealis* and *S. tatarica tatarica*. Although we recorded significant morphometric differences between their skulls and horns, the small number of discriminant features and their overlapping ranges do not justify the status of true species. The observed significant differences between Pleistocene and recent forms as well as between various geographical subgroups indicate that the saiga population was subjected to temporal and spatial differentiation. The observed dissimilarities between the extinct '*borealis*' and extant '*tatarica*' forms are most probably consequences of the past diversity when this steppe antelope was widely widespread in a vast area from the whole Eurasia to North America. Additional morphometric studies based on a more complete material and ancient DNA analyses are necessary to describe fully this differentiation and the saiga evolutionary history.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quaint.2015.09.040>.

Appendix

Table A.1
Measurements of *Saiga tatarica* L., 1766 skulls from Poland and Ukraine.

Measurement	Poland			Ukraine		
	Maszycka Cave	Jasna Strzegowska Cave	Słupianka Cave	Ol'viya		Mirne
	No number	No 261	No MF/285	No 8-6443	No 8-6449	No number
m1 [mm]	87.5	91.6	94.3			
m2 [mm]	55.1	62.8	62.1			
m3 [mm]	121.3	118.5	119.3			
m4 [mm]	31.1; 31	29.6; 29.9	29.6; 30.4	32	34.1	33.4
m5 [mm]		130.8	123.2			
m6 [mm]	50.8	49.3	49.1			
m7 [mm]	102.4	103.1	100.9			
m8 [mm]	29.5; 28.8	31.3; 29.5	30.5; 30.2	29.4	29.3	29.3
m10 [mm]	75.9	75.4	72.0			
m11 [mm]	77.6	86.8	89.4			
m12 [mm]	49.6	48.1	49.3			
m13 [mm]	49.3	48.2	46.1			
m16 [°]	24	25	25			

Table A.2Measurements of *Saiga tatarica* L., 1766 skulls from Crimea.

Measurement	Kruber Cave		Prolom II	Zaskalnaya IX	Emine – Bair – Khosar							
	Skull	Horncore	No number	No 1	Ba2 3726	Ba2 3301	Bb 636	Bb 637	Bc 292	Bc 445	Bc 454	Exposition
m1 [mm]	88.9								81.4			
m2 [mm]	47.1								55.6			
m3 [mm]	124.1								116.3			
m4 [mm]	35.4; 37.3	31.8		34.4; 25	32.9	36	37.6		31.0; 25.7	35.5	29.8; 29.4	33
m5 [mm]	145.8								121.6		124.5	
m6 [mm]	52.9								48.4		52.2	
m7 [mm]	105.2								96.2		102.7	
m8 [mm]	33.4; 35.4	26.1	30.9		28.3	32	31.5		28.5; 24.8	34.1	29.2; 28.1	33.3
m10 [mm]	78.7								70.8		73.8	
m11 [mm]	89.4							48	77.4			
m12 [mm]									50.1			
m13 [mm]									44.8			
m16 [°]									36			

Table A.3Measurements of *Saiga tatarica* L., 1766 skulls from Eastern Europe and Western Siberia, Russia and Kazakhstan.

Measurement	Romanovskaya	Grigorievka	Krasnyi Yar			
	No number	MP PGPI 1188	PM TSU 5/805	PM TSU 5/206	PM TSU 5/936	PM TSU 5/5143
m1 [mm]	96.1		93			
m2 [mm]	59.2		62			
m3 [mm]	133.3		119			
m4 [mm]	33.8; 34.4	37	34	34	37.5	30.2
m5 [mm]		143	116			
m6 [mm]	56.6		48			
m7 [mm]	108.5	102	100			
m8 [mm]	33.9; 34.5	32	31.5	28.1	31	27.2
m9 [mm]		54	58			
m10 [mm]	75.3		73			
m11 [mm]			85			
m12 [mm]			45.5			
m13 [mm]			50			
m14 [mm]			107			
m15 [mm]			118			
m16 [°]		48	37			
m17 [°]		53	56			

Table A.4Measurements of *Saiga tatarica* L., 1766 skulls from Central Siberia, Russia.

Measurement	Aydorakh River	Novoselovo		Mokhovo
	ZIAS No 15097	ZM KHSU 6458	ZM KHSU 6194	ZM KHSU 6349
m1 [mm]	96			
m2 [mm]	65.9			
m3 [mm]	123.4			
m4 [mm]	30; 29.9	32; 31		28
m5 [mm]	133	110	30	
m6 [mm]	51.3	47		
m7 [mm]	105.6	97		
m8 [mm]	32.1; 31.4	31; 31	29.7	26.8
m9 [mm]	50.5	50.5		
m10 [mm]	72.8	54		
m11 [mm]	91.2			
m12 [mm]	53			
m13 [mm]	48.1			
m14 [mm]	165.5	86	139	
m15 [mm]	155	85	129	
m16 [°]	34	25		
m17 [°]		44		

Table A.5

Summary statistics and p-values of pairwise tests based on cranial measures for two *Saiga* taxa: mean [minimum–maximum]; sample number. For schema of measurements, see Fig. 5; p-values (corrected) lower than 0.05 were **bolded**.

Measurement	<i>S. borealis</i>	<i>S. tatarica</i> (fossil and recent)	p-value
m1 [mm]	96.4 [89.1–101]; 14	89.3 [81.4–97]; 15	0.0008
m2 [mm]	64.9 [60.5–67.2]; 14	59.3 [47.2–64]; 15	0.0008
m3 [mm]	121.5 [115.5–129.1]; 10	122.2 [116.3–133.4]; 6	0.8745
m4 [mm]	31 [25.2–37.5]; 26	33.8 [26–40]; 38	0.0024
m5 [mm]	125.1 [109.5–137.2]; 18	122.7 [85–145.8]; 21	0.6596
m6 [mm]	50.3 [40.5–55]; 14	48.6 [39–56.6]; 14	0.6596
m7 [mm]	99.9 [90.6–110.1]; 20	99.9 [88–108.9]; 25	0.9880
m8 [mm]	28.5 [24–32.2]; 26	30.3 [24.3–34.4]; 40	0.0081
m10 [mm]	68.4 [50–77.5]; 16	64.4 [46–78.8]; 24	0.6596
m11 [mm]	48.7 [44–53]; 12	49.3 [48–50.4]; 6	0.6596
m12 [mm]	87.1 [82–92.8]; 12	85.4 [77.5–91.5]; 6	0.6596
m13 [mm]	48.1 [45–51.2]; 12	47.2 [44.8–49.4]; 4	0.6596
m16 [°]	27.8 [22–37]; 11	30.5 [23–48]; 6	0.6596

Table A.6

Coefficients of discriminant functions.

Measurement	Standardized coefficients		Structure correlation coefficients	
	Function 1	Function 2	Function 1	Function 2
m1	–0.806	–0.276	–0.672	–0.171
m2	0.138	–0.571	–0.499	–0.611
m4	0.355	–0.375	0.354	0.167
m7	–0.627	1.016	–0.337	0.649
m8	0.747	0.020	0.254	0.393

Table A.7

Summary statistics and p-values of pairwise tests based on cranial measures for Pleistocene and recent *S. tatarica*: mean [minimum–maximum]; sample number. For schema of measurements, see Fig. 5; p-values (corrected) lower than 0.05 were **bolded**.

Measurement	Pleistocene	Recent	p-value
m1 [mm]	91.6 [81.4–97]; 6	87.8 [82–94]; 8	0.3950
m2 [mm]	58.2 [47.2–62.8]; 6	60.8 [54–64]; 8	0.5992
m4 [mm]	33.6 [26–38]; 27	34.7 [32–40]; 9	0.8262
m5 [mm]	125.4 [85–145.8]; 8	121 [96–136]; 13	0.6457
m6 [mm]	50.1 [41.2–56.6]; 8	45.7 [39–51]; 5	0.3875
m7 [mm]	103.9 [96.2–108.8]; 13	94.9 [88–103.5]; 11	0.0015
m8 [mm]	30.4 [24.3–34.5]; 28	30.3 [29–32]; 10	0.6457
m10 [mm]	71.6 [60–78.8]; 10	58 [46–75]; 13	0.0252

Table A.8

Summary statistics based on cranial measures for *S. borealis* skulls classified into groups according to localization of their excavation sites: mean [minimum–maximum]; sample number. For schema of measurements, see Fig. 5.

Measurement	Eastern Europe	Western-Central Siberia	Eastern Siberia	North America
m1 [mm]	99.3 [97.5–101]; 2	95.7 [93–97.8]; 5	95.9 [89.1–99.3]; 6	97
m2 [mm]	66.5 [66.4–66.5]; 2	64 [60.5–66.1]; 5	65.2 [63–67.2]; 6	65
m3 [mm]	123.8 [120.7–126.8]; 2	122.6 [119–129.1]; 5	118.1 [115.5–121.7]; 3	NA
m4 [mm]	29.9 [28.3–31.5]; 2	32 [28–37.5]; 13	30.5 [26.5–33.6]; 9	27.4 [25.2–29.6]; 2
m5 [mm]	127.2	125.5 [109.5–137.2]; 8	125.5 [113–133.8]; 8	116
m6 [mm]	52.1 [50.4–53.7]; 2	50.9 [47–55]; 8	48.1 [40.5–52.8]; 4	NA
m7 [mm]	100.2 [96.4–104]; 2	102.8 [97–110.1]; 8	97.1 [90.6–102.9]; 8	99.2 [94–104.4]; 2
m8 [mm]	26.5 [25.9–27]; 2	29.5 [26.8–31.8]; 13	28.2 [25.8–32.2]; 9	25.8 [24–27.6]; 2
m10 [mm]	75 [74.4–75.6]; 2	68 [54–77.5]; 7	66.2 [50–73.9]; 5	68.6 [68–69.2]; 2
m11 [mm]	49.7 [48.7–50.6]; 2	50.9 [45.5–53]; 5	46 [45.7–46.4]; 3	46 [44–48]; 2
m12 [mm]	87.8 [84.9–90.7]; 2	89.5 [85–92.8]; 5	85.1 [83.1–86.5]; 3	83.4 [82–84.8]; 2
m13 [mm]	49.8 [48.4–51.2]; 2	47.5 [45–50]; 5	47.8 [45.2–49.7]; 3	48.2 [47–49.3]; 2
m16 [°]	27	31.2 [25–37]; 5	23 [22–24]; 4	31

Table A.9

Summary statistics based on cranial measures for *S. tatarica* skulls classified into groups according to localization of their excavation sites: mean [minimum–maximum]; sample number. For schema of measurements, see Fig. 5.

Measurement	Western Europe	Poland	Eastern Europe	Azerbaijan	North America
m1 [mm]	NA	91.2 [87.6–94.3]; 3	89 [81.4–97]; 11	86	NA
m2 [mm]	NA	60 [55.1–62.8]; 3	59.1 [47.2–64]; 11	60	NA
m3 [mm]	NA	119.7 [118.6–121.3]; 3	124.6 [116.3–133.4]; 3	NA	NA
m4 [mm]	35.3 [32.1–38]; 11	30.3 [29.8–31.1]; 3	34.2 [28.4–40]; 22	NA	26.2 [26–26.4]; 2
m5 [mm]	NA	127.1 [123.26–130.88]; 2	128.2 [118–145.8]; 12	112.1 [85–136]; 7	NA
m6 [mm]	NA	49.8 [49.2–50.8]; 3	52.6 [48.4–56.6]; 4	45.8 [39–51]; 7	NA
m7 [mm]	107.9 [107–108.5]; 3	102.2 [101–103.1]; 3	97 [88–108.9]; 13	99.8 [91–103.5]; 4	103.4 [98.8–108]; 2
m8 [mm]	30.7 [27–34]; 11	30 [29.2–30.4]; 3	30.7 [26.2–34.4]; 23	30	24.5 [24.3–24.6]; 2
m10 [mm]	NA	74.5 [72.1–76]; 3	60.6 [46–78.8]; 12	64 [47–75]; 7	73.7 [73.4–74]; 2
m11 [mm]	NA	49.1 [48.2–49.7]; 3	49.5 [48–50.4]; 3	NA	NA
m12 [mm]	NA	84.7 [77.7–89.5]; 3	86.1 [77.5–91.5]; 3	NA	NA
m13 [mm]	NA	47.9 [46.1–49.4]; 3	44.8	NA	NA
m16 [°]	NA	25.3 [24–27]; 3	35.7 [23–48]; 3	NA	NA

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