



Research Article

Temporal and spatial differentiation of Pleistocene and recent *Saiga* deduced from morphometric analyses of cranial remains

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Keywords:
morphometry
Saiga borealis
Saiga tatarica
skull
Pleistocene

Article history:

Received: 20 May 2020

Accepted: 15 April 2021

Acknowledgements

This work was supported by the National Science Centre Poland (Narodowe Centrum Nauki, Polska) under Grant no. 2020/37/B/NZ8/02595 as well as the Faculty of Biological Sciences, University of Wrocław (the internal grant for the young scientists, grant number 0420/2315/2017). We are very grateful to anonymous reviewers for their insightful comments and remarks, which significantly improved the manuscript.

Abstract

The saiga antelope was one of important components of the Pleistocene steppe-tundra faunal complex. Although the species is critically endangered now and inhabits several isolated regions in Central Asia, it was widely spread in the Pleistocene in Europe, across Asia up to North America. Such a broad spatial and temporal distribution caused that many authors described several morphological forms. Most often, two forms are recognized and assigned to the species rank as *Saiga borealis* and *S. tatarica*, or in the subspecies rank as *Saiga tatarica borealis* and *S. t. tatarica*. The former became extinct at the beginning of the Holocene, and the latter has survived to the present. To comprehend the morphological diversity of this genus, we conducted extensive morphometric analyses of the cranial material of saiga covering the whole region of its distribution. The study showed that *S. borealis* was larger in several length skull dimensions and occipital region than *S. tatarica*, which in turn showed larger diameters of the horncore base. Moreover, we found a significant decrease in many skull measurements of saiga since the Middle Pleistocene till modern times, which was probably associated with the appearance of unfavourable climatic and ecological conditions. The observed significant distinctions between the Pleistocene and recent forms as well as between some geographical subgroups indicate that the saiga population was subjected to temporal and spatial differentiation, the former factor being more important for variation of the saiga skull than the latter.

Introduction

The genus *Saiga* (Gray, 1843) belongs to the family Bovidae and subfamily Antilopinae (Grubb, 2005). A characteristic feature of this antelope is a pair of closely-set, bloated nostrils directed downwards and forming a short proboscis (Heptner et al., 1988; Sokolov, 1974). In addition, males have thick and slightly twisted horns with pronounced rings. Saiga is a relic from the Ice Age, well-adapted to temperate-arctic climatic zones. Although it is now restricted to several isolated regions in Central Asia, it was widely distributed in the Pleistocene from Western Europe across the central and northern Eurasia up to North America (Baryshnikov and Tikhonov, 1994; Kahlke, 2014). In the past, saiga herds numbered millions but currently this species is considered to be critically endangered because its population is continuously decreasing (Arylov et al., 2004; IUCN SSC Antelope Specialist Group, 2018; Milner-Gulland et al., 2001; Young et al., 2010).

The earliest occurrence of *Saiga* was reported in the Olyorian Complex in Yakutia dated from the late Early to early Middle Pleistocene (1.2–0.6 Ma) (Kahlke, 2014; Sher, 1968). During the Middle Pleistocene, this mammal expanded its geographical distribution occupying the Western Siberia and Europe for the first time (Baryshnikov and Tikhonov, 1994; Kahlke, 1975, 1990, 1991, 1992, 2014). The saiga reached the maximum of its distribution in the Last Glacial period (MIS 5d–MIS 2, 115–12 ka), especially at the end of this period (MIS 3 and MIS 2), when its geographical range longitudinally spanned from the Pyrenees to Alaska and north-western Canada (Aaris-Sørensen et al., 1999; Alvarez-Lao and Garcia, 2011; Bachura and Kosintsev, 2007; Baryshnikov and Tikhonov, 1994; Baryshnikov et al., 1990; Haring-

ton, 1984; Kahlke, 1975, 1991, 2014; Kosintsev and Bachura, 2013; Markova et al., 2010; Nadachowski et al., 2016; Ridush et al., 2013; Sher, 1968).

The wide distribution of saiga in time and space caused its differentiation. Many authors recognized different morphological forms and deliberately elevated them to species or subspecies rank. Most of present saiga populations are classified into one species *Saiga tatarica* but with two genetically confirmed subspecies: *Saiga tatarica tatarica* and *S. t. mongolica* (Kholodova et al., 2006). The former inhabits the Republic of Kalmykia and Kazakhstan, whereas the latter is endemic to western Mongolia (Bannikov, 1954).

A much greater confusion is related to the Pleistocene forms, because many researchers described different *Saiga* species: *S. borealis* from Yakutia (Tchersky, 1876); *S. prisca* from Moravia (Nehring, 1891), *S. ricei* from Alaska (Frick, 1937) and *S. binagadensis* from Azerbaijan (Aleperova, 1955). Moreover, many authors applied different taxonomical classifications of saiga. As a result, its history and taxonomic status are still fiercely debated. Sher (1968) tried to order the classification by assuming the existence of the extant *S. tatarica* and the extinct *S. ricei*. According to him, *S. borealis* was midway between the two other species, but he left its status unsolved due to the lack of main diagnostic measurements and indices. In contrast, more recently, R.D. Kahlke (Kahlke, 1991) defined only one species, *S. tatarica*, with three subspecies: (1) *S. t. borealis* from north-eastern Siberia, extinct at the beginning of the Holocene, (2) the extant *S. t. tatarica* including also the fossil saiga from the Crimea and Eastern Europe, and (3) the extant *S. t. mongolica*. *Saiga prisca* and *S. ricei* were considered younger synonyms of *S. tatarica borealis*.

The taxonomical status of *Saiga* was further complicated by Baryshnikov and Tikhonov (Baryshnikov and Tikhonov, 1994). They analysed

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13 skull and horn measurements of both fossil and recent saigas from Alaska and Eurasia. Their results suggested the existence of two *Saiga* species: a larger and more massive *S. borealis* and a smaller and more delicately built *S. tatarica*. To *S. borealis*, they classified three subspecies: (1) the extinct *S. b. borealis* from Eastern Siberia and Alaska, (2) the extinct *S. b. prisca* from Europe, the Urals and Western Siberia, and (3) *S. b. mongolica*, which survived till the present in western Mongolia. *Saiga ricei* was included into *S. borealis borealis*. *Saiga tatarica* was divided into: (1) the extant *S. t. tatarica*, which was previously widely distributed in steppe and semi-desert zones of Eurasia, and (2) the extinct *S. t. binagadensis*, which inhabited arid landscapes of Transcaucasia and Kazakhstan. It should be noted that the two extant forms were separated into different species in this classification.

Ratajczak et al. (2016) presented the most recent morphological analysis of saiga. Their comparisons of skull and horn measurements revealed significant differences between the two forms distinguished by Baryshnikov and Tikhonov (1994), i.e. the bigger *S. borealis* and the smaller *S. tatarica*. However, the samples were not numerous enough to fully describe the saiga differentiation in time and space. Therefore, we conducted more extensive research by analysing over twice as many skull remains. Since the saiga constituted a substantial component of the Pleistocene steppe and steppe-tundra (Kahlke, 2014), the knowledge about the diversity of this antelope is important to fully reconstruct the faunal changes in the Last Glacial.

Materials and methods

Analysed specimens

The new material analysed in this study included 53 skulls and 62 horns. The specimens represented only adult males but not females, so the analyses were not biased due to sexual dimorphism. Representative crania of *S. borealis* and *S. tatarica* are presented in Fig. 1 and Fig. 2, respectively. These data were enriched by those already obtained by Ratajczak et al. (2016) and collected from various literature resources (Aaris-Sorensen et al., 1999; Alekperova, 1955; Baryshnikov and Tikhonov, 1994; Harington, 1984; Kahlke, 1990; Petrova, 2009; Sher, 1968; Vladimirovich et al., 2014). In total, we considered 106 skulls and 94 horns (Tab. S1). The specimens temporally spanned from the Middle Pleistocene to present days, whereas geographically included Eurasian and North American individuals. Further details about the specimens are included in Tab. S1. The location of the sites with saiga skull analysed in this study is shown in Fig. 3. However, it does not include sites whose location was not precise or not possible to exactly determine. Nevertheless, all data were included in Tab. S1.

Measurements

The skull and horns were measured according to Sher (1968), Baryshnikov and Tikhonov (1994), von del Driesch (1976) and Ratajczak et al. (2016). The diagram of measurements is shown in Fig. 4. For convenience and clarity, we labelled the morphometric measurements by “m” with a corresponding number, e.g. m1. Such abbreviations were used in the whole paper. The measurements were conducted with slide caliper (0.01 mm Nonius), tape measure (0.1 mm Nonius) and pro-

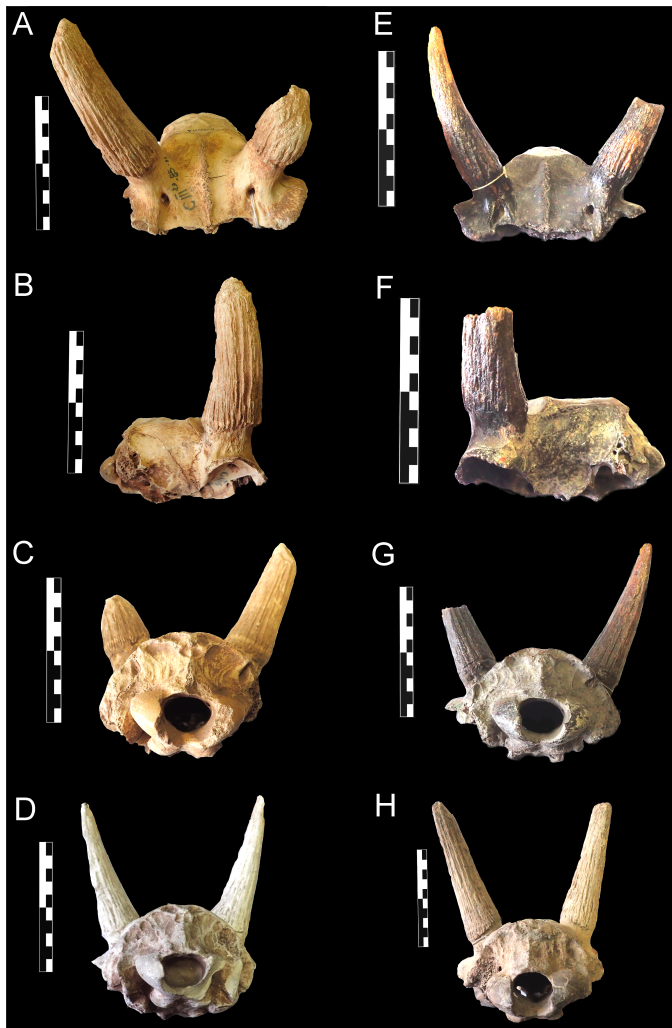


Figure 1 – Skulls of *S. borealis*. Jajva River: A. Anterior view, B. Lateral view, C. Posterior view; Leopold's channel (ZIN 5): D. Posterior view; near Tomsk Ushaika River: E. Anterior view, F. Lateral view G. Posterior view; Kuznetsk (ZIN 3250): H. Posterior view.

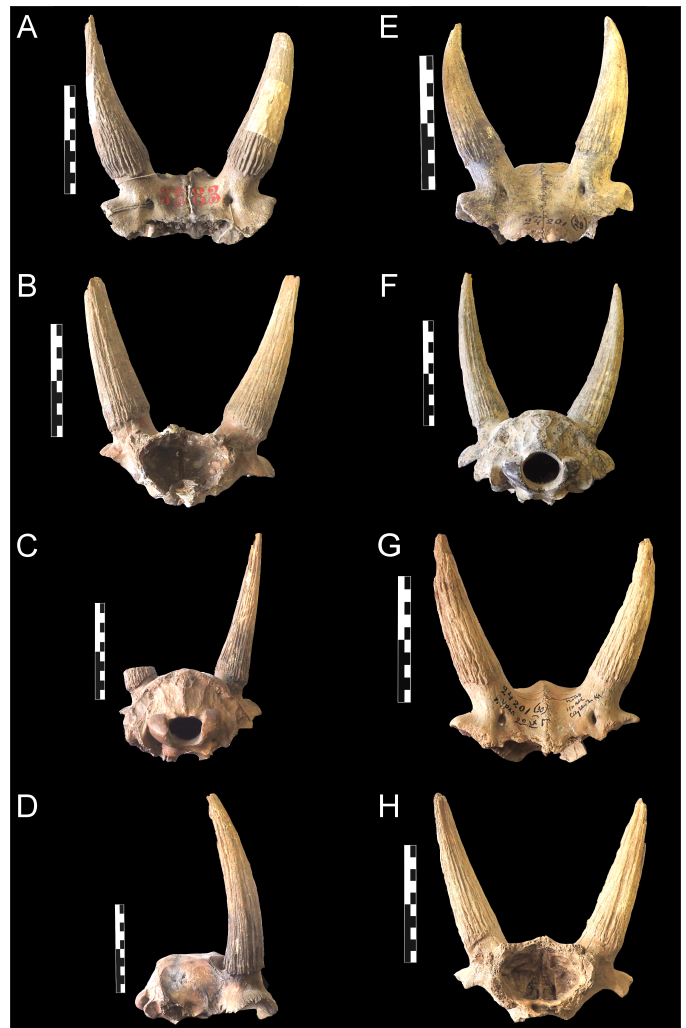


Figure 2 – Skulls of *S. tatarica*. Salarika River: A. Anterior view, B. Posterior view; Bolkha River: C. Posterior view, D. Lateral view; Ural River (ZIN 24201 29): E. Anterior view, F. Posterior view; Ural River (ZIN 24201 30): G. Anterior view, H. Posterior view.

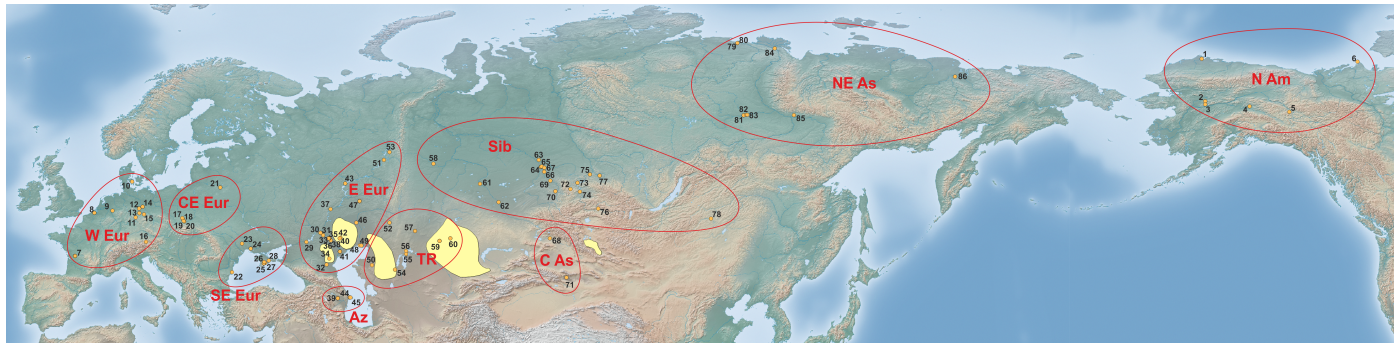


Figure 3 – Distribution of excavation sites with saiga skulls used in this study: 1-Ustutuk River; 2-Lilian Creek; 3-Lost Chicken Creek; 4-Gold Hill; 5-Bluefish III Cave; 6-Baillie Islands; 7-Le Placard; 8-Leopold Canal; 9-Bottrop; 10-Boltingaards Skov; 11-Königsee; 12-Bernburg; 13-Zeuchfeld; 14-Knigrotte; 15-Pharen; 16-Garsitz; 17-Krucza Skala shelter; 18-Jasna Strzegowska Cave; 19-Słupianka Cave; 20-Maszycka Cave; 21-Smargoń; 22-Durankulak; 23-Mirne; 24-Ōl’viya; 25-Emine-Bair-Khosar Cave; 26-Karan-Koba; 27-Kruber Cave; 28-Prolom 2; 29-Romanovskaya; 30-Sarepta; 31-Volga River near Luchka; 32-near Sukhokumsk and Bazhigan; 33-Astrakhan Region; 34-Sotinskje Lake; 35-Cherniy Yar; 36-Astrakhan Region; 37-Tungus; 38-Astrakhan Region; 39-Azerbaijan; 40-Kirghiz; 41-Astrakhan Region; 42-Astrakhan Region; 43-Volga River; 44-Binagady; 45-Binagady; 46-Ural River; 47-Ural River; 48-Guryev Region; 49-Guryev Region; 50-Mangstau; 51-Domashnij Log; 52-Taldysaysk; 53-Jajva River; 54-Komsomolsk-na-Ustyurte; 55-Barsa-Kelmes Iland; 56-Barsa-Kelmes Iland; 57-Aktubinsk Region; 58-Salaikra River; 59-Baikonur Akshala; 60-Kazakhstan; 61-Omsk; 62-Girgirievka; 63-Southern-western Siberia; 64-Krasny Yar; 65-Ob River; 66-Ushaika River; 67-Ob River; 68-Black Irtysh River; 69-Kutznetsk Depression; 70-Kutznetsk Depression; 71-Bogdo Uul; 72-Andarakh River; 73-Novoselovo; 74-Mokhovo; 75-Yenissey River; 76-Tuva Region; 77-Krasnojarski Region; 78-Nizhniy Tsasuchey; 79-Bolkah River; 80-Olenek River; 81-Vilui River; 82-Vilui River; 83-Vilui River; 84-Lena River; 85-Tumara River; 86-Kolyma River. The sites were grouped into geographic regions: North America (N Am); Western Europe (W Eur); Central/Eastern Europe (CE Eur); South-eastern Europe (SE Eur); Eastern Europe (E Eur); Azerbaijan (Az); Transcaspian region (TR); Siberia (Sib); Central Asia (C As) and North East Asia (NE As). Yellow polygons indicate the current distribution of saiga populations (IUCN SSC Antelope Specialist Group, 2018).

tractor (°). The measurements for anterior-posterior and lateral-medial diameters of the horncore base from the left and right side were averaged (m4, m8 and m9). The analysis did not include the measurements 14 and 15, because horns were not always fully preserved. Overall, we considered 1415 measurements from 200 specimens. The linear measurements (m1 to m13) were expressed in millimetres, whereas angles in degrees (m16 and m17).

Statistical analyses

All data were divided into various groups in terms of taxonomy (*S. borealis* and *S. tatarica*), geological age (the Middle/Late Pleistocene and recent) and locality. The following geographic regions were determined: North America (N Am); Western Europe (W Eur); Central/Eastern Europe (CE Eur); South-eastern Europe (SE Eur); Eastern Europe (E Eur); Azerbaijan (Az); Transcaspian region (TR); Siberia (Sib); Central Asia (C As); and North East Asia (NE As) (Fig. 3). We also conducted analyses for these regions grouped into larger spatial areas.

Statistical tests were performed on data sets including at least five samples for a given type of measurement and group. We applied the Shapiro-Wilk test to verify if the analysed variables followed the normal distribution. The homogeneity of variance in the analysed groups was checked using the Lévene test. Two groups were compared us-

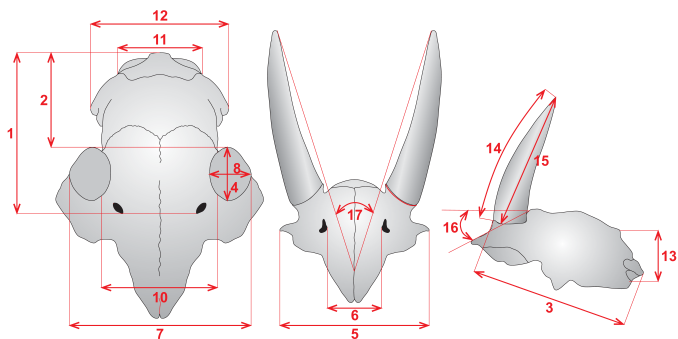


Figure 4 – Scheme of saiga antelope skull measurements: 1. Upper neurocranium length: akrocranium–supraorbital, 2. Length behind horns: akrocranium–hind surface of horncore bases, 3. Cranial length: akrocranium–bregma, 4. Anterior-posterior diameter of horncore base (DAP), 5. Greatest breadth across orbits: ectorbitale–ectorbitale, 6. Width between supraorbital foramina, 7. Width between horns, 8. Lateral-medial diameter of horncore base (DT), 9. Circumference of horncore base, 10. Smallest breadth of parietal, 11. Greatest breadth of occipital condyles, 12. Greatest mastoid breadth otion–otion, 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 del Driesch, 1976; Ratajczak et al., 2016).

ing the unpaired Welch’s t-test if the assumption on the normality of distribution was fulfilled. Otherwise, its non-parametric counterpart, i.e. the unpaired Wilcoxon-Mann-Whitney test, was applied. In the comparison of more than two groups, we used the parametric one-way Analysis of Variance (ANOVA) with moderately conserved Tukey HSD post-hoc test, when the assumptions about normality of distribution and variance homogeneity were fulfilled. When at least one of these assumptions was violated, we applied the non-parametric counterpart of ANOVA, Kruskal-Wallis test with Dunn’s post-hoc test in pairwise comparisons between groups. Spearman correlation coefficient and their significance were calculated for particular skull measurements based on geological classification of the remains. In this post-hoc test and 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*-value was smaller than 0.05.

Discriminant Function Analysis (DFA) including Canonical Analysis (CA) was carried out on two types of sets: (i) the original data excluding cases with missing values and (ii) the data in which the missing values were replaced by an appropriate mean calculated for a corresponding group to which a given case belonged. The second approach was applied when more than two groups were analysed. Multidimensional scaling (MDS) was based on the matrix of Euclidean distances calculated between medians of 15 cranial measurements for saiga groups divided by their geographical location and geological age. Before the distance calculation, the values were min-max normalized in columns.

Statistical analyses and MDS were performed in R software 3.5.1 (R Core Team, 2018), whereas DFA with CA were done using Statistica (data analysis software system, version 13, TIBCO Software Inc. 2017). We used the following R packages: *car*, *FSA* and *stats*.

Results

A large amount of data on saiga remains enabled us to compare them statistically in terms of geological age, geographic distribution and taxonomy, i.e. recognition of *S. borealis* and *S. tatarica*. In the presented descriptions, we focused on variables, which were statistically significant in the intragroup comparisons.

Comparison of skull measurements in respect to two saiga forms

Six out of 15 skull measurements significantly differentiated two saiga forms in statistical tests. *Saiga borealis* was larger than *S. tatarica* in three measurements related to the skull length: the upper neurocranium length (m1), the length behind horns (m2) and the cranial length (m3)

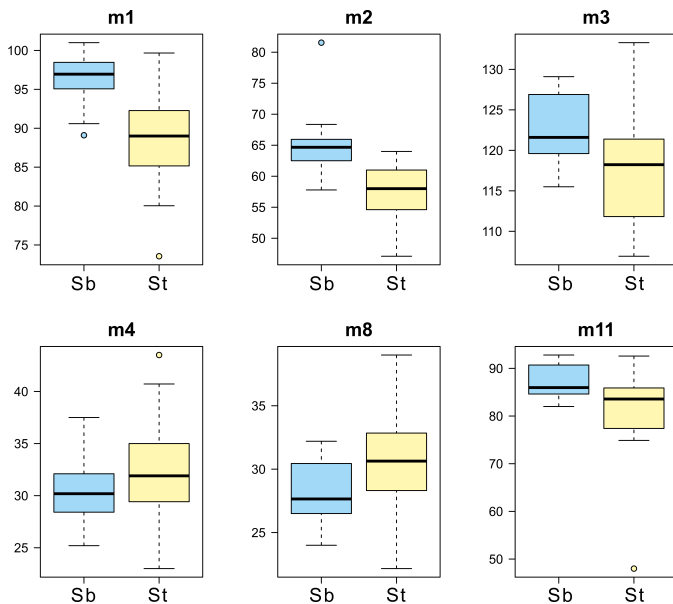


Figure 5 – Box-plots of selected cranial measurements for *Saiga borealis* (Sb) and *S. tatarica* (St). The thick line indicates median, the box shows quartile range and the whiskers denote the range without outliers. For the full description of the measurements see Fig. 4.

(Fig. 5, Tab. S2). Moreover, the extinct form was characterized by the wider greatest breadth of occipital condyles (m11). On average, the variable m2 was 13% larger in *S. borealis* than *S. tatarica*. The other variables differed from 5% to 9%. On the other hand, *S. tatarica* exceeded *S. borealis* in two diameters of the horncore base (m4 and m8). The average percentage difference in these variables was 5% and 9%, respectively.

In order to further determine a discrimination power of skull measurements, discriminant function analysis (DFA) was applied. In this approach, we included 35 most complete saiga skulls for which all 13 measurements (m1–m8, m10–m13 and m16) were obtained. The analysis identified one discriminant function (root), which was significant with $p=0.003$ and clearly separated the two forms of saiga (Fig. 6). This function was best correlated with: the length behind horns (m2, correlation coefficient $r=0.48$), the smallest breadth of parietal (m10, $r=0.41$), the upper neurocranium length (m1, $r=0.39$) and the cranial length (m3, $r=0.34$) (Tab. S3). The lowest values of the discriminative function showed contemporary skulls assigned to *S. tatarica* from the Gurev region in Kazakhstan (Fig. 6). On the other hand, *S. borealis* skulls from the late Pleistocene found at Jajva (in Perm region) and Ushaika (near Tomsk) rivers exhibited the largest values of the function. The skull excavated at the Yenisei river near Krasnoyarsk and attributed to *S. borealis* showed values most similar to *S. tatarica*. Only this sample was incorrectly classified in the DF analysis.

Comparison of skull measurements in respect to geological age

Skulls grouped into Pleistocene and recent forms showed a much larger number of significant differences. Only four out of 15 measurements turned out to be not statistically significant (m5, m13, m16 and m17). The older skulls were substantially bigger both in the lengthwise measurements (m1–m3) and the breadthwise measurements (m6, m7 and m10–m12) as well as the horncore base diameters (m4 and m8) (Fig. 7, Tab. S4). The largest 15-percent difference was shown by the greatest mastoid breadth (m12). The upper neurocranium length (m1), the length behind horns (m2) and the smallest breadth of parietal (m10) were on average 9% larger in Pleistocene saiga than the recent one. Interestingly, the contemporary saiga revealed the circumference of horncore base (m9) significantly greater.

The DF analysis based on the best preserved 35 skulls also provided one significant function ($p<0.001$), which clearly separated the sets of

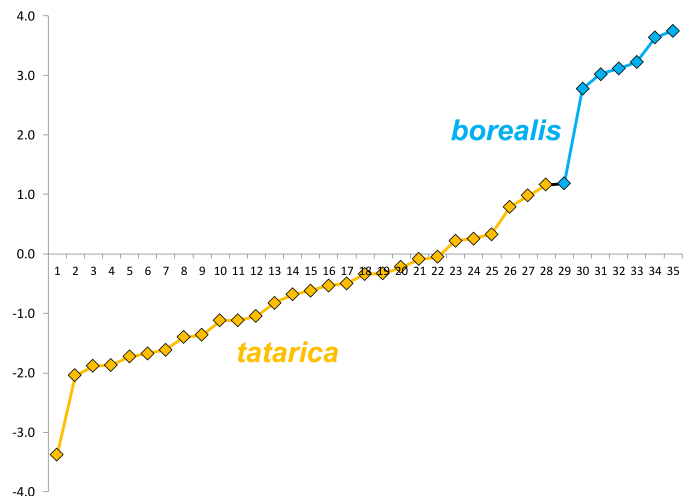


Figure 6 – Values of discriminant function for 35 saiga skulls divided into *S. borealis* and *S. tatarica*. Sites where the skulls were found: 1-Guryev Region; 2-Mangystau; 3-location unknown; 4-Ural River; 5-Baikunur Akshala; 6-near Sukhokumsk and Bazhigan; 7-Komsomolsk-na-Ustyurte; 8-Tuva Region; 9-Astrakhan; 10-Ural River; 11-Aktyubinsk Region; 12-Ulkayak River; 13-location unknown; 14-Volograd; 15-Guryev Region; 16-Kirghiz; 17-Emine-Bair-Khosar Cave; 18-Ural River; 19-Sotinskies Lake; 20-Komsomolsk-na-Ustyurte; 21-Ural River; 22-Bogdo Uul; 23-Jasna Strzegowska Cave; 24-Bogdo Uul; 25-Kazakhstan; 26-Slupianka Cave; 27-Ural River; 28-Bolklah River; 29-Yenisey River; 30-Volga River near Luchka; 31-Krasny Yar; 32-Andarakh River; 33-Binagady; 34-Ushaika River; 35-Jajva River.

fossil and recent skulls (Fig. 8). The best correlated with the function were: the width between horns (m7, $r=-0.36$), the cranial length (m3, $r=-0.35$), the smallest breadth of parietal (m10, $r=-0.35$) and the length behind horns (m2, $r=-0.32$) (Tab. S5). The minimum value of this function was shown by the Pleistocene *S. tatarica* skull from Binagady in Azerbaijan and the maximum value was demonstrated by the recent *S.*

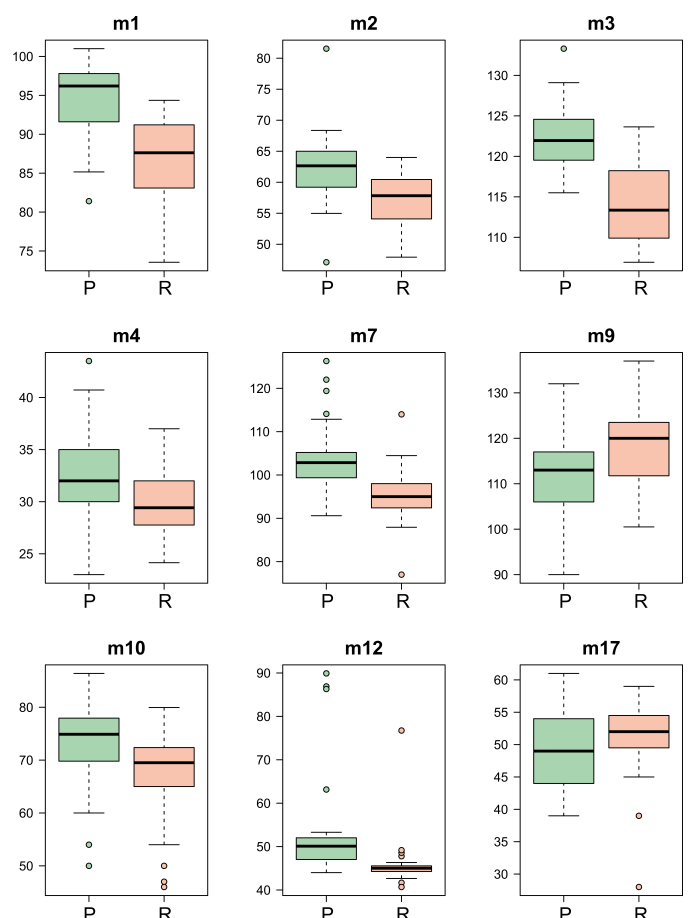


Figure 7 – Box-plots of selected cranial measurements for Pleistocene (P) and recent (R) saiga. Other explanations as in Fig. 5.

tatarica skull from Tuva region. All the samples were correctly classified to their groups.

In the collected data set, we separated the group of the oldest Middle Pleistocene saigas and compared the morphometric changes in the three periods (Fig. 9, Tab. S6). Ten measurements revealed a gradual decrease in time, from the Middle Pleistocene, through the Late Pleistocene to the modern times: m1–m4, m6–m8 and m10–m12. The Spearman correlation coefficient (ρ) calculated for these variables was significantly smaller than zero (Tab. S7). The most negative ρ was observed for the cranial length (m3) and the greatest mastoid breadth (m12): -0.68, and next for the upper neurocranium length (m1): -0.64 and the width between horns (m7): -0.63. The decline was statistically significant in pairwise tests comparing the recent saiga with the two fossil groups in the case of m4, m7 and m12. For m1–m3, m8, m10 and m11, the difference was significant between the Late Pleistocene and the recent saigas, whereas for m7, also between the two Pleistocene groups. The greatest mastoid breadth (m12) decreased on average in 55% from the Middle Pleistocene to the recent, whereas the anterior-posterior diameter of horncore base (m4), and the width between horns (m7) became smaller on average in 17% and 16%, respectively. The only significant increase in time was found for the circumference of horncore base (m9), with $\rho=0.32$. This diameter enlarged on average in 10% from the oldest to the modern saiga.

Comparison of skull measurements considering both saiga forms and geological age. Since the set of *S. tatarica* included both fossil and modern specimens, we decided to exclude the modern forms and compare only the Pleistocene *S. tatarica* skulls with *S. borealis*, thereby eliminating the potential influence of temporal differences. *Saiga borealis* was still significantly larger in the upper neurocranium length (m1) and the length behind horns (m2) in 4% and 10%, respectively (Fig. 10, Tab. S8). Moreover, it had also the height of occiput (m13) greater in 4%. On the other hand, Pleistocene *S. tatarica* skulls showed the diameters of horncore base (m4 and m8) longer in 7% and 12%, respectively. Interestingly, the Pleistocene *S. tatarica* also revealed the width between horns (m7) greater in 6% than *S. borealis*.

Furthermore, to eliminate the potential influence of *S. borealis* in the set of Pleistocene saiga, we compared in terms of geological age only the skulls assigned to *S. tatarica*. This allowed us to check, which cranial features changed from the Pleistocene to the recent in one saiga form. The modern saigas occurred still significantly smaller in respect of the lengthwise measurements (m1 and m3) and the breadthwise measurements (m6, m7, m10 and m12) — Fig. 11, Tab. S9. The largest av-

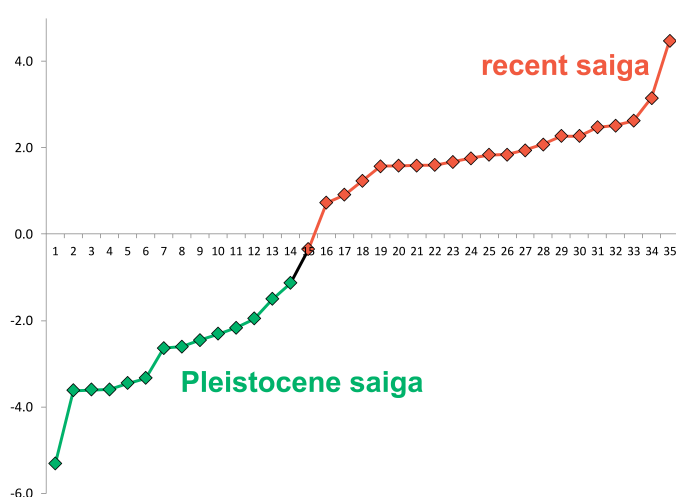


Figure 8 – Values of discriminant function for 35 saiga skulls divided into two Pleistocene and recent saiga. Sites where the skulls were found: 1-Binagady; 2-Ural River; 3-Andarakh River; 4-Ushaika River; 5-Jajva River; 6-Volga River near Luchka; 7-Ural River; 8-Jasna Strzegowska Cave; 9-Yenissey River; 10-Shupianka Cave; 11-Ural River; 12-Bolkah River; 13-Krasny Yar; 14-Emine-Bair-Khosar Cave; 15-Ulkayak River; 16-Aktyubinsk Region; 17-Kazakhstan; 18-Bogdo Uul; 19-location unknown; 20-Baikunur Akshala; 21-Komsomolsk-na-Ustyurte; 22-Mangystau; 23-Ural River; 24-Guryev Region; 25-Sotinskie Lake; 26-location unknown; 27-Bogdo Uul; 28-Astrakhan; 29-Komsomolsk-na-Ustyurte; 30-Kirghiz; 31-Guryev Region; 32-Volograd; 33-Ural River; 34-near Sukhokumsk and Bazhigan; 35-Tuva Region.

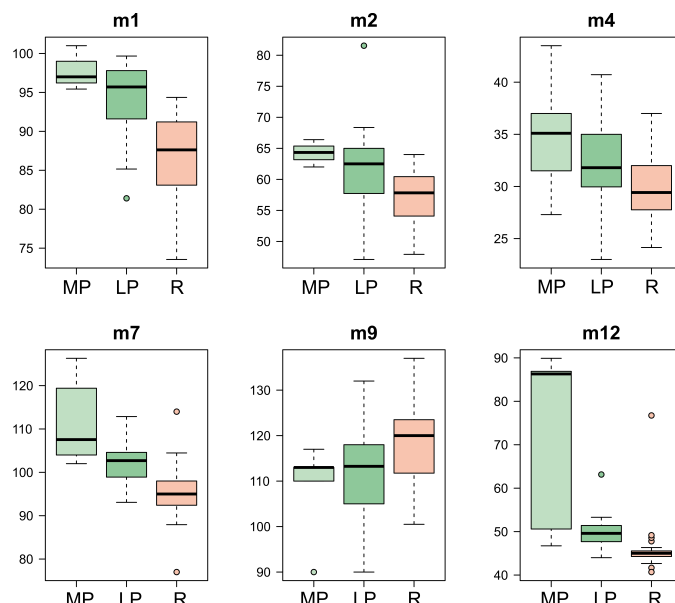


Figure 9 – Box-plots of selected cranial measurements for the Middle Pleistocene (MP), the Late Pleistocene (LP) and recent (R) saiga. Other explanations as in Fig. 5.

erage 23% — decrease concerned the greatest mastoid breadth (m12). The width between horns (m7) and the smallest breadth of parietal (m10) declined on average in 10%. The other parameters decreased on average in 6–7%. The recent saiga showed also the diameters of horncore base (m4 and m8) significantly smaller on average in 10% and 9%, respectively. We found only three measurements that significantly increased over time in *S. tatarica* in 6%, 9% and 11% on average: the circumference of horncore base (m9), the height of occiput (m13) and the angle of divergence of horncores (m17).

Finally, to exclude the potential effect of geographic distribution, we compared Pleistocene and recent *S. tatarica* skulls, which came only from the restricted area, i.e. Eastern Europe and Western Asia. The analyses confirmed the significant differences in measurements referring to the skull length (m1 and m3) — Fig. 12, Tab. S10. The average percent difference was 9% and 10%, respectively. Similarly, the fossil and recent forms differed significantly in the breadthwise parameters: m7 in 14%, m10 in 10% and m12 in 39%. The Pleistocene saiga had also a significantly longer in 9% the anterior-posterior diameter of horncore base (m4). Five other parameters (m2, m5, m8, m11 and m16) were also larger in the extinct forms in 2% to 18%, although the tests showed p -values >0.05 in the comparisons or the differences between groups were not statistically tested due to a small sample size. On the other hand, the angle of divergence of horncores (m17) was wider in the recent form on average in 15%, but the sample of the Pleistocene group was quite small and the difference was not tested either.

In order to obtain a data set sufficient for discriminant analysis, we replaced the missing measurements for individual specimens by an appropriate mean values. The data set consisted of three saiga groups: *S. borealis*, Pleistocene *S. tatarica* and recent *S. tatarica*. The χ^2 test identified two discriminant functions ($p<0.001$). The separation of these groups was very effective because 98% of cases were correctly classified. The first function explaining 72% of variance well separated the Pleistocene and recent *S. tatarica*, which created only slightly overlapping sets (Fig. 13). The second function explaining 28% of variance was responsible for the discrimination of *S. borealis* and *S. tatarica* into non-overlapping groups. The first function was highly positively correlated with the cranial length (m3, $r=0.65$), the width between horns (m7, $r=0.41$), the greatest mastoid breadth (m12, $r=0.36$) and the upper neurocranium length (m1, $r=0.35$) — Tab. S11. The second function was most negatively correlated with the length behind horns (m2, $r=-0.62$), the upper neurocranium length (m1, $r=-0.51$), the angle of divergence of horncores (m17, $r=-0.44$) and the greatest breadth of occipital condyles (m11, $r=-0.41$).

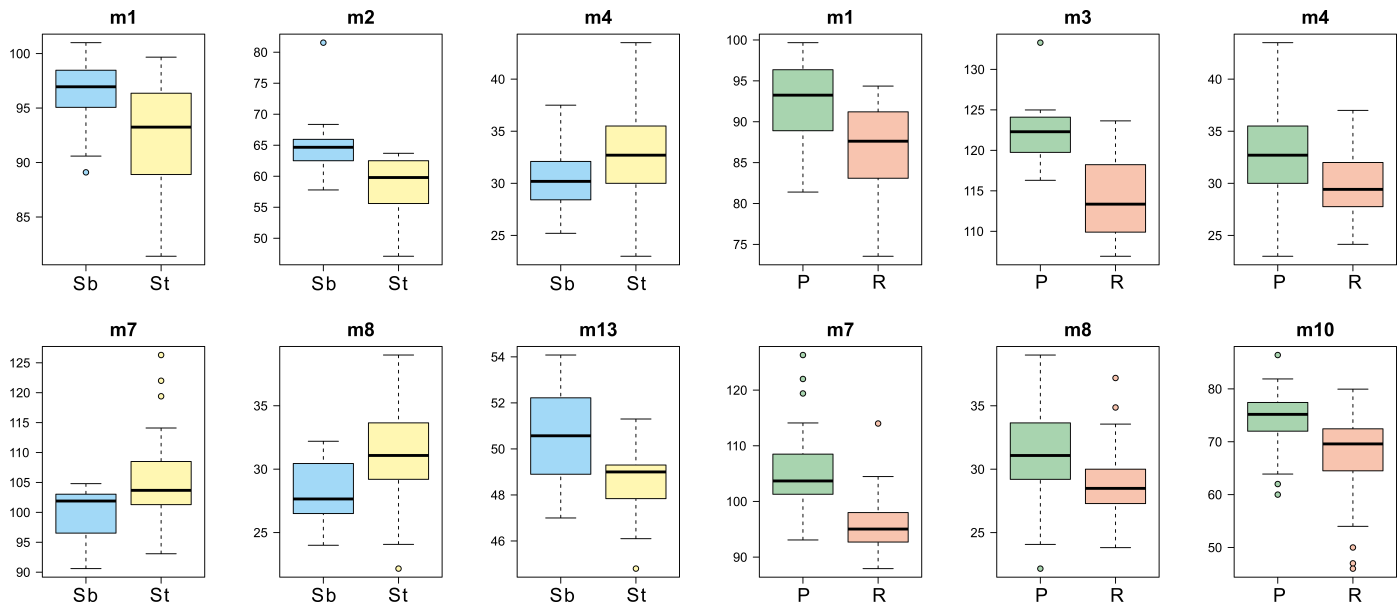


Figure 10 – Box-plots of selected cranial measurements for two Pleistocene *Saiga* divided into *S. borealis* (Sb) and *S. tatarica* (St). Other explanations as in Fig. 5.

General comparison of temporal and spatial saiga groups

To gather results including both geographical location and geological time, we performed multidimensional scaling based on the median values of 15 measurements obtained for nine groups of saiga (Fig. 14). The potential similarities/differences between these groups correspond to the distances of points representing these groups on the two-dimensional plot. The analyses showed non-random distribution of these groups. Two points representing contemporary specimens from two localities, Eastern Europe/Western Asia and Siberia/Central Asia are close to each other in the plot but are rather distant from Pleistocene groups. Among the Pleistocene group, the relatively close points are represented by fossil skulls found in North East Asia and North America, which in the Pleistocene created Beringia, a land connecting today's eastern Siberia with Alaska. Similarly, two points representing adjacent regions Western/Central Europe and Eastern Europe/Western Asia are closely located in the plot. The point representing more distant geographic region, i.e. Siberia/Central Asia is quite separated. The Middle Pleistocene specimens from Eastern Europe/Western Asia and Siberia/Central Asia are clearly separated from all other groups.

An outstanding position is occupied by the point referring to South-eastern European skulls because it is distantly located from other European representatives. In agreement with that, the skulls of Pleistocene *S. tatarica* from South-eastern Europe are the shortest in respect to the measurements, m1 and m2. The percentage difference in the comparison with skulls from other regions was mostly more than 10% and up to 19% on average. In contrast, Western/Central Europe skulls had a significantly longer in 10% the anteriorposterior diameter of horncore base (m4) than those from South-eastern Europe.

Discussion

Thanks to the availability of large amount of Saiga cranial remains, we were able to study the material in terms of taxonomy, geological age and geographic distribution. In comparison to the previous study (Ratajczak et al., 2016), we found more characters in which the studied saiga groups differed and obtained a much greater support for spatial and temporal differentiation of this antelope. Our results justify distinction of two saigas, usually described under the species *S. borealis* and *S. tatarica* or the subspecies level *S. t. borealis* and *S. t. tatarica*. The skulls assigned to these forms are clearly separated in the discriminant analysis. The former form was characterized by a significantly longer skull, specifically its posterior part. The upper neurocranium length (m1) and the length behind horns (m2) were the best discrimi-

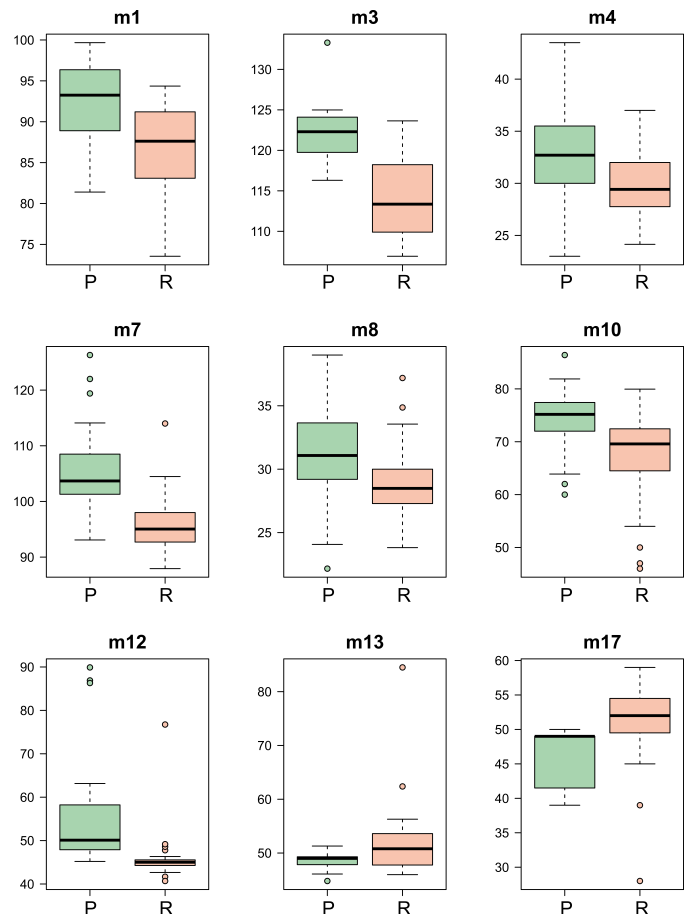


Figure 11 – Box-plots of selected cranial measurements for Pleistocene (P) and recent (R) *Saiga tatarica*. Other explanations as in Fig. 5.

nating features, which agrees with previous analyses (Baryshnikov and Tikhonov, 1994; Ratajczak et al., 2016). We did not conduct separate analyses of forms described under the names *binagadensis*, *mongolica*, *prisca* and *ricei* due to insufficient data.

In the present study, however, we also noticed the greatest breadth of occipital condyles (m11) and the height of occiput (m13) significantly larger in *S. borealis*, which suggests a better development of muscles supporting its bigger skull. A greater development of the neck muscles can be also associated with larger head-to-head butting forces in the case of males. Contractions of the neck muscles can oppose torques during the impact (Schaffer, 19968). However, the *S. tatarica* skull showed the larger diameters of horncore base (m4 and m8), which suggests that males of this saiga had more massive horns. We hypothesize that the sexual dimorphism was more pronounced and a stronger sexual selection operated in *S. tatarica* (Emlen, 2008). In fact, the males are frequently involved in fights and the winner has an opportunity to creates a “harem” of 5 to 10 (up to 50) females before the rut (Sokolov, 1974). Males are very protective of their “harem”, so violent fights are often between males. It is not uncommon for a male saiga to kill its intraspecific combat rival during these battles (Heptner et al., 1988).

Similarly, the horncore base diameters were also larger in the Pleistocene saigas than the recent ones, which can be associated with a stronger sexual selection pressure on males due to a higher population density in the past. A counteracting factor for large horns is heat loss through the horn surface, which may cause an important energetic load to animals living in cold climate conditions (Picard et al., 1996, 1994). Therefore, we should expect smaller horns in the Pleistocene forms existing in much colder environments. Apparently, this factor was less important than the sexual selection, because food was available in that time for saigas, which could sustain these metabolic costs.

Our results clearly showed that the saiga antelope significantly changed over time. The skulls analysed in three periods: the Middle

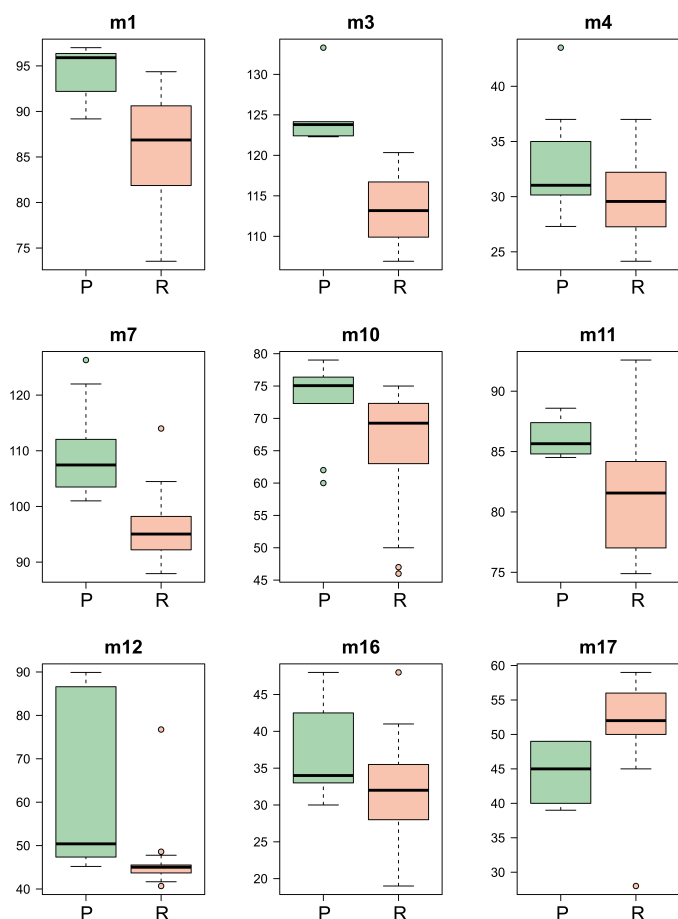


Figure 12 – Box-plots of selected cranial measurements for Pleistocene (P) and recent (R) *Saiga tatarica* found in one locality, Eastern Europe and Western Asia. Other explanations as in Fig. 5.

Pleistocene, the Late Pleistocene and modern times, became smaller in the later period compared with the previous ones. Such trends were also observed for other mammals (Guthrie, 2003; Marciszak et al., 2019; Smith et al., 1995; Stefaniak et al., 2019; van der Made et al., 2014; Wilson, 1996). The decrease applied to almost all cranial measurements of the saiga considered not only as one taxon (i.e. including both *S. borealis* and *S. tatarica*) but also only *S. tatarica*. The only feature that significantly increased in *S. tatarica* was the angle of divergence of horncores (m17). This change could be related with sexual dimorphism and sexual selection.

The changes in the saiga skull, especially those referring to the size, can be associated with climatic and geographical transformations during the Pleistocene and up to the present. The larger size of Pleistocene forms compared to more recent ones can be interpreted according to Bergmann's rule assuming that populations and species in colder conditions are usually larger than those in warmer environments (Bergmann, 1848). The larger size brings benefits in cold climate because bigger animals have a lower surface area to volume ratio than smaller forms. Therefore, they radiate less body heat per unit of mass. However, this interpretation was criticized because there are many other factors that can influence the body size. One of them is abundance and availability of nutrient which provide energy during periods of growth (Geist, 1987; Guthrie, 1984; McNab, 2010; Rosenzweig, 1968; Yom-Tov and Geffen, 2006). Poorer food resources can restrict population and finally lead to a smaller body size of individuals (Clauss et al., 2013). Moreover, bigger species can have a higher probability of survival in environments with seasonal availability of resources because they metabolize fat stores at lower weight-specific rates than smaller species (Dunbrack and Ramsay, 1993; Lindstedt and Boyce, 1985). Similarly, in colder conditions, larger organisms can more efficiently manage their larger fat reservoir to provide the energy needed for survival and can better tolerate periods of food shortages (Ashton et al., 2000). It was

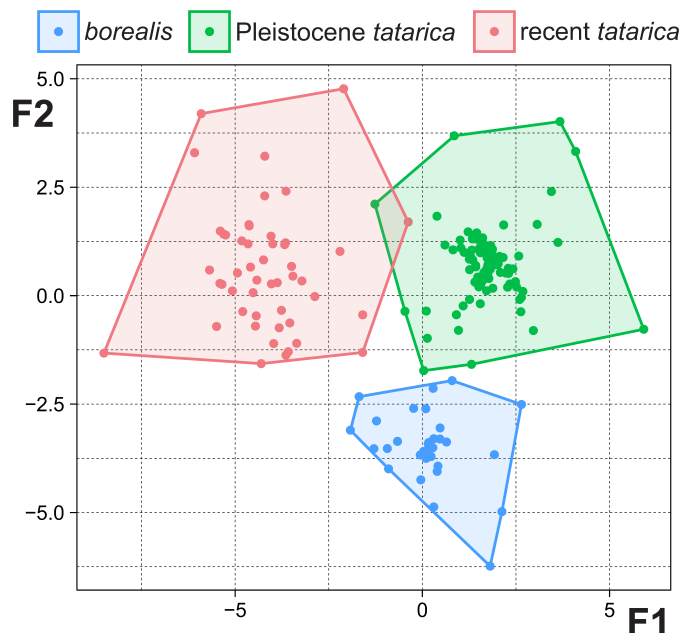


Figure 13 – Discriminant function analysis plot for three saigas.

also proposed that food of low nutritional value is better tolerated by larger body-sized organisms because they have larger rumens, wider mouths and lower relative metabolism rates (Adamczewski et al., 1994; Hanley and Hanley, 1980; Hofmann, 1989; Illius and Gordon, 1987). The body size can be also influenced by sexual selection, especially in males. Accordingly, the sexual dimorphism is present in saiga.

Following these considerations, we can assume that in the Pleistocene, there existed more suitable conditions for saiga than at the end of this epoch and in the Holocene. In fact, this antelope was a typical representative of *Mammuthus–Coelodonta* faunal complex, which included cold-adapted species preferring steppe, steppe-tundra and tundra (Kahlke, 2014). Such ecosystems provided more food resources for saiga, i.e. grasses and herbaceous plants, and thus resulted in its wider occurrence in Eurasia up to Canada during the Pleistocene. The continental and dry climate was also more favourable for this nomadic herbivore because it allowed for long-distant migrations across steppes across the whole Eurasia. At the end of the Pleistocene, the climate warmed up, became more humid and open habitats were replaced by forests, mainly taiga (Kahlke, 2014; Kuhn and Mooers, 2010). The disappearance of favourable conditions caused that the saiga individuals become smaller, whereas populations retreated from already occupied areas and reduced significantly during the postglacial time to the region from the Carpathians to Altai (Sokolov, 1974). The shrinkage of habitats and decrease in the population size could also contribute to the lower genetic variation.

A unique feature of *Saiga* is a short mobile proboscis, which is a good adaptation to filter out dust kicked up by the herd during summer migrations and also acts as a thermoregulatory organ during the summer season (Sokolov, 1974). On the other hand, in winter, it heats up and moistens the frigid and dry air before it gets into the lungs. This characteristic made the saiga well adapted to the climatic and environmental conditions in the Pleistocene. Therefore, it would be interesting to verify how this organ changed over time. Unfortunately, it has a null preservation potential in the fossil record. The anterior part of cranium (viscerocranium) could be correlated with the size of proboscis and the volume of nasal cavity. However, it is very rarely preserved as fossil. Therefore, we can only indirectly hypothesize about these features based on the rest of the cranium. If we assume that the width of the preserved part of cranium is correlated with the anterior part, we can infer that wider skulls possessed a more capacious nasal cavity, which was more effective at warming cool air, e.g. in glacial periods during the Pleistocene. Interestingly, we found that the Pleistocene skulls were characterized by significantly larger breadthwise dimensions than those

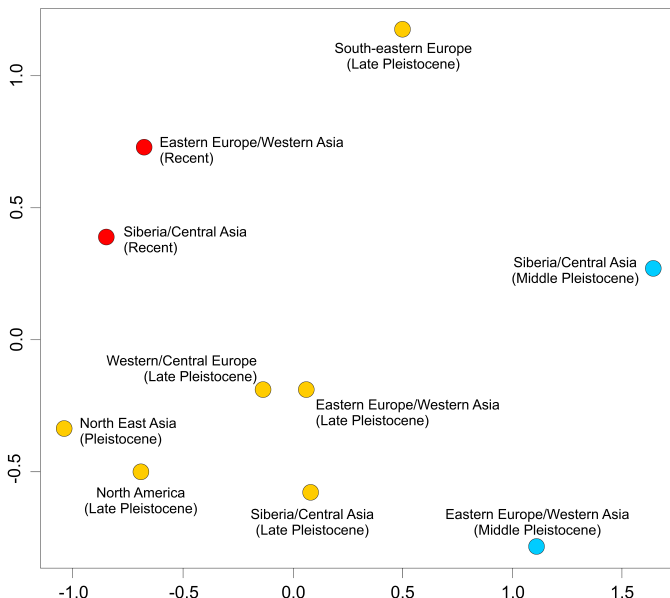


Figure 14 – Multidimensional scaling plot for nine groups of *Saiga* determined according to geographical location and geological time.

in recent forms. It would mean that the Pleistocene forms were better adapted to cold and continental climate. In agreement with that, the recent analyses of stable carbon and nitrogen isotope revealed that the extinct saiga showed a greater ecological and dietary flexibility than the modern populations (Jurgensen et al., 2017). However, it may be associated with poor and restricted forage resources available to the modern saiga living in semideserts, less diverse environments.

The influence of the regional climatic and environmental conditions on the differentiation of Saiga can also explain the distinction in skull measurements observed between Pleistocene *S. tatarica* and *S. borealis*. The former was exclusively found in South-eastern Europe and dominated in Western/Central Europe, which were characterized by a milder climate. In turn, *S. borealis* prevailed in regions with more cold and continental conditions, i.e. Siberia and North East Asia, as well as it could be more common in North America. The territory in which the distributions of the two saigas could more overlapped was Eastern Europe/Western Asia, where, however, relatively more skulls of *S. tatarica* was reported. The results indicate that two different saiga forms existed in the Pleistocene occupying regions with different climatic and ecological conditions, which were reflected in the cranial material.

The general comparisons of saiga groups in the multidimensional scaling showed that the samples of the same geological age are closer located in the plot than those of the same geographical location. It indicates that the temporal factor was more important in variation of saiga skull than the spatial distribution. However, the skulls of a similar age were more similar if they came from geographically adjacent regions. It implies a continuity between their populations and intense migrations, which prevented development of specific features.

An interesting exception are the above-mentioned South-eastern European saigas, which probably represented a separated population with independent changes in the skull. They are characterized by smaller measurements. Many of them were found in Crimean Peninsula, where saiga survived even till the 20th century (Vremir, 2004). The isolation of saiga in Crimea in the interglacials could have resulted from the rise of the Black Sea level and development of the Crimean Island. It is not inconceivable that the decrease in skull (and body) size of this saiga was associated with diminishing of its population. Saiga herds could be isolated, also in other regions, due to various geographic barriers, e.g. mountains, as well as thick snow cover, expanding glaciers or dense forests, which significantly limited the saiga spread in the past (Aaris-Sorensen et al., 1999; Baryshnikov and Tikhonov, 1994; Baryshnikov et al., 1990; Kahlke, 1990, 1992, 2014; Shpansky, 2006; Vereshchagin

et al., 1982). In consequence, the isolated populations could develop different features observed in skulls.

The taxonomic status of the two saigas, *S. borealis* and *S. tatarica*, is not easy to determine. Our analyses showed only quantitative difference in some skull measurements between them. Taking into account this finding and migratory character of this antelope, we can conclude that these saigas probably do not represent separate species, *S. borealis* and *S. tatarica*. The preliminary analyses of ancient DNA seem confirm this concept (Campos et al., 2014, 2010). They did not justify recognizing them as separate species. If we regard that these two saigas dominated in different geographic regions, we can consider them as separate subspecies, *S. t. borealis* and *S. t. tatarica*, as proposed by R.D. Kahlke (Kahlke, 1991) and assuming that subspecies are populations of a species occupying a distinct breeding range and showing some diagnostic features. However, the ranges of these two saigas could not be completely separated but could overlap because their remains were found in some of the same regions. Unfortunately, their fossils are not precisely dated, so we are not able to decide if these saigas co-existed at the same time in these regions. If we agree that their ranges considerably overlapped, they could be considered ecotypes (genetically distinct populations within a species, which are adapted to or determined by specific environmental conditions) or ecophenotypes (phenotypic modifications caused by environmental factors). Nevertheless, it cannot be excluded that the two saigas evolved initially allopatrically as subspecies in different regions. Consequently, the insufficient contacts and the low genetic flow between these two *Saiga* subspecies could be the cause of their morphological differentiation. Additional genetic analyses involving Pleistocene *Saiga* are required to assess differentiation and taxonomic status of this antelope.

Conclusions

The study of the collected cranial material of *Saiga* revealed differentiation of this taxon in time and space as well as significant differences between two main saigas commonly identified by other authors. The extinct *S. t. borealis* proved to have a longer skull and a larger occipital region than *S. t. tatarica*. On the other hand, the latter showed larger diameters of the horncore base, which could be associated with a stronger sexual selection in *S. t. tatarica*. The differences in *S. t. borealis* and *S. t. tatarica* living in the Pleistocene epoch could be driven by regional climatic and environmental conditions. *Saiga tatarica borealis* dominated in Siberia and North East Asia characterized by colder and continental conditions, whereas the Pleistocene *S. t. tatarica* preferred South-eastern and Western/Central Europe with a milder climate. Therefore, it is not inconceivable that the two saigas emerged as subspecies in different regions, but after spreading their populations could mixture when they got into the contact zone. Alternatively, they could be considered ecotypes or ecophenotypes. The same problem concerns to forms described under the names *binagadensis*, *mongolica*, *prisca* and *ricei* as well as specific samples from Crimean Peninsula and adjacent regions, whose skulls showed substantially smaller measurements. The latter probably represented an isolated population, in which these features evolved. These different saiga forms could represent an intraspecific variation within *S. t. borealis* and *S. t. tatarica* associated with the regional conditions on a smaller scale. Additional genetic analyses including Pleistocene forms can help to solve the issue of taxonomic status of various saiga forms. The skull of saiga became significantly smaller in almost all cranial measurements since the Pleistocene till modern times. These changes could be linked with disappearance of favourable conditions, e.g. contraction of open steppes, strongly preferred by saiga. The only angle of divergence of horncores became significantly wider over time in *S. t. tatarica*, which was probably related with sexual selection. ☞

References

- Aaris-Sorensen K., Petersen K.S., Henriksen M.B., 1999. Late Weichselian record of saiga (*Saiga tatarica* (L.)) from Denmark and its implications of glacial history and environment. *Quartaer*. 49–50: 87–94.

- Adamczewski J.Z., Kerr W.M., Lammerding E.F., Flood P.F., 1994. Digestion of low-protein grass hay by muskoxen and cattle. *Journal of Wildlife Management* 58: 679–685.
- Alekperova N.A., 1955. The fossil Saiga from Bynagady. *Trudy Estestvenno-istoricheskogo museya AN Azerb. SSR*. 10: 10–64.
- Alvarez-Lao D.J., Garcia N., 2011. Geographical distribution of Pleistocene cold-adapted large mammal faunas in the Iberian Peninsula. *Quaternary International*. 233(2): 159–170.
- Arylov Y., Badmaev V., Bekenov A., Chimeg J., Entwistle A., Grachev Y.A., Lhagvasuren B., Lushchekina A., Mallon D., Milner-Gulland E.J., Ukrainsky V., 2004. The saiga antelope — teetering on the brink but still cause for hope. *Oryx* 38(3): 250–251.
- Ashton K.G., Tracy M.C., Queiroz A.D., 2000. Is Bergmann's Rule Valid for Mammals? *The American Naturalist* 156(4): 390–415.
- Bachura O., Kosintsev P., 2007. Late Pleistocene and Holocene small- and large-mammal faunas from the Northern Urals. *Quaternary International* 160: 121–128.
- Bannikov A.G., 1954. *Mammals of the Mongolian People's Republic*. Nauka, Moscow, Russia.
- Baryshnikov G., Tikhonov A., 1994. Notes on skulls of Pleistocene saiga of northern Eurasia. *Historical Biology* 8(1–4): 209–234.
- Baryshnikov G.F., Kasparov A.K., Tikhonov A.N., 1990. Saiga of the Paleolithic of the Crimea. *Trudy Zoologicheskogo Instituta* 212: 3–48.
- Bergmann C., 1848. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Vandenhoeck und Ruprecht, Göttingen*. [in German]
- Campos P.F., Hofreiter M., Orlando L., Willerslev E., Gilbert M.T., 2014. Corrigendum. *Mol Ecol*. 23(22): 5646–5648.
- Campos P.F., Kristensen T., Orlando L., Sher A., Kholodova M.V., Gotherstrom A., Hofreiter M., Drucker D.G., Kosintsev P., Tikhonov A., Baryshnikov G.F., Willerslev E., Gilbert M.T., 2010. Ancient DNA sequences point to a large loss of mitochondrial genetic diversity in the saiga antelope (*Saiga tatarica*) since the Pleistocene. *Mol Ecol*. 19(22): 4863–4875.
- Clauss M., Dittmann M.T., Müller D.W.H., Meloro C., Codron D., 2013. Bergmann's rule in mammals: a cross-species interspecific pattern. *Oikos* 122(10): 1465–1472.
- Dunbrack R.L., Ramsay M.A., 1993. The allometry of mammalian adaptations to seasonal environments: a critique of the fasting endurance hypothesis. *Oikos* 66: 336–342.
- Emlen D.J., 2008. The evolution of animal weapons. *Annual Review of Ecology Evolution and Systematics* 39: 387–413.
- Frick C., 1937. Horned Ruminants of North America. *Bulletin of the American Museum of Natural History* 69: 1–669.
- Geist V., 1987. Bergmann's rule is invalid. *Canadian Journal of Zoology* 65(4): 1035–1038.
- Grubb P., 2005. Order Artiodactyla. In: Wilson D.E., Reeder D.M. (Eds.) *Mammal Species of the World: A Taxonomic and Geographic Reference*. Johns Hopkins University Press, Baltimore, USA. 688.
- Guthrie D.R., 2003. Rapid body size decline in Alaskan Pleistocene horses before extinction. *Nature* 426(6963): 1476–1487.
- Guthrie R.D., 1984. Mosaics, allelochemicals and nutrients. An ecological theory of late Pleistocene megafaunal extinctions. In: Martin P.S., Klein S. (Eds.) *Quaternary extinctions*. University of Arizona Press, Tucson. 254–298.
- Hanley T.A., Hanley K.A., 1980. Food resource partitioning by sympatric ungulates on Great Basin rangeland. *Journal of Range Management* 35: 152–158.
- Harington C.R., 1984. Quaternary marine and land mammals and their paleoenvironmental implications, some examples from northern North America. *Special Publications Carnegie Museum Natural History* 8.
- Heptner V., Nasimovich A., Bannikov A., 1988. *Mammals of the Soviet Union*, 1. Amerind Publishing Co., New Delhi.
- Hofmann R.R., 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* 78: 443–457.
- Illius A.W., Gordon I.J., 1987. The allometry of food intake in grazing ruminants. *Journal of Animal Ecology* 56: 989–999.
- IUCN SSC Antelope Specialist Group, 2018. *Saiga tatarica*. The IUCN Red List of Threatened Species 2018 <http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T19832A50194357>. en [Accessed 05 December 2018]
- Jurgensen J., Drucker D.G., Stuart A.J., Schneider M., Buuveibaatar B., Bocherens H., 2017. Diet and habitat of the saiga antelope during the late Quaternary using stable carbon and nitrogen isotope ratios. *Quaternary Science Reviews* 160: 150–161.
- Kahlke H.D., 1975. Der Saiga-Fund von Bottrop/Westfalen. *Quartär* 26: 135–146. [in German]
- Kahlke H.D., 1991. Pleistocene Distributional and Evolutionary History of the Genus *Saiga* Gray, 1843 (Mammalia, Artiodactyla, Bovidae) in the Palaearctic. *Vertebrata Palasiatica* 10: 314–322.
- Kahlke R.D., 1990. Der Saiga-Fund von Pahren. Ein Beitrag zur Kenntnis der palaarktischen Verbreitungsgeschichte der Gattung *Saiga* Gray 1843 unter besonderer Berücksichtigung des Gebietes der DDR. *Eiszeitalter und Gegenwart* 40: 20–37. [in German]
- Kahlke R.D., 1992. Repeated immigration of Saiga into Europe. *Courier Forschungsinstitut Senckenberg* 153: 187–195.
- Kahlke R.D., 2014. The origin of Eurasian Mammoth Faunas (Mammuthus-Coelodonta Faunal Complex). *Quaternary Science Reviews* 96: 32–49.
- Kholodova M.V., Milner-Gulland E.J., Easton A.J., Amgalan L., Arylov I.A., Bekenov A., Grachev I.A., Lushchekina A.A., Ryder O., 2006. Mitochondrial DNA variation and population structure of the Critically Endangered saiga antelope *Saiga tatarica*. *Oryx* 40(1): 103–107.
- Kosintsev P.A., Bachura O.P., 2013. Late Pleistocene and Holocene mammal fauna of the Southern Urals. *Quaternary International*. 284: 161–170.
- Kuhn T.S., Mooers A.O., 2010. Missing saiga on the taiga. *Mol Ecol*. 19(22): 4834–4836.
- Lindstedt S.L., Boyce M.S., 1985. Seasonality, fasting endurance, and body size in mammals. *The American Naturalist* 125: 873–878.
- Marciszak A., Schouwenburg C., Gornig W., Lipecki G., Mackiewicz P., 2019. Morphometric comparison of *Panthera spelaea* (Goldfuss, 1810) from Poland with the lion remains from Eurasia over the last 700 ka. *Quaternary Science Reviews* 223.
- Markova A.K., Puzachenko A.Y., van Kolfschoten T., 2010. The North Eurasian mammal assemblages during the end of MIS 3 (Brianskian–Late Karginian–Denekamp Interstadial). *Quaternary International* 212(2): 149–158.
- McNab B.K., 2010. Geographic and temporal correlations of mammalian size reconsidered: a resource rule. *Oecologia* 164(1): 13–23.
- Milner-Gulland E.J., Kholodova M.V., Bekenov A., Bukreeva O.M., Grachev I.A., Amgalan L., Lushchekina A.A., 2001. Dramatic declines in saiga antelope populations. *Oryx* 35(4): 340–345.
- Nadachowski A., Lipecki G., Ratajczak U., Stefaniak K., Wojtal P., 2016. Dispersal events of the saiga antelope (*Saiga tatarica*) in Central Europe in response to the climatic fluctuations in MIS 2 and the early part of MIS 1. *Quaternary International* 420: 357–362.
- Nehring A., 1891. Diluviale Reste von *Cuon*, *Ovis*, *Saiga*, *Ibex* und *Rupicapra* aus Mähren. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* 2: 107–155. [in German]
- Petrova E.A., 2009. Istoria formirovaniya fauny krupnykh mekopitajusczich Volzhko — Komskogo regiona v srednim i pozdnim neopleistocene. *Sankt Petersburg: 1–301*. [in Russian]
- Picard K., Festa-Bianchet M., Thomas D., 1996. The cost of horniness: heat loss may counter sexual selection for large horns in temperate bovids. *Ecoscience* 3(3): 280–284.
- Picard K., Thomas D.W., Festa-Bianchet M., Lanthier C., 1994. Bovid horns: an important site for heat loss during winter? *Journal of Mammalogy* 75(3): 710–713.
- R Core Team, 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at <https://www.r-project.org/>
- Ratajczak U., Shpansky A.V., Malikov D.G., Stefaniak K., Nadachowski A., Wojtal P., Ridush B., Krakhmalnaya T.V., Stepanchuk V., Mackiewicz P., 2016. Quaternary skulls of the saiga antelope from Eastern Europe and Siberia: *Saiga borealis* versus *Saiga tatarica* — One species or two? *Quaternary International* 420: 329–347.
- Ridush B., Stefaniak K., Socha P., Proskurnyak Y., Marciszak A., Vremir M., Nadachowski A., 2013. Emine-Bair-Khosar Cave in the Crimea, a huge bone accumulation of Late Pleistocene fauna. *Quaternary International* 284: 151–160.
- Rosenzweig M.L., 1968. The strategy of body size in mammalian carnivores. *The American Midland Naturalist* 80(2): 299–315.
- Schaffer W.M., 1968. Intraspecific combat and the evolution of the Caprini. *Evolution Lancaster Pa.* 22: 817–825.
- Sher A.V., 1968. Fossil Saiga in Northeastern Siberia and Alaska. *International Geology Review* 10(11): 1247–1260.
- Shpansky A.V., 2006. Quaternary mammal remains from the Krasny Yar locality (Tomsk region, Russia). *Quaternary International* 142: 203–207.
- Smith F.A., Betancourt J.L., Brown J.H., 1995. Evolution of Body Size in the Woodrat Over the Past 25,000 Years of Climate Change. *Science* 270(5244): 2012–2014.
- Sokolov E.V., 1974. *Saiga tatarica*. *Mammalian Species* 38: 1–4.
- Stefaniak K., Lipecki G., Nadachowski A., Semba A., Ratajczak U., Kotowski A., Roblíčková M., Wojtal P., Shpansky A.V., Malikov D.G., Krakhmalnaya T.V., Kovalchuk O.M., Boeskorov G.G., Nikolskiy P.A., Baryshnikov G.F., Ridush B., Jakubowski G., Pawłowska K., Cyrek K., Sudol-Procyk M., Czyżewski L., Krajcarz M., Krajcarz M.T., Żeromska A., Gagat P., Mackiewicz P., 2019. Diversity of muskox *Ovibos moschatus* (Zimmerman, 1780) (Bovidae, Mammalia) in time and space based on cranial morphology. *Historical Biology*: 1–16.
- Tchersky I.D., 1876. *Antilope (Saiga) borealis* n. spec. fossilis. *Izvestia Sibirskogo otdela Imperatorskogo Geographicheskogo Obschestwa*. 7(4,5): 145–151.
- van der Made J., Stefaniak K., Marciszak A., 2014. The Polish fossil record of the wolf *Canis* and the deer *Alces*, *Capreolus*, *Megaloceros*, *Dama* and *Cervus* in an evolutionary perspective. *Quaternary International* 326–327: 406–430.
- Vereshchagin N.K., Baryshnikov G.F., 1982. Paleoeology of Mammoth fauna in the Eurasian Arctic. In: Hopkins D.M., Matthews J.V., Schweger C.E., Young S.B. (Eds.) *Paleoecology of Beringia*. Academic Press, New York. 267–280.
- Vladimirovich G.M., Lozovskaya M.V., Hossain A., Viktorovich M.A., 2014. Saiga fossils in the Southern-Lower Volga of Astrakhan, Russia. *Songklanakarinn Journal Science Technology* 36(1): 27–35.
- von den Driesch A., 1976. A guide to the measurement of animal bones from archaeological sites. *Peabody Museum Bulletin* 1: 1–136.
- Vremir M.M., 2004. New approach on the saiga antelopes (*Saiga tatarica/borealis*; Bovidae) from the Late Pleistocene and Holocene of Crimea (SE Ukraine). *Studia Universitatis Babeş-Bolyai Geologia* 49(2): 105–108.
- Wilson M.C., 1996. Late Quaternary vertebrates and the opening of the ice-free corridor, with special reference to bison. *Quaternary International* 32: 97–105.
- Yom-Tov Y., Geffen E., 2006. Geographic variation in body size: the effects of ambient temperature and precipitation. *Oecologia* 148: 213–218.
- Young J.K., Murray K.M., Strindberg S., Buuveibaatar B., Berger J., 2010. Population estimates of Endangered Mongolian saiga *Saiga tatarica mongolica*: implications for effective monitoring and population recovery. *Oryx* 44(2): 285–292.

Associate Editor: P. Raia

Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table SI-SII Results of various statistical analyses cited in the main text.