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ARTICLE



Diversity of muskox *Ovibos moschatus* (Zimmerman, 1780) (Bovidae, Mammalia) in time and space based on cranial morphometry

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ABSTRACT

Muskox *Ovibos moschatus* is a Pleistocene relic, which has survived only in North America and Greenland. During the Pleistocene, it was widely distributed in Eurasia and North America. To evaluate its morphological variability through time and space, we conducted an extensive morphometric study of 217 *Praeovibos* and *Ovibos* skull remains. The analyses showed that the skulls grew progressively wider from *Praeovibos* sp. to the Pleistocene *O. moschatus*, while from the Pleistocene to the recent *O. moschatus*, the facial regions of the skull turned narrower and shorter. We also noticed significant geographic differences between the various Pleistocene *Ovibos* crania. Siberian skulls were usually larger than those from Western and Central Europe. Eastern European muskoxen also exceeded in size those from the other regions of Europe. The large size of Late Pleistocene muskoxen from regions located in more continental climatic regimes was probably associated with the presence of more suitable food resources in steppe-tundra settings. Consistently, radiocarbon-dated records of this species are more numerous in colder periods, when the steppe-tundra was widely spread, and less abundant in warmer periods.

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Introduction

Muskox, *Ovibos moschatus* (Zimmerman, 1780), was an important representative of the *Mammuthus-Coelodonta* faunal complex, which was widely distributed in the Pleistocene from Eurasia to North America (Kahlke 1999, 2014). This species survived the global faunal extinction at the end of the Pleistocene in North America and Greenland, but not in Eurasia and Beringia (Lorenzen et al. 2011; Cooper et al. 2015). Since then, its range significantly reduced. *Ovibos moschatus* is now distributed in Northeast and North Greenland as well as on the largest islands covering the Nunavit and northwestern territories of the Canadian Arctic Archipelago (Lent 1999; Gunn and Forchhammer 2008). This species was re-introduced into Alaska and West Greenland as well as into Siberia and Norway territory. This mammal is well

adapted morphologically and physiologically to cold climatic conditions. It is covered with thick wool, which enables it to reduce its metabolism and use previously stored fat reserves. Thus, the muskox is a good indicator of glacial environments.

The oldest remains of this species were found in Süssenborn (Germany) in the layers dated to the early Middle Pleistocene (MIS 16, 640–620 ka) (Kahlke 1963) although it probably appeared in the circumpolar tundra zone (Kahlke 2014). In the subsequent cold periods of the Pleistocene, it was widespread in Eurasia, from north-eastern Spain, southern France and Great Britain in the west, across Germany, the central part of Europe, southern Scandinavia, the Baltic countries and Russia to Chukotka in eastern Asia (Sher 1971; Tikhonov 1994, 1998; Kahlke 1999, 2014; Raufuss and von Koenigswald 1999; Markova et al. 2015; Pawłowska 2015); it also migrated into North America (Sher 1971;

Kurtén and Anderson 1980). Its maximum distribution was reached during the Vistulian glacial, the Denekamp Interstadial (uncal. 33–25 ka BP, cal. 37–29 ka BP) and the Late Glacial Transition (uncal. 17–12.4 ka BP, cal. 20.5–14.4 ka BP) (Markova et al. 2015). Then followed a sudden decline during the Older (uncal. 12.4–10.8 ka BP, cal. 14.4–12.7 ka BP) and the Younger Dryas Stadials (uncal. 10.8–10.3 ka BP, cal. 12.7–12.1 ka BP) (Markova et al. 2015). Based on the literature, the most recent record of muskox in Eurasia is dated to uncal. 2700 ± 70 yr BP (cal. 2819 yr BP) from the Taymyr Peninsula (Sulerzhitsky and Romanenko 1997; Orlova et al. 2004). *Ovibos* became extinct in Eurasia because of increasing global temperature and humidity and not because of human activity (Currant and Jacobi 2001; Campos et al. 2010b; Lorenzen et al. 2011; Markova et al. 2015; Krakhmalnaya and Kovalchuk 2018).

The genus *Ovibos* is thought to be related with the older genus *Praeovibos*, which appeared in the Early Pleistocene (ca. 1.8–1.1 Ma) (Crégut-Bonnoure 2007) or even the late Pliocene, zone MNQ18 (Garrido 2008). *Praeovibos* was widespread in the Middle Pleistocene from Western Europe, including the British Isles, to north-western Canada (Sher 1974, 1987; Crégut-Bonnoure 1984, 2007; McDonald et al. 1991). Unlike *Ovibos*, which is typical of the periglacial environment, *Praeovibos* was probably not specialised to cold conditions; in fact, its remains were also found in Mediterranean region (Crégut-Bonnoure 1984; McDonald et al. 1991). It is hypothesised that *Ovibos* had directly derived from *Praeovibos* or that both genera have had originated from a common ancestor (Lent 1999; Mol et al. 1999; Campos et al. 2010a; Markova et al. 2015). These two muskoxen likely coexisted in the Middle Pleistocene and perhaps competed for resources (Kahlke 1964; Kurtén 1968). *Praeovibos* differed from *Ovibos* by having poorly developed horn-cores, higher and rounded skull and narrower forehead. In the cheek teeth, *Praeovibos* had better developed cingula and additional islets on the occlusal surface. Its metapodia were also slender and more elongated.

The Eurasian Pleistocene muskox included a subspecies, *O. moschatus pallantis*, which was originally described as *O. pallantis* by H. Smith in 1827 (Ryziewicz 1955; Baryshnikov 1981; Tikhonov 1998). However, not all authors share this opinion (Lent 1999); genetic analyses on both ancient and modern DNA revealed that the extinct and modern representatives do not belong in separate clades and should be regarded as a single species (Campos et al. 2010b). Morphological comparisons between the present *Ovibos moschatus* and *Praeovibos* were conducted by several authors (Ryziewicz 1955; Sher 1971; Tikhonov 1994), revealing several differences, e.g. the absence or presence of the endostyle in upper molars, lacrimal bones of different size and shape, horn-core bases of distinct size and located in different position, cheek tooth rows of different length. These comparisons, however, were performed on a small amount of specimens, too small to reliably represent the whole range of morphological variation of muskoxen. In the present analysis, we carried out a more extensive morphometric study based on a higher number of Pleistocene and recent skulls of Eurasian and North American muskoxen. The muskox was an important component of the Pleistocene steppe-tundra faunal complex because it was one of the most numerous

herbivorous mammals at that time (Vereshchagin and Baryshnikov 1982; Kahlke 2014). Therefore, improved knowledge of its diversity is crucial to fully understand how ecosystems changed at the Pleistocene/Holocene transition. The results of our study can also be helpful for a better understanding of the factors that led to the demise of muskox. Obtained results can aid in the implementation of conservation and protection actions for this endangered species (Gunn and Forchhammer 2008).

Materials and methods

Measurements

We studied remains of 104 skulls of muskoxen of both the Middle Pleistocene *Praeovibos* as well as the Pleistocene and recent *Ovibos*, from Eurasia and North America (Table S1). Measurements were taken following the procedures described by Ryziewicz (1955), Sher (1971) and von Den Driesch (1976); see Figure 1 for the scheme of the measurements. The measurements were obtained with a slide electronic calliper Mitutoyo with 0.01 accuracy and with a Nonius tape measuring instrument with 0.1 mm accuracy. We added ‘m’ next to the number indicating each of the measurements used (Figure 1). In total, we considered 32 types of measurements and nine indexes of selected dimensions: m9/m1, m4/m1, m3/m1, m4/m3, m24/m18, m28/m9, m27/m9, m11/m15 and m15/m18. The measurements for the left and right horn-core bases (m11) and orbits (m22 and m23) were averaged. We also measured the minimum breadth between the bases of the horn-cores (m14), but finally, we did not include it because it occurred unreliable due to variable preservation of horn-core bases. Additional measurements about muskox skulls were taken from literature. The list of specimens and references are contained in Table S2. The description of selected studied muskox remains found in Polish sites is included in the Supplemental material (Text). In total, we used 2295 measurements taken from 217 skull remains (Table S3). All measurements were expressed in mm.

Dated records

In the study, we collected all available 215 muskox radiocarbon dates, which were carefully selected from literature (see Table S4 for references and other details). We discarded the dates without dating error and those of remains with unclear affiliation to the muskox. We also included five dates that have been recently obtained from cranial remains from sites in Poland: Perspektywiczna Cave (Poz-83555; uncal. 12,910 ± 60 yr BP) and Spławie near Pyzdry (Poz-34506; uncal. 30,400 ± 300 yr BP), in Ukraine: Zbranki (Poz-89281; uncal. 13,880 ± 70 yr BP), as well as in Russia: Minusinsk (UBA-37843; uncal. 20,725 ± 156 yr BP) and Chernilshchikovo (UBA-38454; uncal. 29,603 ± 451 yr BP) (Shpansky 2000). The Polish and Ukrainian samples were radiocarbon-dated in Poznań Radiocarbon Laboratory in Poland and the Russian ones using in the 14CHRONO Centre for Climate, the Environment and Chronology at the Queen’s University Belfast in the United Kingdom. All the dates were calibrated to years before present (BP) in OxCal v4.3 (Bronk Ramsey and Lee 2013) using IntCal13 atmospheric curve

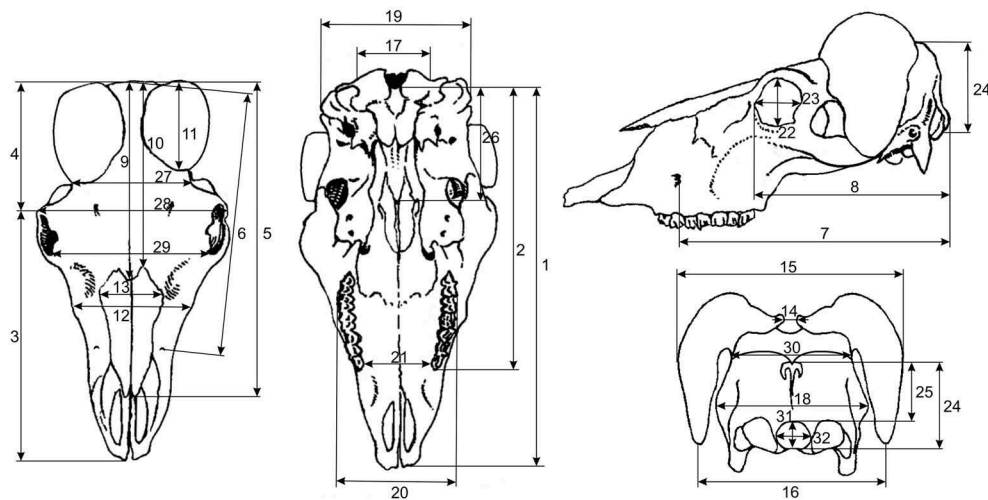


Figure 1. Scheme of muskox skull measurements according to Sher (1971), modified by other authors. 1. Basal length – from basion to prosthion; 2. Short skull length – from basion to premaxilla; 3. Cranial length – from akrocranial to ectorbital; 4. Facial length – from ectorbital to prosthion; 5. Short upper cranial length – from akrocranial to rhinion; 6. From akrocranial to infraorbital on one side of the skull; 7. From the aboral border of one occipital condyles to the infraorbital on the same side of the skull; 8. From basion to the entorbital on the same side of the skull; 9. Median frontal length – from akrocranial to nasion; 10. Small frontal length – from akrocranial to median point of intersection of the line joining the oral points of the frontals; 11. Greatest (oro-aboral) diameter of the horn-core base; 12. Facial breadth – across the facial tuberosities; 13. Greatest breadth across the nasal; 14. Minimum breadth between the bases of the horn-cores; 15. Greatest tangential distance between the outer curves of the horn-cores; 16. Minimum distance between the horn-core tips; 17. Greatest breadth of occipital condyles; 18. Greatest breadth at the bases of the paraoccipital processes; 19. Greatest mastoid breadth – between otion; 20. Greatest palatal breadth – across the outer borders of the alveoli; 21. Minimum palatal breadth – across the inner borders of P2 alveoli; 22. Greatest inner height of the orbit: perpendicular to measurement 23; 23. Greatest inner length of the orbit – from ectorbital to entorbital; 24. Greatest height of occiput – from akrocranion to basion; 25. Minimum height of occiput – from akrocranion to opisthion; 26. Basicranial axis – from basion to synsphenion; 27. Minimum frontal breadth – breadth of the narrowest part of the skull behind the orbits; 28. Greatest frontal breadth – between ectorbital; 29. Minimum orbital breadth – between entorbital; 30. Minimum occipital breadth below horn-cores; 31. Height of the foramen magnum – from basion to opisthion; 32. Greatest breadth of the foramen magnum.

(Reimer et al. 2013). In counting the number of dated muskox records in time intervals of 1.5 ka, multiple records from the same locality were included only once for each time interval to remove the bias in the number of preserved and collected samples from one location.

Statistical analyses

All statistical analyses were performed only on data from adult cranial remains of the Middle Pleistocene *Praeovibos* as well as of the Pleistocene and recent *Ovibos moschatus* (see Figure 2 for examples). The material was divided into groups based on their stratigraphic and geographic provenance. The Pleistocene skulls of *Ovibos moschatus* were additionally subdivided depending on the geographic regions of provenance: Western Europe, Central Europe, Eastern Europe, Northern Europe, Northern Siberia and Southern Siberia. The distinction between groups in individual measurements was expressed by the percentage difference between median of appropriate measurements calculated for the compared groups. The basic statistical parameters were included in Table S5 and S6. All the available specimens were treated statistically, in order to eliminate or anyhow attenuate potential biases due to sexual differences. The data sets were too small to conduct separated analyses for the two sexes. Additional biases could arise from the fact that not all the specimens could be reliably sexed and the data sets were imperfectly discriminated by sex. Analysing all the skull remains avoided these issues. In cases when sex was reliably determined, the sex ratio for individual groups was not biased, which ensures the trustworthiness of the approach adopted.

Statistical tests were conducted on data sets including at least three samples for a given type of measurement and group. A Shapiro–Wilk test was performed to see if the differences between the observed distributions and a normal distribution were statistically significant, while the homogeneity of variance in the analysed groups was checked using a Lévene test. If the assumption of normality of distribution in the data was fulfilled, two groups were compared using the unpaired t-Student test. Otherwise, the non-parametric Wilcoxon-Mann-Whitney test for unpaired samples was used. When we compared more than two groups and the assumptions about normality of distribution and variance homogeneity were fulfilled, we used the parametric one-way Analysis of Variance (ANOVA) with moderately conserved Tukey HSD post-hoc test. If at least one of these two assumptions was violated, we applied the non-parametric Kruskal–Wallis test with Dunn’s post-hoc test in pairwise comparisons between groups. In the post-hoc tests and when many hypotheses were tested, we applied the Benjamini-Hochberg method for p-value correction to control the false discovery rate. Spearman’s rank correlation coefficient and its significance level were calculated for particular skull measurements with different stratigraphic origins as well as between the number dated muskox records and average $\delta^{18}\text{O}$ curve values (Cooper et al. 2015) calculated for given time intervals. Percentage differences in medians of individual measurements were compared with the equal distributions of positive and negative values using χ^2 test. Differences were considered significant when p-value was smaller than 0.05. In Discriminant Function Analysis (DFA) including Canonical Analysis (CA), we replaced the missing measurements of individual specimens with appropriate average values in a given stratigraphic or geographic group. To assess the

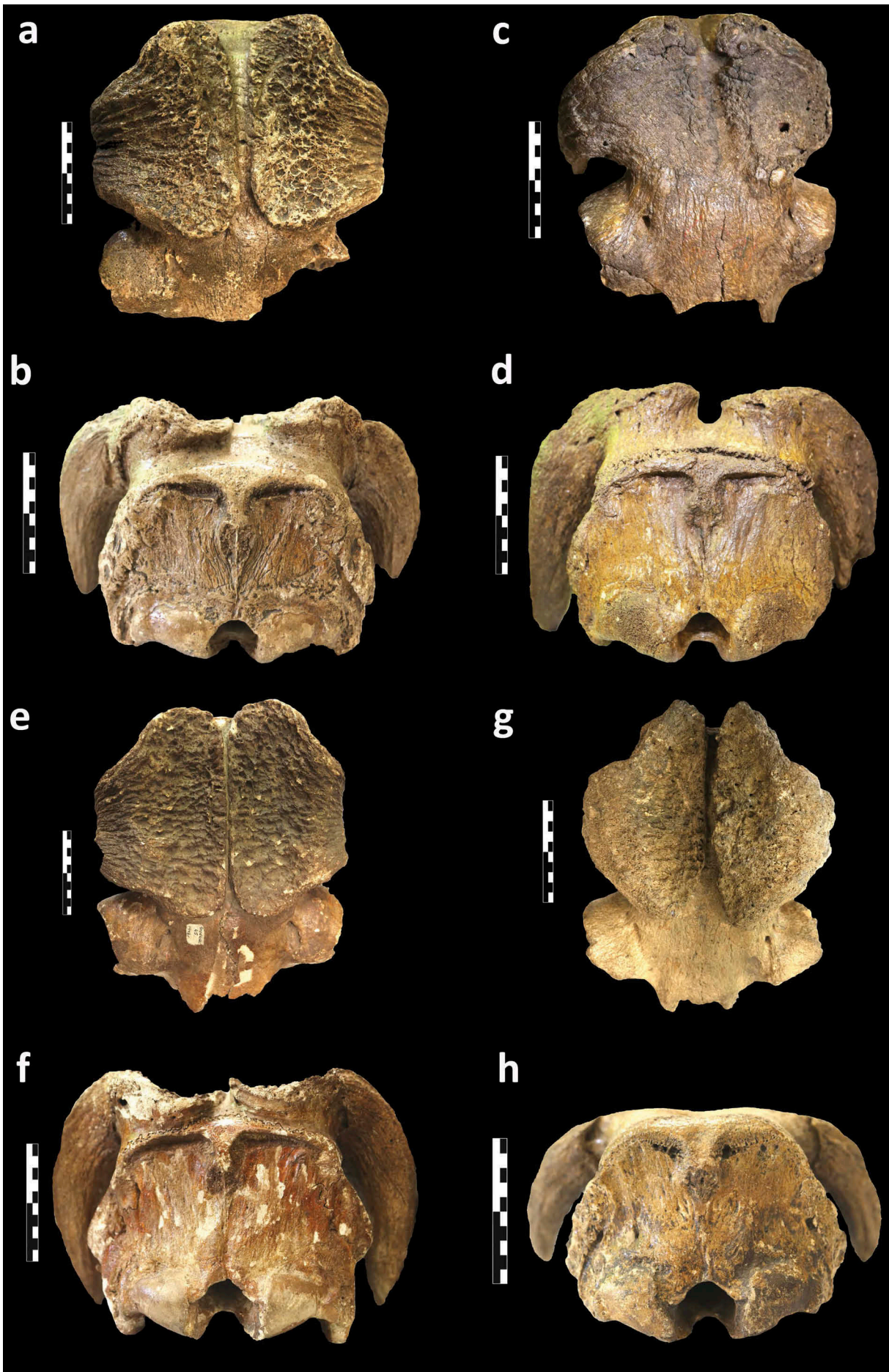


Figure 2. Selected skulls of *Ovibos moschatus* found in Poland. a. b. Lower Silesia, Ovm/M1/3; c. d. Milowice, MIL/M1/4/896; e. f. Grodziec, BED/M1/2; g. h. Milowice, MIL/M1/5/1042. a, c, e and g, top view. b, d, f and h, back view.

relation of each cranial measurement to the discriminant functions, we calculated structure coefficients, which are the correlations between a given variable and the discriminant scores associated with the corresponding function.

Statistical tests were carried out in R package 3.5.1 (A language and environment for statistical computing, R Core Team 2018, R Foundation for Statistical Computing, Vienna, Austria), whereas DFA with CA were done using Statistica (Data analysis software system, version 13, TIBCO Software Inc. 2017).

Results

Comparison of cranial measurements with respect to stratigraphy and genus

Many of the measurements of the Middle Pleistocene *Praeovibos* and of the Pleistocene and recent *Ovibos* showed statistically significant differences. We reported here only differences in median of appropriate measurements exceeding the 10% level; smaller values were presented only when they were statistically significant (Figure 3).

The Pleistocene skulls of *Ovibos* are wider than those of *Praeovibos* (Figure 4). In the groups including at least three samples, the skulls of *Ovibos* are 40% wider in the greatest tangential distance between the outer curves of the horn-cores (m15), 34% in the minimum frontal breadth (m27), 27% in the minimum occipital breadth below the horn-cores (m30), 25% in the greatest breadth at the bases of the paraoccipital processes (m18), 13% in the greatest frontal breadth (m28) and 9% in the greatest mastoid breadth (m19). They are also 14% longer than the skulls of *Praeovibos* in the basicranial axis (m26). The biggest difference was observed in the greatest diameter of the horn-core base (m11), which was 122% larger in the Pleistocene *Ovibos* than in *Praeovibos*. The skull of *Ovibos* is 30% higher in the minimum height of the occiput (m25) and 24% smaller than *Praeovibos* in the minimum distance between the horn-core

tips (m16). Statistically significant differences were obtained in m11, m19, m25, m26, m27 and m30.

Some dimensions could only be measured in specimens of two *Praeovibos*. Compared with *Praeovibos*, the skulls of the Pleistocene *Ovibos* are 41% wider in the greatest breadth across the nasal (m13), 20% in the facial breadth (m12) and 11% in the index m11/m15, i.e. the greatest diameter of the horn-core base by the greatest tangential distance between the outer curves of the horn-cores. Some measurements taken only on an individual skull of *Praeovibos* show that this taxon is 29% smaller in the facial length (m4) and 14% in the greatest inner length of the orbit (m23) (Figure 4).

Differences between skulls of Pleistocene and recent *Ovibos* are generally not very strong (Figure 4). The recent skulls are sometimes shorter lengthwise, on average 22% in the cranial length (m3) and 14% in the basicranial axis (m26). They are also often narrower breadthwise in (i) the viscerocranium: 15% in the facial breadth (m12), 14% in the greatest breadth across the nasal (m13), 11% in the greatest (m20), 10% in the minimum palatal breadth (m21), and in (ii) the neurocranium: 10% in the greatest breadth of the foramen magnum (m32) and 8% in the minimum occipital breadth under the horn-cores (m30). Moreover, the recent crania have become 19% and 14% smaller, respectively, in the greatest inner length (m23) and the height of the orbit (m22), respectively, as well as they are 24% lower in the posterior part of skull, i.e. the minimum height of the occiput (m25). The differences result statistically significant in m20, m22, m23, m25, m30 and m32.

On the other hand, some dimensions of neurocranium have increased from the Pleistocene to the recent representatives, i.e. the small frontal length (m10) is 15% and the greatest breadth of the occipital condyles (m17) 10% larger (Figure 4). The minimum distance between the horn-core tips (m16) is even 148% larger. The differences in m10 and m16 are statistically significant.

The skull shape of muskoxen has also changed since the Pleistocene. The viscerocranium became on average 35%

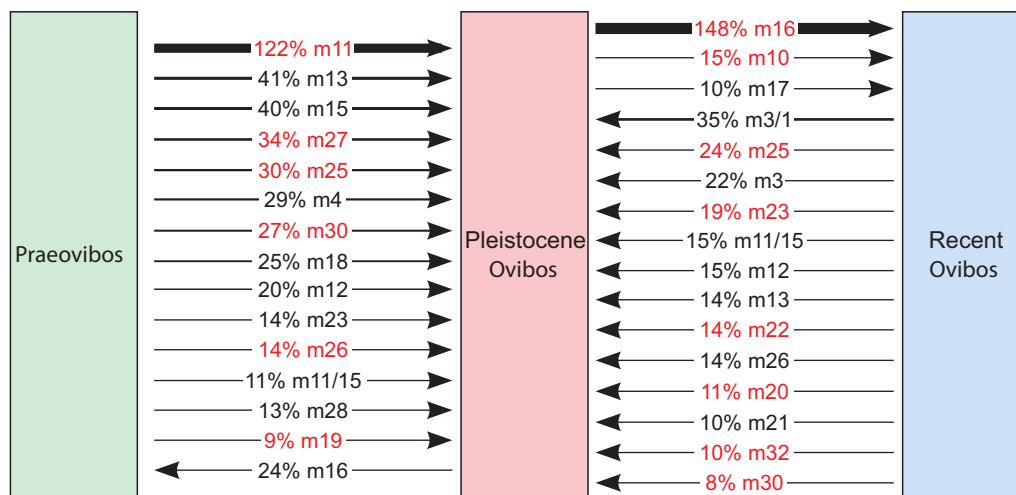


Figure 3. Diagram showing at least 10% differences in median of cranial measurements between *Praeovibos*, the Pleistocene *Ovibos* and the recent *Ovibos*. Smaller values were presented only when they were statistically significant (marked in red). Arrowhead indicates the group that has a given median value larger.

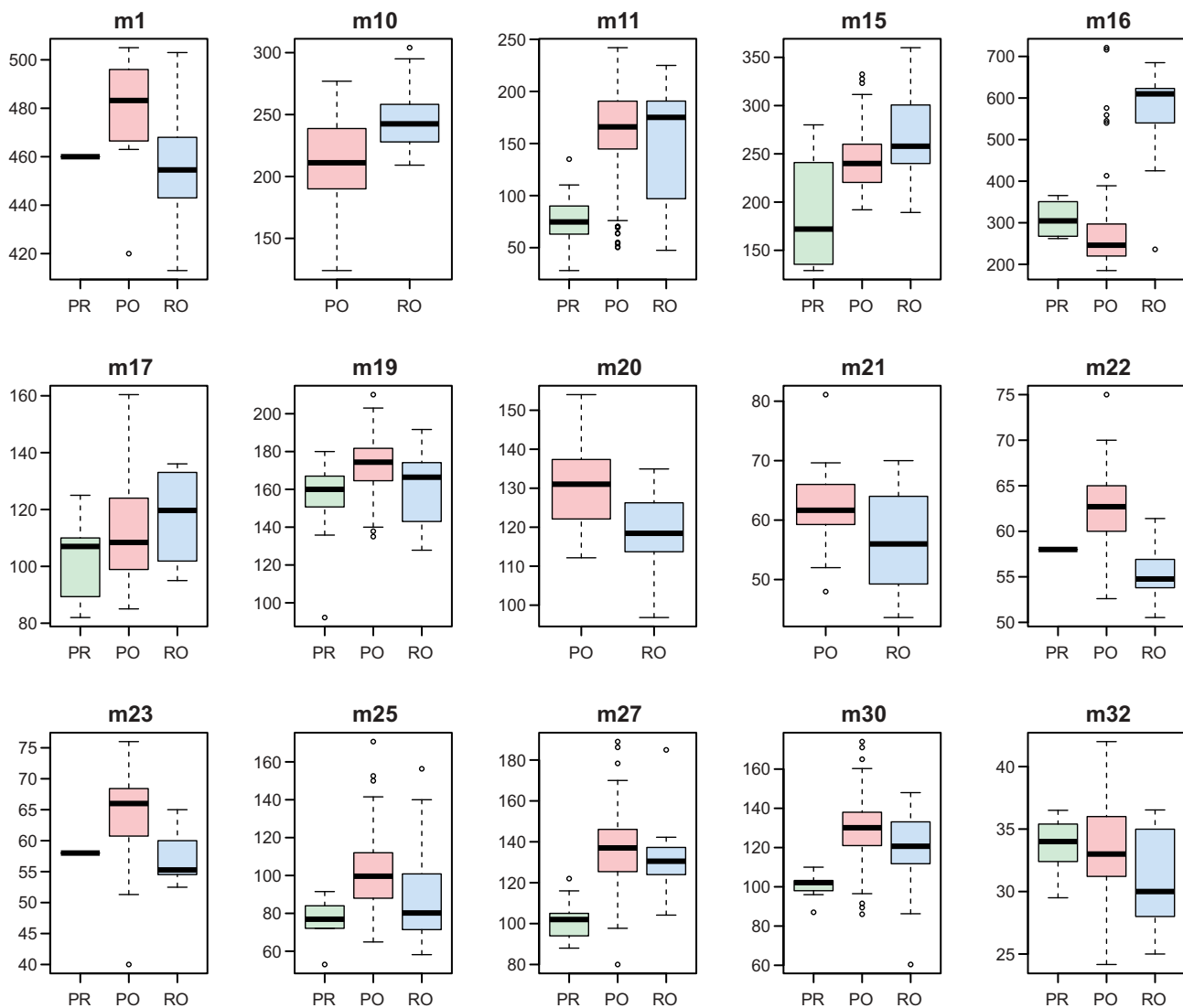


Figure 4. Box-plots of selected cranial measurements of the Middle Pleistocene *Praeovibos* (PR), the Pleistocene *Ovibos* (PO) and the recent *Ovibos* (RO). Thick line indicates median, box shows quartile range and whiskers denote range without outliers. Values are given in mm.

shorter in relation to the whole length (m3/m1) and the greatest diameter of the horn-core base 15% shorter relative to the greatest tangential distance between the outer curves of the horn-cores (m11/m15).

Comparing the measurements of the skulls of all three groups reveals several trends over time. Most of the cranial dimensions grew progressively larger from the Middle Pleistocene *Praeovibos* and reached the highest values in the Pleistocene *Ovibos*; then they decreased again in the recent representatives (Figure 4). This trend can be observed in the breadth of the anterior (m12) and posterior (m18, m19, m28, m30) parts of the skull as well as in the occipital height (m25). A similar trend is observed in relation between the greatest diameter of the horn-core base and the greatest tangential distance between the outer curves of the horn-cores (m11/m15). Also, the greatest diameter of the horn-core base (m11) and the minimum frontal breadth (m27) grew wider from *Praeovibos* to the Pleistocene *Ovibos* but stabilised thereafter (Figure 4).

In contrast, the greatest tangential distance between the outer curves of the horn-cores (m15) and the greatest breadth of the occipital condyles (m17) gradually increases

from the Middle Pleistocene *Praeovibos* to the Pleistocene *Ovibos* and then decreased thereafter. The Spearman's rank correlation coefficient (ρ) calculated for these two variables was 0.24 and 0.22, and statistically significant with the p-values 0.017 and 0.026, respectively. At the same time, the greatest breadth of the foramen magnum (m32) grew gradually narrower ($\rho = -0.21$, $p = 0.017$), while the minimum distance between the horn-core tips (m16) first grew narrower in the Pleistocene *Ovibos* and then wider again in the extant representatives.

The variations in the median of many of the individual measurements taken for this study can effectively summarise the modifications that the muskox skulls underwent over time. The Pleistocene *Ovibos* exceeds in size the Middle Pleistocene *Praeovibos* in almost 86% of the median cranial measurements, whereas almost 68% of the medians are smaller in the modern than in the Pleistocene *Ovibos*. The skulls therefore grew larger from the Middle Pleistocene *Praeovibos* to the Pleistocene *Ovibos* and decreased thereafter. The biased distributions of these medians deviated significantly from their equal distribution ($p = 0.001$ and $p = 0.048$, respectively).

The discriminant analysis indicates that there is a significant difference between the three groups of skulls (Figure 5). The χ^2 test identified two discriminant functions ($p < 0.001$); the first explains 83.6% of variance and shows how the Pleistocene *Ovibos* skulls are separated from the others. This distinction is associated with the larger dimensions of these skulls in comparison to older *Praeovibos* and younger *Ovibos* specimens. Below, we reported the correlation coefficients (r) between a given variable and the discriminant function greater than $|0.25|$. The first function (root) was most negatively correlated with the greatest breadth across the nasal, m13 ($r = -0.39$) and the basal length, m1 ($r = -0.26$), as well as with the dimensions of the orbit, m22 ($r = -0.33$) and m23 ($r = -0.26$). These measurements reach the largest values in the Pleistocene skulls of *Ovibos*. In contrast, the second function, explaining 16.4% of variance, was responsible for the separation of most recent skulls of *Ovibos* from the others, especially from those of *Praeovibos*. This function showed a high negative correlation with the measurements that were substantially smaller in *Praeovibos* than in the recent muskox, i.e. the distance between the horn-cores described by m16 ($r = -0.62$) and m15 ($r = -0.48$), the greatest diameter of the horn-core base, m11 ($r = -0.26$), the breadths m13 ($r = -0.30$) and m27 ($r = -0.28$) as well as the length of the neurocranium, m4 ($r = -0.29$). The measurements m16 and m15, which are most negatively correlated with the function, reached also the largest values in the extant *Ovibos*. In turn, the greatest inner height of the orbit, m22 was positively correlated ($r = 0.29$) and was larger in *Praeovibos* than those of the recent *Ovibos*.

Comparison of cranial measurements grouped based on geographic locality

In order to study the spatial differentiation of muskox skulls, we conducted cross-comparisons between different cranial

measurements of the Pleistocene specimens of *Ovibos*. We excluded data of both the Middle Pleistocene *Praeovibos* and the recent *Ovibos* from this analysis to eliminate the potential influence of taxonomic and temporal differences, which were described above. In the comparison, we grouped the skulls into five sets, two Asian ones (Northern and Southern Siberia) and three European sets (Central, Eastern and Western Europe). A potential Northern European set would be represented only by one skull and is therefore excluded from the statistical analysis. In the description presented below, we focused on the measurements for which the statistical tests showed significant intergroup differences as well as some of those for which the differences were greater than 15% and the compared groups were represented by at least three specimens (Figure 6).

Among the determined groups, muskox skulls from Northern Siberia are characterised by the largest values of many measurements (Figure 7). Compared to those from Central Europe, these skulls are 20% wider in the greatest breadth of the occipital condyles (m17), 19% longer in the basicranial axis (m26), 13% wider in the greatest frontal breadth (m28) and 8% wider in the greatest breadth of the foramen magnum (m32) and 15% longer in the median frontal length (m9). Only the latter difference is not statistically significant. The skulls from Northern Siberia are 17% larger than those from Western Europe in the basicranial axis (m26) and 37% in the minimum orbital breadth (m29) (Figure 7). The Western European skulls provided a 23% lower index between the greatest tangential distance between the outer curves of the horn-cores and the greatest breadth at the bases of the paraoccipital processes (m15/m18). This is associated with the statistically significant 13% increase in m18 of Western European crania compared with those from Northern Siberia. Northern Siberian skulls are also 17% significantly higher in the greatest inner height of the orbit (m22) than skulls from Eastern Europe (Figure 7).

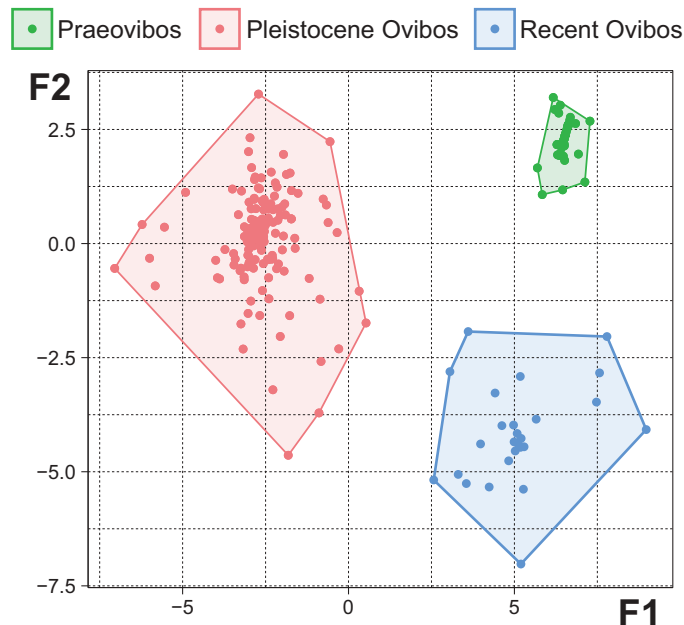


Figure 5. Discriminant function analysis plot for three groups of muskoxen of various genera and geological age.

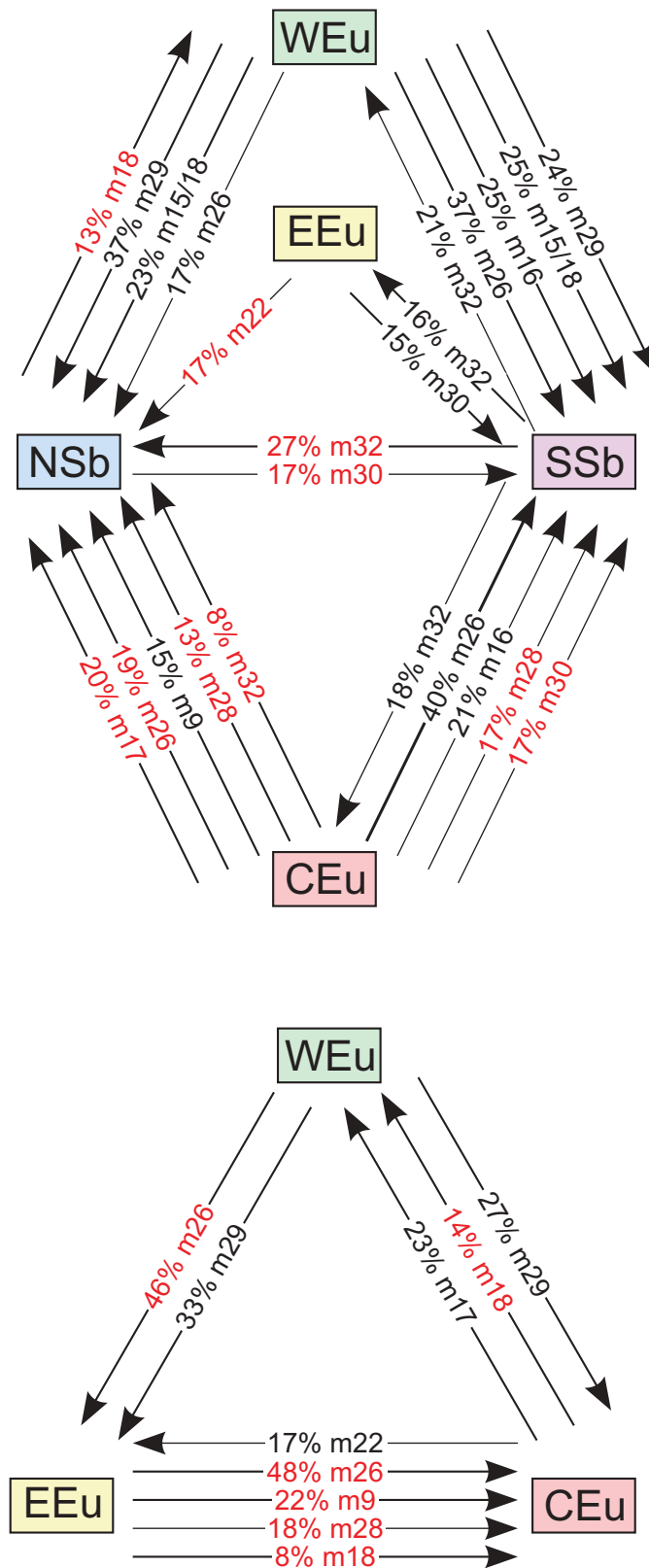


Figure 6. Diagrams showing at least 15% differences in median of cranial measurements between Pleistocene *Ovis* subdivided geographically: Western Europe (WEu), Central Europe (CEu), Eastern Europe (EEu), Northern Siberia (NSb) and Southern Siberia (SSb). Results for groups represented by at least three specimens were only shown. Other explanations as in Figure 3.

Skulls from Southern Siberia are also 40% and 37% longer than those from Central and Western Europe in the basicranial axis (m26) as well as 21% and 25% wider in the

minimum distance between the horn-core tips (m16), respectively (Figure 7). Moreover, the Central European crania are 17% significantly narrower than those from Southern Siberia

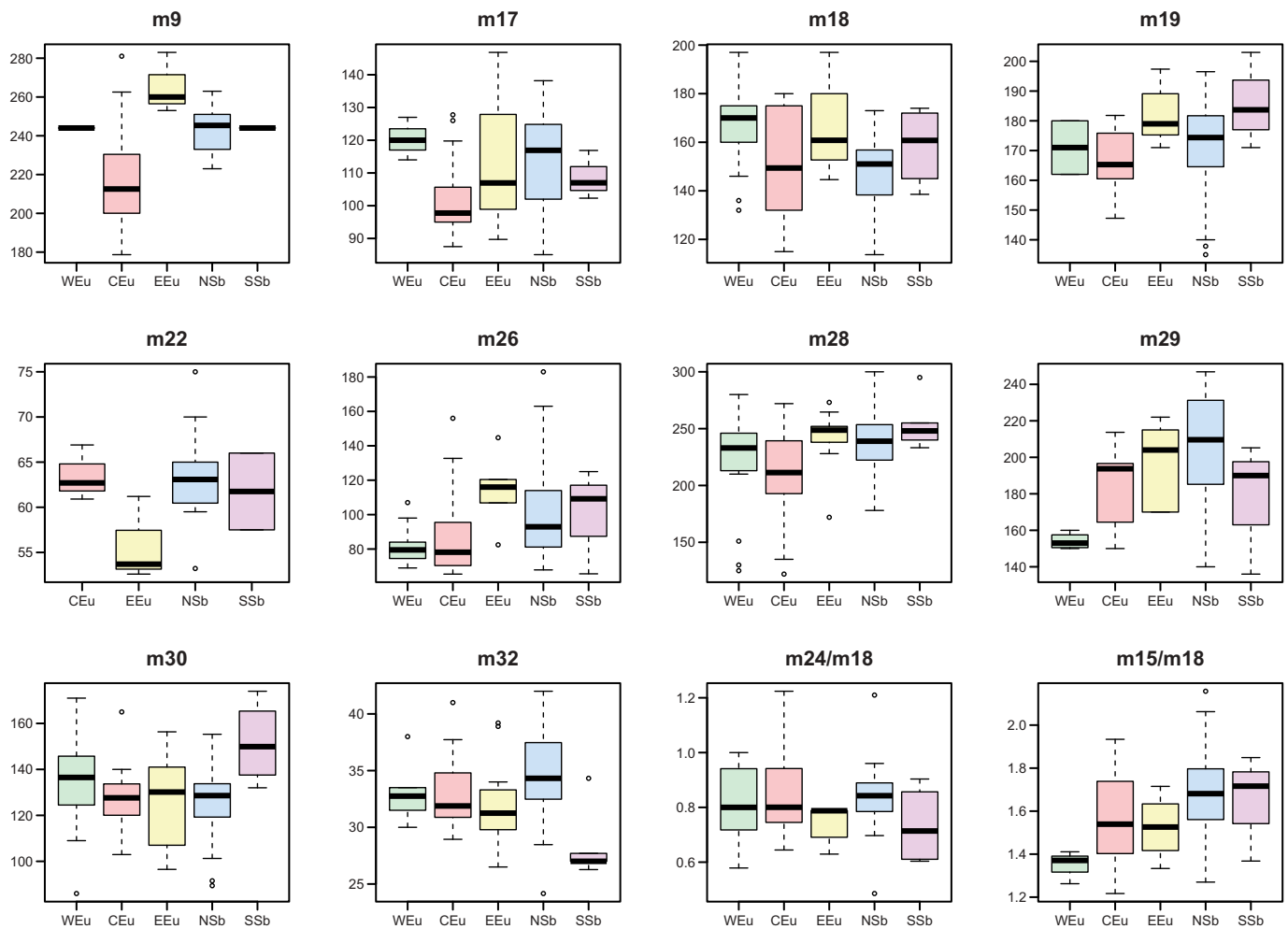


Figure 7. Box-plots of selected cranial measurements of Pleistocene *Oribos* subdivided geographically: Western Europe (WEu), Central Europe (CEu), Eastern Europe (EEu), Northern Siberia (NSb) and Southern Siberia (SSb). Other explanations as in [Figure 4](#).

in the greatest frontal breadth (m28) and the minimum occipital breadth below horn-cores (m30). Eastern European skulls are also 15% narrower than those from Southern Siberia in m30 ([Figure 7](#)). When compared with the Southern Siberian crania, those from Western Europe are 24% narrower in the minimum orbital breadth (m29) and have 25% smaller m15/m18. The Siberian skulls are 16%, 18% and 21% narrower in the greatest breadth of the foramen magnum (m32) than those from Eastern, Central and Western Europe, respectively.

We noticed some statistically significant differences between the Siberian skulls ([Figure 7](#)). Those from the northern region are 27% wider in the greatest breadth of the foramen magnum (m32), while those from the south are 17% wider in the minimum occipital breadth below horn-cores (m30).

Interestingly, we found quite a large diversity in skull dimensions among the European muskoxen ([Figure 7](#)). Crania from Eastern Europe are 48% longer than those from Central Europe in the basicranial axis (m26), 22% longer in the median frontal length (m9), 18% wider in the greatest frontal breadth (m28) and 8% wider in the greatest mastoid breadth (m19). All these differences are statistically

significant. On the other hand, the skulls from Eastern Europe are 17% lower in the greatest inner height of the orbit (m22) than those from Central Europe. Eastern European skulls also exceed those from Western Europe in the basicranial axis (m26) in 46% and the minimum orbital breadth (m29) in 33% ([Figure 7](#)). The former difference is statistically significant. Compared with Central European skulls, those from Western Europe are also 27% narrower in m29 but 23% wider in the greatest breadth of occipital condyles (m17) and 14% wider in the greatest breadth at the bases of the paraoccipital processes (m18). The latter difference is statistically significant.

The Pleistocene muskox skulls from Siberia are generally the largest among the studied ones, whereas those from Central and Western Europe are the smallest. There is an average percentage difference of 5% between the groups of at least three specimens (Siberia vs Central/Western Europe), whereas 69% of the measurements yield greater median values for Siberian skulls than for the European ones. This unequal distribution of measurements is significantly different from the equal (i.e. 50%) one ($p = 0.002$). In the comparison including the Southern Siberian group, the average difference reached more than 7%, whereas 71% of medians

exceed those of the European set ($p = 0.02$). Skulls from Central and Western Europe in comparison to other sets are on average 5% smaller, whereas 68% of medians are lower than in the other groups ($p = 0.0003$). The comparison of the skulls from only Central Europe to others, excluding those from Western Europe, gives 6% and 77% ($p = 1.6 \times 10^{-5}$), respectively. East-European skulls are also larger in comparison to those from Central and Western Europe. The average difference is more than 5%, and 67% of medians are greater in the former than in the latter set ($p = 0.056$).

The discriminant analysis shows a clear separation of the skulls subdivided geographically (Figure 8). Four discriminant functions resulted significant with $p < 0.000001$. They explained 82.3%, 10.2%, 5.5% and 2.0% of variance, respectively. The first function clearly distinguished West-European muskox skulls, which are one of the smallest among the studied data. Based on the correlation coefficients $> |0.25|$, this function is most negatively correlated with the index $m27/m9$, i.e. the minimum frontal breadth to the median frontal length ($r = -0.53$), as well as with the minimum orbital breadth, $m29$ ($r = -0.34$). It indicates that crania from Western Europe are very narrow, both in total and in relation to their length. The second function clearly separates Central European skulls from East-European ones, which partially overlap skull sets from Siberia. This function shows a highly negative correlation coefficient with the index $m27/m9$ ($r = -0.56$) as well as a positive one with the median frontal length, $m9$ ($r = 0.71$) and the greatest breadth of the occipital condyles, $m17$ ($r = 0.26$). This indicates that skulls from Eastern Europe have longer and wider neurocrania than those from central regions of Europe. The third function yields a partial isolation of numerous skulls from Northern Siberia, which may be associated with their large size. Consequently, this function is negatively correlated with the minimum orbital breadth, $m29$ ($r = -0.40$), the greatest breadth of the foramen magnum, $m32$ ($r = -0.38$) and the index $m15/m18$, which is the ratio between the distance between the horn-cores and the breadth of the occipital region of the cranium ($r = -0.29$). The highest positive correlation is reached with the greatest breadth at the bases of the paraoccipital processes, $m18$ ($r = 0.32$), which is relatively small in the Northern Siberian skulls.

Distribution of dated records

Figure 9 presents the geographic distribution of the 215 sites for which radiocarbon dates are available. We divided them into seven groups distinguished geographically as Western Europe (12 dates), Northern Europe (4 dates), Central Europe (8 dates), Eastern Europe (34 dates), Southern Siberia (3 dates), Northern-middle Siberia (106 dates) and Eastern Siberia (48 dates). The oldest dates, most of which infinite, >50 ka BP or even >60 ka BP, were recorded from Bol'shoy Lyakhovsky Island in Eastern Siberia, whereas the oldest date in Europe is 47.6 ka BP from Jämtland (Sweden). These, however, are not the oldest remains of *Ovibos* known so far, which, in contrast, were discovered in the Middle Pleistocene deposits of Süssenborn (Germany) (Kahlke 1963). The abundance of dates and remains from Siberia can indicate the north-eastern part of Asia as a place where much of the evolution of muskoxen took place and where they were commonly distributed. However, this conclusion should be considered with a caution because the high relative abundance of muskoxen remains may also depend on other factors, e.g. favourable taphonomic and preservation circumstances as well as greater exploration of the area.

The youngest dates also come from Siberia: ca. 2620 yr BP (Republic of Sakha, Eastern Siberia) and ca. 2820 yr BP (Logata River, Northern-middle Siberia), see Figure 9 and Table S4. This indicates that some muskox population survived in these regions until the Subboreal period of the Holocene. In contrast, the most recent European dates of ca. 12.9 ka BP (Bugorok site, Central Europe) and ca. 12.7 ka BP (Medvezhya cave, Eastern Europe) indicate that muskox persisted in Central and Eastern Europe probably only up to the Younger Dryas. In Western Europe, the species likely became extinct earlier, at the end of the deglaciation (the Late Glacial Transition), ca. 15 ka BP, as suggested by the remains from the Goyet Cave system (Belgium).

The sets of dates from Eastern Siberia reveal a discontinuity during the time period ca. 43–33 ka BP (Figure 9). A similar gap is shown by the dates from Eastern Europe (ca. 44–31 ka BP) and Western Europe (ca.

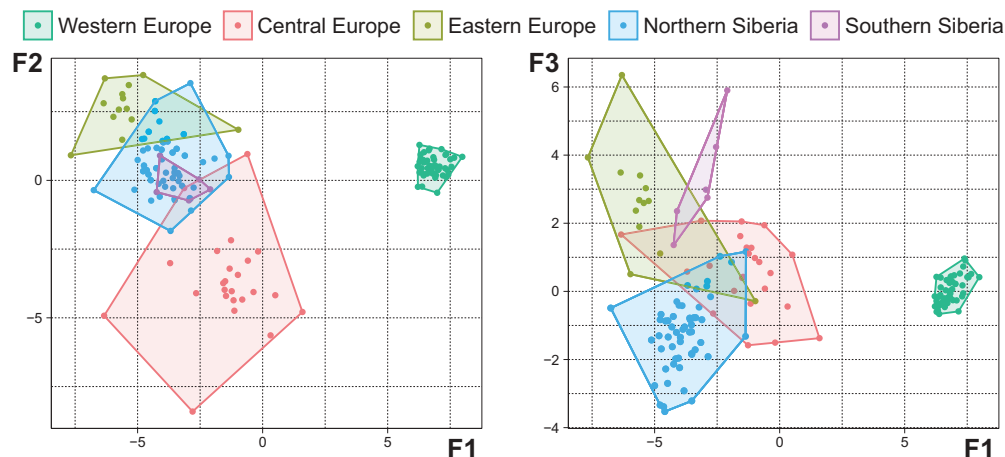


Figure 8. Discriminant function analysis plots of Pleistocene *Ovibos* discriminated based on geographic regions of provenance.

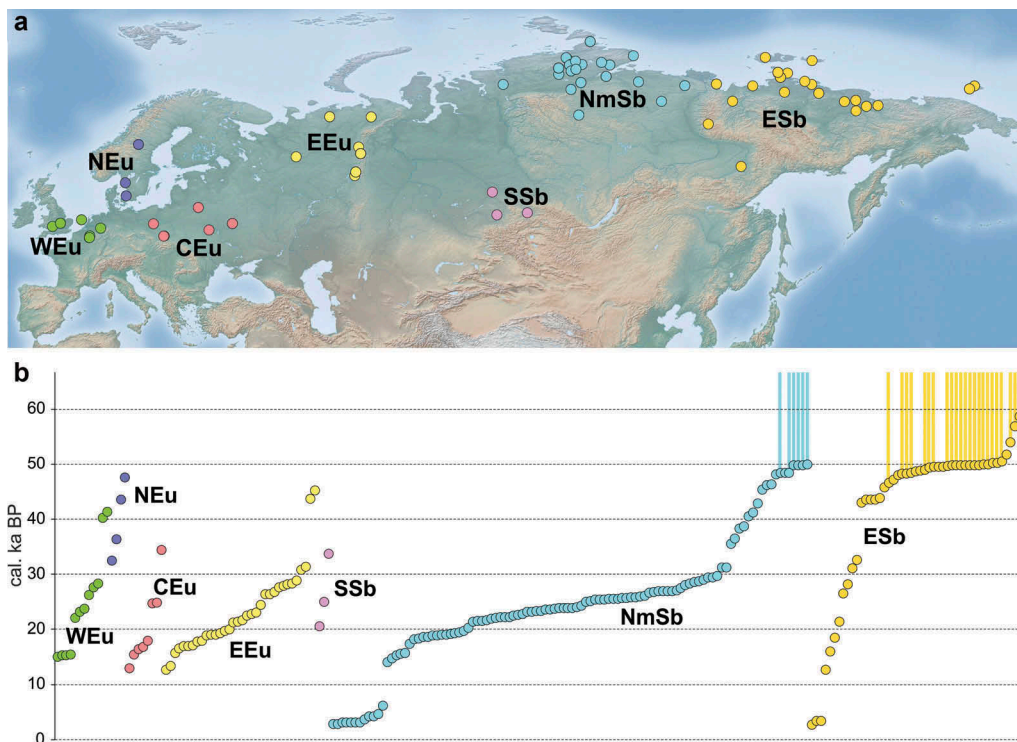


Figure 9. Radiocarbon-dated records of *Ovibos* in space and time. The records are categorised in seven groups: Western Europe (WEu), Northern Europe (NEu), Central Europe (CEu), Eastern Europe (EEu), Southern Siberia (SSb), Northern-middle Siberia (NmSb) and Eastern Siberia (ESb). a. Location of sites. b. Distribution of the dated records in time scale. The dates are sorted from the youngest to the oldest for each group. Vertical lines beginning from some points indicate open dates.

40–28 ka BP). Only individual dates were reported from other regions. This time interval falls within the so-called ‘interple-niglacial’ of the Last Glacial Period (MIS 3), which was characterised by a comparatively warmer climate than other periods of the Last Glacial Period (Rasmussen et al. 2006; Svensson et al. 2008). Another long gap in the datings from Northern-middle Siberia (ca. 14–6.1 ka BP) and Eastern Siberian (ca. 12.7–3.4 ka BP) was found in the time period of sudden climate warming at the Pleistocene/Holocene transition.

In order to check the influence of climatic changes on the muskox population, we compared the distribution of the dated muskox records with the pattern of the revised $\delta^{18}\text{O}$ curve in the Greenland ice core (Figure 10). The curve was obtained by combining the Cariaco Basin (Hulu Cave) and Greenland ice core (GICC05) records and contains reliable climate proxy variables reflecting climatic changes in the Pleistocene (Cooper et al. 2015). By combining the Cariaco Basin (Hulu Cave) radiocarbon record of shifts in the Intertropical Convergence Zone with Greenland temperature, the authors were able to bring abrupt interstadial transitions and high-resolution radiocarbon records into the same calendar time scale. The combined Cariaco-Greenland chronology greatly reduced the uncertainty surrounding the onset of interstadial events by 18% to 79%.

Generally, the number of dated muskox records negatively correlates with the $\delta^{18}\text{O}$ curve: the Spearman’s rank correlation coefficient is $\rho = -0.56$ and statistically significant ($p = 0.002$). There are more dated records available for colder

periods (Greenland stadials) than for warmer ones (Greenland interstadials) – Figure 10. The oldest peak in the number of dated muskox records (ca. 49 ka BP) is correlated with the cold stadial GS-13. It is followed by a decrease peaking at ca. 46 ka BP, at the time of the warm interstadial GI-12. Then again, the number of dated muskox records increased at ca. 46 ka BP at the time of the stadial GS-12. Since this time until ca. 32 ka BP, the number of *Ovibos* dated records is very low. There is a gap in the dated records from the three regions mentioned in the previous paragraph. This was a time of major climatic fluctuations, i.e. rapid alternation of at least six interstadials and six stadials. The number of dated muskox records rises again only after ca. 32 ka BP, i.e. the relatively cold GS-6. This trend peaks at ca. 23 ka BP in the Last Glacial Maximum (LGM). This period was dominated by relatively longer stadials (GS-5.2, 5.1, 4, 3 and 2.2), with only few intervening short interstadials (GI-5.1, 4, 3, 2.2 and 2.1). The dated records vary considerably in the period of the deglaciation (the Late Glacial Transition). Although this entire interval is referred to the GS-2.1, it contains evident fluctuations in the $\delta^{18}\text{O}$ values, which are well correlated with the changes in the number of dated muskox records. A higher numbers (at ca. 18.75 ka BP and ca. 15.75 ka BP) correlate with the lowest $\delta^{18}\text{O}$ values, and decreasing numbers of dated records (at ca. 17.25 ka BP) are connected with higher $\delta^{18}\text{O}$ values. From the time of the GS-2.1, the number of dated records dropped considerably during the Bølling-Allerød interstadial warming, GI-1 (ca. 14.25 ka BP) and somewhat increased again in the Younger Dryas Stadial, GS-1 (ca. 12.75

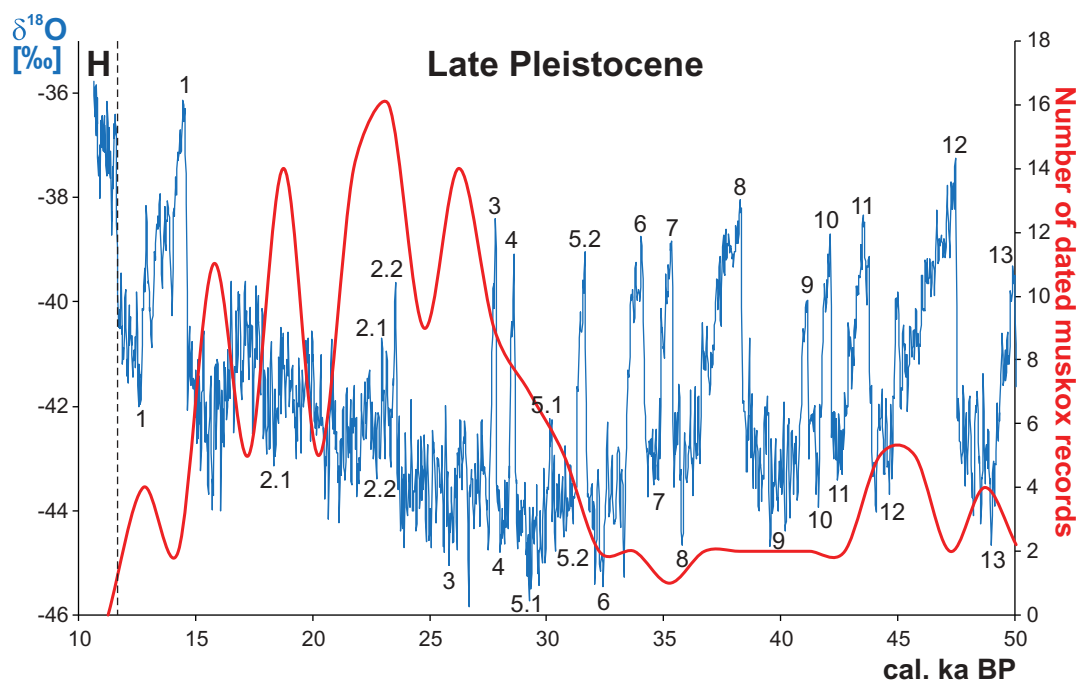


Figure 10. Curve of the number of dated muskox records (red) against the revised $\delta^{18}\text{O}$ curve in the Greenland ice core (blue) obtained by combining the Cariaco Basin (Hulu Cave) and Greenland ice core (GIACC05) records (Cooper et al. 2015). The number of dated muskox records was calculated in time intervals of 1.5 ka. Multiple records from the same locality were counted only once for each time interval. Corresponding Greenland stadials (GS) and interstadials (GI), as determined by Rasmussen et al. (2014) and Seierstad et al. (2014) are indicated by numbers placed below or above the $\delta^{18}\text{O}$ curve, respectively. H stands for the Holocene.

ka BP), and finally reached zero at the beginning of the Holocene. Since 6.1 ka BP, no dated fossil *Ovibos* records were reported.

Discussion

A relatively rich amount of cranial remains of muskox was analysed to verify the taxonomic consistency as well as the stratigraphic and geographic distribution of the genus. The study is based on 32 different measurements and nine indexes. Unfortunately, the poor preservation prevented us from taking all the required measurements of each specimen. Although the poor sample preservation did not allow to test if the differences in some measurements, especially of the oldest remains, are statistically significant, the groups of skulls considered for this study show clear tendencies and evolutionary trends. The present conclusions need to be verified in the light of new evidence.

Based on the available material, skulls assigned to *Praeovibos* resulted being smaller in a number of dimensions as compared to the Pleistocene *Ovibos*. In particular, the latter exceeds the former especially in width measurements and has horn-cores more widely separated from one another and with thicker bases.

A controversial issue is whether *Praeovibos* was a direct ancestor of *Ovibos* or both genera derived from a common ancestor during the Early Pleistocene (Villafranchian) (Lent 1999; Mol et al. 1999; Campos et al. 2010a; Markova et al. 2015). The Late Pliocene genus *Boopsis*, discovered in China, could be related with the potential common ancestor of both genera (Lent 1999). Finding the remains of both genera in Middle Pleistocene deposits would support the second hypothesis (Kahlke 1964; Kurtén 1968). However,

mitochondrial DNA-based phylogenetic analyses demonstrated that *Praeovibos* sequences fall in the diversity of the recent *Ovibos*, which may imply that *Praeovibos* is an earlier morphotype of the extant *O. moschatus* (Campos et al. 2010a). If *Praeovibos* evolved into *Ovibos*, the transition occurred after a small group of individuals became isolated, evolved independently, and then radiated, replacing the remaining populations of *Praeovibos* (Lent 1999).

Nevertheless, the potential ancestor of *Ovibos* most likely resembled *Praeovibos*. Therefore, we can assume that the differences between these genera reflect evolutionary changes through time in a phylogenetic lineage leading to *Ovibos*. In agreement with this assumption, *Praeovibos* is considered less specialised than *Ovibos* (Mol et al. 1999) and is regarded as an early, more cosmopolitan, variety of muskox (Campos et al. 2010a) with greater ecological variability (Kahlke 2014). Early and Middle Pleistocene faunal assemblages including *Praeovibos* are typical of vast, temperate and moist grasslands and wooded steppes (Crégut-Bonnoure 1984; McDonald et al. 1991) and also Caucasian mountain landscapes (Baryshnikov 2007) and are not exclusive of cold tundra settings as are the Late Pleistocene and recent muskoxen (Mol et al. 1999). Thus, *Praeovibos* seems not to have been a typical member of the cold fauna of the mammoth steppe-tundra in contrast to *Ovibos*. Therefore, we can assume that the increase in muskoxen size was associated with climatic and ecosystem transformations during the Pleistocene, specifically with the cooling and the spread of steppe-tundra in Eurasia and North America.

On the other hand, recent representatives of *Ovibos* are significantly smaller than the Pleistocene ones. The viscerocranium and neurocranium have become narrower in a number of dimensions and the anterior part of the skull has visibly

shortened. The general decrease in the skull size, however, is not a simple reversion to the Middle Pleistocene representatives of *Praeovibos* because not all dimensions were subjected to the same changes. Worth noting is that, compared with its Pleistocene counterpart, the present muskox has horn-cores with reduced bases and separated more widely from one another. This implies a mosaic evolution of the muskox skull, where various parts changed at different rates and in different directions.

Our analyses also showed significant differences between the Pleistocene muskoxen skulls collected from various geographic regions. The muskoxen that inhabited Siberia had wider and longer skulls than their European relatives, especially those from the western and central parts of the continent. The skulls from Southern Siberia also have the horn-cores separated more widely than those in other representatives. The differences between the Northern and Southern Siberian skulls are rather small, which probably reflects the proximity of these regions. Similarly, the skulls from Eastern Europe were also larger than those from other regions of Europe and similar to those from Northern Siberia, which also reflects the contiguity of these regions as well as the presence of similar environmental conditions in the past. In contrast, skulls from Western and especially Central Europe are the smallest in the studied set, both in length and width. Moreover, the specimens from Western Europe had horn-cores placed very close to one another. These results indicate that during the Pleistocene there were geographically distinct populations of *Ovibos*. The populations from regions dominated by more continental conditions (Siberia and Eastern Europe) were generally larger-sized than those from regions with a more humid climate (Western and Central Europe). This east-west cline in the skull dimensions could also be associated with a greater habitat fragmentation, which implied the splitting up of the European populations into subpopulations or metapopulations more or less isolated from one another and distributed wider than their Western European relatives, extended from Eastern Europe to east Asia. The isolation was probably temporary, induced by the expansion of Scandinavian ice sheet or to the development of thick snow cover during the periods of increased precipitation. These barriers probably prevented or at least limited the exchanges between the western and eastern populations of muskox.

The larger size of the extinct Pleistocene *Ovibos*, especially that from the Late Pleistocene, as compared to the older *Praeovibos* and the recent *Ovibos* shows a trend that was reported in other mammals (Smith et al. 1995; Wilson 1996; Guthrie 2003; van der Made et al. 2014; Ratajczak et al. 2016). These changes, and in particular the larger size of the Pleistocene *Ovibos* from the colder and more continental, as compared to other parts of Europe, Siberian and East-European environments appear to conform to Bergmann's rule (Bergmann 1848). The theory postulates that large body-sized organisms living in cold conditions can gain energetic advantage due to smaller heat loss per unit of mass, which results from a decreased body surface area to volume ratio. This rule, however, admits numerous exceptions, because body size is actually the resultant of a complex of factors. In fact, morphology, pelage, physiology, behaviour, type and access to food resources as well as primary plant production

and precipitation in a given habitat are all variables that play an important role in determining the body size of mammals.

Species can become larger or smaller depending on the abundance and availability of resources (Rosenzweig 1968; Guthrie 1984; Geist 1987; Yom-Tov and Geffen 2006; McNab 2010; Clauss et al. 2013). Compared to Holocene settings, the Pleistocene steppe-tundra assured the availability of higher quality forage for the muskox, which was better adapted to such environmental conditions. Therefore, the decrease in size from the Pleistocene to modern times was probably driven by the climatic changes at the Pleistocene/Holocene transition. When the climate became warmer and more humid, open habitats, such as steppe and tundra, were replaced by forests, e.g. taiga (Kuhn and Mooers 2010; Kahlke 2014). The increased humidity resulted in more intense snowfall and excessive snow cover, which dramatically limits an access to food. Muskox was well adapted to the cold and dry conditions of steppe-tundra with shallow or patchy winter snow cover (Vibe 1967; Lent 1978); hence, the climatic and environmental changes that occurred at the Pleistocene/Holocene transition possibly led to the withdrawal of muskox populations from their original habitats as well as to their fragmentation into isolated groups (Markova et al. 2015). Our comparison of the distribution through the time of dated records of *Ovibos* with the curve of $\delta^{18}\text{O}$ cycle is consistent with these conclusions. It revealed a clear influence of climatic changes on muskoxen populations. Overall, the number of dated muskox records increased in colder periods (stadials), when the steppe-tundra likely spread, and decreased in warmer intervals (interstadials), when this ecosystem probably shrank. Frequent alternations of cold and warm periods could have also adverse effects on the distribution of muskoxen.

The distribution area of *Ovibos* was drastically reduced between ca. 15–10 ka BP under the drive of climate warming at the transition between the Late Pleistocene and the Holocene, see also Markova et al. (2015). Consequently, the size of the muskox population decreased and the individuals grew smaller. Genetic analyses, also including ancient DNA samples, showed that populations of muskoxen underwent several gene-associated expansions and contractions over the past 60,000 years, finishing at the end of this period with a population of smaller size than it was earlier (Campos et al. 2010b). These analyses also show that the recent samples come from the ancient muskox lineage and not from a separate one. Therefore, the morphometric changes observed in the muskox skull likely evolved in response to climatic and environmental changes in a residual population that survived the Pleistocene/Holocene transition. Similarly, the differences between the muskoxen from Siberia and Eastern Europe and those from Western and Central Europe may reflect the different local environmental conditions that existed in these regions. The former areas were exposed to more continental and colder conditions as well as offered more widespread steppe-tundra ecosystems than the latter.

This reconstruction is consistent with the study of present muskoxen populations. Interestingly, even small contemporary muskox populations, which are genetically homogenous

and distributed over a much smaller area than in the past, show evident body size differences. Muskoxen living in regions with greater abundance and availability of forage plants as well as lower precipitation show longer rows of lower jaw dentition, larger adult body size, higher ontogenetic and reproduction rates as well as reach sexual maturity earlier (Olesen et al. 1994; Lyberth et al. 2007). Smith et al. (2002) also noticed that maxillary tooth row length increases with latitude from 60°N to 83°N, which was thought to reflect differences in diet associated with the different availability of plants in the studied regions.

The muskox remains from the last 50,000 years show regional and temporal differences in the stable carbon and nitrogen isotope content (Raghavan et al. 2014). Fluctuations in this content followed changes in precipitation and were associated with climatic events such as the Last Glacial Maximum, Bølling-Allerød interstadial, Younger Dryas stadial and the Holocene. Regional differences in the isotopic composition were also noticed in various regions: Greenland, Canada, Northeast Siberia, Taimyr and Urals. This indicates that *Ovibos* inhabited different environments and had different dietary habits. It also suggests that muskox can adapt to various food resources. This supposed relative dietary flexibility of *Ovibos* may explain why this species survived climate-induced the Holocene megafaunal extinctions.

During the Pleistocene, food availability and abundance were subjected to strong seasonal fluctuations. In such conditions, larger organisms are favoured by being able to metabolise fat reservoirs at lower rate per weight unit than smaller forms (Lindstedt and Boyce 1985; Dunbrack and Ramsay 1993). They can also more effectively manage their larger fat reserves to produce energy especially in cold conditions (Ashton et al. 2000). The steppe-tundra environment provided appropriate food resources for muskoxen, but of low nutritional value, more suitable for larger body-sized organisms with larger rumens, wider mouths and lower relative rates of metabolism (Hanley and Hanley 1980; Illius and Gordon 1987; Hofmann 1989; Adamczewski et al. 1994b). Due to the fact that food retention time in the rumen of muskox is longer than in those of other ruminants, *Ovibos* is able to extract more energy from food with a high roughage and low nutrient content (Adamczewski et al. 1994a, 1994b).

Our findings indicate that the cold continental climate and steppe-tundra environment are the optimal conditions for the muskox, and promoted a development of its populations during the Pleistocene. Therefore, similar conditions, e.g. in the northernmost regions of North America and Asia, should be ensured to effectively protect this endangered species.

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Disclosure statement

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