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Mammoths at the margins: new $\delta^{13}C$ and $\delta^{15}N$ isotope data from the southeast of the Western Siberian plain

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ABSTRACT

This study investigates the carbon and nitrogen isotopic composition of woolly mammoth (Mammuthus primigenius) remains from three Late Pleistocene paleontological sites in the southeast of the Western Siberian Plain (SEWS): Shestakovo, Krasnoyarskaya Kurya, and Volchia Griva. This region and time interval (28–22 ka cal BP) remain underrepresented in isotopic records, particularly for $\delta^{13}C$ and $\delta^{15}N$ values. We analysed 29 mammoth dentine samples, alongside dentine from one horse and one deer. Preservation quality was rigorously evaluated using established criteria, including C:N atomic ratios, collagen yields, and elemental carbon and nitrogen content. Our results reveal the densest concentration of the highest mammoth $\delta^{15}N$ values reported for the Northern Hemisphere. We attribute this isotopic enrichment to the unique local environmental conditions at Volchia Griva, including saline soils and intensive trampling, which may have altered nitrogen cycling at the site.

1. Introduction

Stable carbon isotope analysis provides valuable insights into an animal's diet, local vegetation, and climate by reflecting the isotopic values of consumed plants and indicating the proportion of C_3 and C_4 forage in the diet (Arppe et al., 2011; Fox-Dobbs et al., 2008; France et al., 2007; Kuitems et al., 2015; Szpak et al., 2010). The isotopic analysis of nitrogen in collagen is instrumental in understanding trophic relationships and nutritional stress. Bone collagen nitrogen $\delta^{15}N$ values directly correlate with the $\delta^{15}N$ value of dietary protein (Deniro and Epstein, 1981; Schoeninger and DeNiro, 1984). The relationship between the $\delta^{15}N$ values of animals, tissues, and biochemical components, and the $\delta^{15}N$ value of their diet suggests that animal nitrogen isotopic compositions can provide insights into an animal's dietary preferences, particularly when potential food sources exhibit varying $\delta^{15}N$ values (Deniro and Epstein, 1981). In addition, the changes in stable carbon and nitrogen isotopes of plants can reflect the local soil characteristics (e.g. Aslam et al., 1984; van Groenigen and van Kessel, 2002), which in turn can influence the $\delta^{15}N$ values of plants and therefore affect herbivores' $\delta^{15}N$ values.

Woolly mammoth (*Mammuthus primigenius*) was a prominent species of the "mammoth steppe" ecosystem, which spanned the northern continents from Europe to North America (Guthrie, 1968; Stuart, 2005) ca. 110,000–12,000 years ago (Koch and Barnosky, 2006). The mammoth steppe resulted from the adaptation of Arctic tundra and central Asian steppe species to increased aridity, colder temperatures, and climatic fluctuations (Kahlke, 2014). This cold and drought-resistant mosaic landcover dominated the nonglaciated parts of the Northern Hemisphere, supporting diverse megafauna (Hibbert, 1982; Schweger, 1982).

The Last Glacial Maximum (LGM) ca 27 to 23 ka cal BP (Hughes and Gibbard, 2015), was the most recent period when continental ice sheets were at their maximum of extension (Drucker, 2022). LGM is considered a pivotal era in the history of mammoth megafauna because it is a key landmark for the many mammoth steppe species, as during this period, Eurasia and North America experienced a large, accelerated loss of megafauna (Cooper et al., 2015; Stuart, 2015). During 34–24 ka cal BP, environmental conditions in the North Siberian parts of the mammoth steppe were characterised by cooler summers compared to earlier periods, although temperatures were high enough to support the steppe species; this interval has been described as a relatively "cool" tundra-steppe phase (Sher et al., 2005). Overall, LGM in Northern Siberia was characterised by arid conditions (Schirrmeister et al., 2002). The existence of the mammoth steppe was maintained by a strongly

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continental climate, with summers that were either comparably warm or only slightly cooler than present, and winters significantly colder (Sher et al., 2005). Despite the harshness of this period, mammoth fauna survived in the Arctic (Sher et al., 2005).

Insight into the mammoth food sources has been gained from the isotopic compositions of megafaunal skeletal remains (e.g. Ayliffe et al., 1992; Kohn and Cerling, 2002). However, the majority of published carbon and nitrogen isotopic data on woolly mammoths have focused predominantly on the northernmost parts of the mammoth steppe, particularly Beringia, which is currently one of the best-documented areas regarding mammoth stable isotope data (Fig. 1). Szpak et al. (2010) conducted a comprehensive carbon and nitrogen isotope study of 58 mammoth bone samples from Eastern Beringia (Alaska and Yukon) and Western Beringia (Siberia), with only five samples from the LGM. They showed that before the LGM, high-latitude Siberia and the Russian Far East were colder and more arid than ecologically more diverse central Alaska and Yukon. However, during the LGM itself, Alaska and Yukon became colder and more arid than western Beringia. Arppe et al. (2019) examined δ^{13}C, δ^{15}N, and δ^{34}S isotopic compositions of 77 mammoth specimens from the last mammoth refugium (Zimov et al., 2012) at Wrangel Island, and Northern Siberia. Out of 77 samples, approximately 12 % are dated to the LGM. They showed that high-latitude Siberian mammoth populations existed in relatively stable environmental conditions until their extinction, suggesting that events too short-lived to have been recorded in bulk-sampled skeletal remains, e.g. a starvation event or changes in water quality, may have played a role in the eventual demise of the species. Iacumin et al. (2000) reported carbon and nitrogen isotope values of mammoth and other herbivore teeth and bones of various ages from the European plain, south-central Siberia, the Taymyr peninsula, and Yakutia, showing that mammoths in Yakutia likely experienced more significant nutritional limitations and incorporated more woody vegetation into their diet than the European Plain populations. The only comprehensive study from the southeastern Western Siberian Plain is a study by Leshchinskiy and Burkanova (2022), who reported the first δ^{13}C and δ^{15}N values from 10 post-LGM mammoth bones and several fox, wolf, bison and horse bones at Volchia Griva. In addition to isotopic records, they also provided pollen records for the site. Environmental reconstructions at Volchia Griva showed a transition from wetter conditions to open forb-grass steppes around 20-14 ka BP.

The lack of carbon and nitrogen isotope data from the LGM in the southeast of the Western Siberian plain presents a significant gap in our understanding of Late Pleistocene ecological and environmental conditions. To fill this gap, this study aims to provide new carbon and nitrogen isotope records from mammoth remains of three sites in the southeast of the Western Siberian Plain: Shestakovo, Krasnoyarskaya Kurya and Volchia Griva (Fig. 1). Each site has yielded large quantities of mammoth remains: at Shestakovo, more than 4500 skeletal remains from at least 18 individuals have been excavated (Derevianko et al., 2000, 2003). Krasnoyarskaya Kurya site has similarly produced approximately 5600 remains representing at least 35 mammoths (Lazarev and Leshchinskiy, 2011; Leshchinskiy et al., 2014; Seuru et al., 2017). Volchia Griva, discovered in the 1950s, has so far yielded over 7000 remains from at least 80 mammoths (Leshchinskiy et al., 2023; Leshchinskiy and Burkanova, 2022). Shestakovo and Volchia Griva were particularly attractive for large herbivores because both of these sites had salt licks („beast solonetz“) (Derevianko et al., 2000, 2003), where animals suffering from a chronic deficiency of calcium and other essential elements would eat rocks and soil to compensate for the mineral deficiency (Leshchinskiy, 2015, 2017). The large fossil assemblages at these sites are comparable to other Late Glacial mammoth sites in Siberia, such as Lugovskoye and Berelyokh, where approximately 5500 and 7200 woolly mammoth remains have been found, respectively (Leshchinskiy, 2006, 2017). In Europe, similarly large collections of mammoth fossils have been found at Kraków Spadzista Street in Poland, and Milovice I and Předmostí in the Czech Republic, respectively (Brugère and Fontana, 2009; Krzemińska and Wędzicha, 2015; Leshchinskiy, 2012; Wojtal, 2004; Wojtal and Sobczyk, 2005). According to radiocarbon-AMS dates of the subfossil-bearing layers, the mammoth materials date to the LGM: 28-27 ka cal BP for Shestakovo, ca. 25-23 ka cal BP for Krasnoyarskaya Kurya, and ca. 24-22 ka cal BP for Volchia Griva (Boiko et al., 2005; Derevianko et al., 2000; Kuzmin et al., 2023;

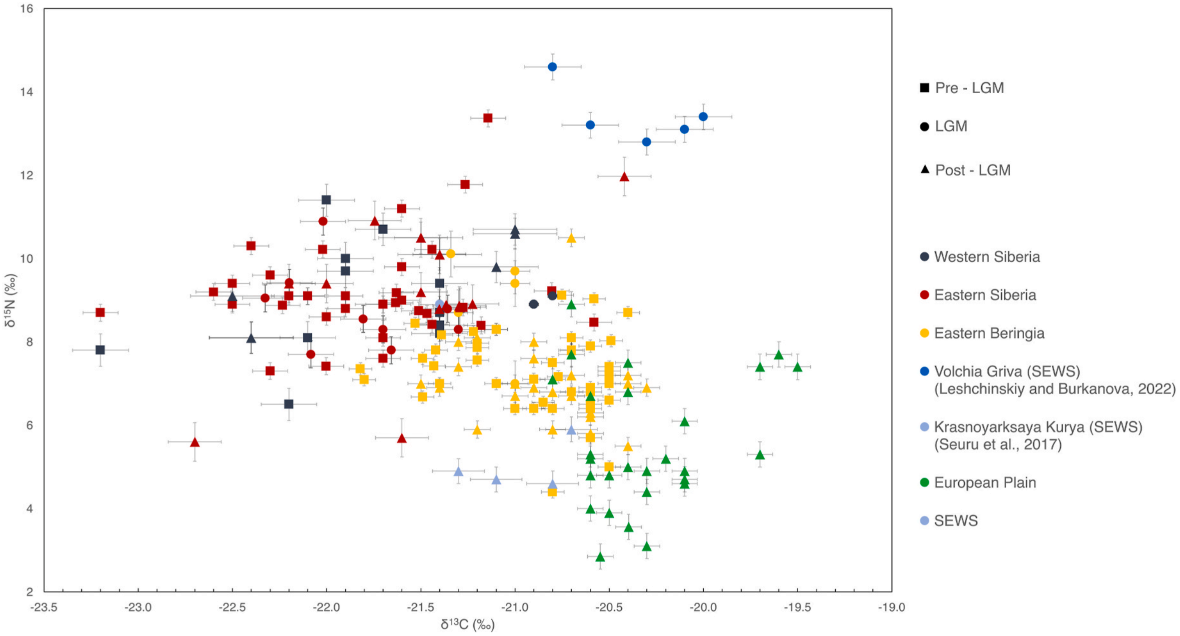

Fig. 1. Comparison between the published δ^{13}C values and δ^{15}N values of mammoths from Western Siberia, Eastern Siberia, Eastern Beringia, SEWS and European Plain for three time periods: pre-LGM (before 27 ka cal BP), LGM (27–23 ka cal BP), and post-LGM (after 23 ka cal BP until 11. 7 ka cal BP. The comparative datasets and radiocarbon dates were taken from the following publications: Szpak et al., (2010), Iacumin et al., (2000), Arppe et al. (2019), Iacumin et al., (2010), Barbieri et al., (2008), Debruyne et al., (2008), Grigoriev et al., (2017), Mann et al., (2013), Bocherens et al., (1994), Metcalfe et al. (2016), Seuru et al., (2017), Drucker et al., (2018), Drucker et al., (2014), Orlova et al., (2004).

Maschenko, 2010; Seuru et al., 2017).

In this paper, we report on the carbon and nitrogen isotope analyses of 29 megaherbivore tooth specimens, mainly representing the woolly mammoth from Shestakovo, Krasnoyarskaya Kurya and Volchia Griva l to provide unique insight into the ecology of the mammoth fauna in an underrepresented sector of the mammoth steppe, the southeast of Western Siberian Plain, significantly contributing to the limited paleoecological records in this region during the LGM. Additionally, we discuss the preservation status of the remains, and its implications for further studies of the mammoth fauna skeletal materials discovered at these sites.

2. Materials & methods

2.1. Material collection

The samples listed in Table 1 were selected from the collection of Tomsk State University. Altogether, 29 specimens belonging to woolly mammoth (*Mammuthus primigenius*, n = 27), with one horse and one deer molar were sampled using a Dremel 300 drill. The samples included: four samples from Shestakovo, eight samples from Krasnoyraskaya Kurya and 17 samples from Volchia Griva (Supplementary data, T1). Based on a visual and tactile inspection of the specimens, as well as the hardness or softness of the material, we assigned the samples to one of three categories (very good, good, or acceptable condition) (Table 1). The samples represent the full spectrum of different condition categories that reflect the typical condition of finds in these sites. Samples were photographed and placed in zip packages. Photos of the samples and their field numbers are given in the Supplementary data. For this study, we analysed one horse molar dentine sample, one deer molar dentine sample, 20 mammoth molar dentine samples and 7 mammoth molar dentine samples.

2.2. Evaluation of preservation

We used the elemental C:N ratio of the extracted collagen as the main preservation assessment criteria, with additional consideration of collagen yields and the total carbon and nitrogen content (weight-% C, weight-% N). In general C:N ratios falling within the range of 2.9–3.6 were considered indicative of well-preserved collagen (Ambrose, 1990; DeNiro, 1985; DeNiro and Weiner, 1988; Sealy et al., 2014; van Klinken, 1999). We considered a stricter C:N range of 3.1–3.3 suggested by Guiry and Szpak (2021). We used the following criteria regarding the elemental contents: C > 13 % and N > 4.8 % (Ambrose, 1990). Generally, if a sample did not meet the target set for one or more of the above criteria, we removed it from the main dataset. However, each sample was considered separately, and preservation was assessed on a case-by-case basis. Collagen yields have been calculated as the weight of extracted collagen divided by the weight of the sample and multiplied by 100 and presented as % (Table 1). Usually, well-preserved bone and dentine have collagen yields of ~20 % (van Klinken, 1999), and generally, contents larger than 0.5–2 % are considered indicative of well-enough preserved collagen for ancient bones and teeth (Ambrose, 1990; DeNiro and Weiner, 1988; Dobberstein et al., 2009; van Klinken, 1999). We did not use collagen yields as definitive criteria for rejection because collagen loss may not necessarily change the sample's isotopic composition. Consequently, the resulting C:N ratios and elemental concentrations can still meet the acceptable criteria (e.g., Dobberstein et al., 2009). Therefore, we accepted samples with collagen yields lower than 0.5 % if their C:N values, C% and N % were within the accepted range and absolute delta values were similar to the rest of the group (e.g. SH 53, SH 56, VG 32, VG 33) (Table 1). Nevertheless, we observed collagen yields in our sample set attentively and, in some cases, removed samples from the main dataset based on low collagen yields. We did not use visual preservation as a criterion for sample rejection because visually unappealing samples may still yield reliable isotopic results.

2.3. Carbon and nitrogen isotopic analysis

For isotopic analyses of carbon (δ^{13}C) and nitrogen (δ^{15}N) in collagen a piece of material weighing 0.5 g was cut off. Collagen extraction for carbon and nitrogen isotope analysis was conducted using the method described in Cersoy et al. (2017) (Protocol F): coarse bone powder (0.3–0.7 mm) was first treated with 1M HCl for 20 min, while being stirred continuously. The resulting solution was filtered through MF-Millipore™ membranes (mixed cellulose ester, 5.0-μm pore size,

Table 1

Carbon and nitrogen isotope values, C and N weight-% concentrations, atomic C:N ratios and collagen yields of the accepted samples. M in the table stands for Mammoth, H for Horse, SH for Shestakovo, KK for Krasnoyrskaya Kurya, VG for Volchia Griva. Bold and italics mark the values that are lower than the recommended range. Asterisk marks abnormally high yield values considered to result from weighing errors.

Sample ID	Visual inspection	Skeletal element type	δ^{15}N (‰, AIR) ± SD	δ^{13}C (‰, V-PDB)	N%	C%	C:N	Collagen yield %
SH 53	Acceptable	H molar	+3.0 ± 0.02	−20.3	10.4	32.0	3.6	*0.4*
SH 55	Good	M molar	+6.1 ± 0.04	−21.0 ± 0.01	12.5	37.0	3.4	0.6
SH 56	Good	M molar	+8.8 ± 0.09	−20.5 ± 0.06	13.0	37.7	3.4	*0.4*
		Min (mammoths)	*+6.1*	*−21.0*				
		Max (mammoths)	*+8.8*	*−20.5*				
		Average (mammoths)	*+7.5*	*−20.7*				
KK 57	Good	M molar	+8.3 ± 0.01	−20.1 ± 0.11	10.7	32.8	3.6	0.6
KK 58	Good	M molar	+7.8 ± 0.02	−21.4 ± 0.12	10.9	32.5	3.5	0.7
KK 59	Good	M molar	+8.6 ± 0.17	−21.5 ± 0.06	12.5	36.5	3.4	0.7
KK 61	Acceptable	M tusk	+7.1 ± 0.02	−21.9 ± 0.0	9.3	29.0	3.6	0.6
KK 64	Very good	M molar	+9.4 ± 0.12	−21.1 ± 0.01	13.8	39.6	3.3	1.4
KK 65	Very good	M tusk	+8.1 ± 0.08	−21.6 ± 0.03	11.7	32.9	3.3	0.5
		Min	*+7.1*	*−21.9*				
		Max	*+9.4*	*−20.1*				
		Average	*+8.2*	*−21.3*				
VG 16	Acceptable	M molar	+12.6 ± 0.06	−20.8 ± 0.04	14.2	40.5	3.3	1.0
VG 26	Very good	M molar	+14.9 ± 0.03	−19.0 ± 0.23	10.1	30.6	3.5	40.1*
VG 27	Very good	M molar	+14.3 ± 0.09	−20.1 ± 0.02	10.8	32.2	3.5	53.3*
VG 31	Acceptable	M molar	+11.3 ± 0.02	−20.5 ± 0.0	11.8	34.5	3.4	0.5
VG 32	Acceptable	M molar	+11.8 ± 0.07	−20.6 ± 0.10	10.5	31.9	3.5	*0.2*
VG 33	Acceptable	M molar	+13.3	−20.7	11.6	34.3	3.4	*0.2*
VG 34	Acceptable	M molar	+14.0 ± 0.13	−20.8 ± 0.04	13.5	38.6	3.3	0.7
		Min	*+11.3*	*−20.9*				
		Max	*+14.9*	*−19.0*				
		Average	*+13.2*	*−20.3*				

Fisher Scientific, France) and rinsed with Milli-Q water. The acid-insoluble residues were then treated with 0.1M NaOH for 20 h, followed by filtration through MF-Millipore™ membranes and rinsing with Milli-Q water. Subsequently, the alkali-insoluble residues were immersed in HCl (pH 2), and extraction was carried out at 100 °C for 17 h. The final extract was filtered once more using MF-Millipore™ membranes before collection. Approximately, 0.5 mg of extracted collagen was placed in tin foil caps, packed and analysed on a Thermo-Finnigan Delta V Plus isotope ratio mass spectrometer (IRMS) paired with an elemental analyser (Thermo Flash 1112) at Tartu University. Altogether, 29 samples were analysed in duplicates. The mean value and SD of the two replicates for each sample are presented in Table 1. Detailed information on the values for each duplicate is included in the Supplementary data, T3.

Differences in the relative content of stable isotopes of a chemical element in a substance were measured in comparison with unified international standards and denoted by the conventional unit δ (delta), which is expressed as a fraction of atoms of the heavy isotope from all atoms of the given element and converted to permille (‰) of deviation from the international standard (DeNiro, 1985). The $\delta^{13}C$ and $\delta^{15}N$ values are reported against the "Vienna" equivalent of the Belemnite PeeDee Formation (VPDB) and atmospheric nitrogen (AIR) standards, respectively. We used IAEA N-1 ($\delta^{15}N = +0.43$ ‰) (Boehlke and Coplen, 1995), IAEA N-2 ($\delta^{15}N = +20.41$ ‰) (Boehlke and Coplen, 1995) and USGS25 ($\delta^{15}N$ = -30.41 ‰) (Brand et al., 2014) reference values to normalise data to the AIR scale and IAEA-CH-3 ($\delta^{13}C$ = -24.72 ‰) (Coplen et al., 2006) and IAEA-CH-6 ($\delta^{13}C = -10.449$ ‰) (Coplen et al., 2006) to normalise data to the VPDB scale. We used urea ($\delta^{15}N = -0.32$ ‰; $\delta^{13}C$ = -41.30 ‰; n = 10) (Iva Analysentechnik, 2025) working standard to monitor quality. The internal precision of measurement for N was ≤0.2 ‰ and for C it was ≤0.1 ‰.

2.4. Data analysis

Differences in isotopic values between Shestakovo, Krasnoyarskaya Kurya and Volchia Griva were tested using RStudio (version R 3.6.0). The means for the three distinct sites were calculated as averages.

Throughout the text, all the mammoth site-related radiocarbon dates discussed in calendar years (cal BP) were calibrated using OxCal v.4,4.4 (Bronk Ramsey, 2009) and calibration curve InCal20 (Reimer et al., 2020).

3. Results

3.1. Sample preservation

Out of 29 analysed samples, 13 samples were removed from the dataset due to quality concerns. The full dataset with rejection reasons is available in the Supplementary data, T1. Sixteen samples remain in the main dataset and are considered to preserve the original isotopic values (Table 1).

The amount of extracted collagen was small for the whole sample set, with a highly variable yield percentage ranging between 0.03 % and 53 %. Not considering two samples with anomalously high yields at 40.1 % (VG 26) and 53.3 % (VG27), the average for the entire dataset was 0.5 %. We attribute these two high collagen yield values to an error during the weighing process. Despite the generally low yields, there was enough collagenous extract to get a reliable IRMS measurement in all cases, however, for VG 26 and VG 27 we were unable to remeasure the samples because there was no material left.

Some of the rejected samples exhibited very low collagen yields, for example, KK 60 (0.04 %) and VG 22 (0.03 %) (Supplementary data, T1). Even though the accepted samples had weight % of C > 13 % and N > 4.8 % (Ambrose, 1990), it has been shown that fresh or well-preserved collagen N contents should range from 11 % to 17 % (Ambrose, 1990; Sealy et al., 2014; van Klinken, 1999). Five of the 16 accepted samples have N contents below 11 %. Regarding carbon content, van Klinken (1999) observed a mean C% of 34.8 ± 8.8 in a substantial collection of acceptable collagens, while higher values ranging from 41 % to 47 % were suggested by Ambrose (1990) and Sealy et al. (2014). In our dataset, all C% values fall within the criteria suggested by van Klinken (1999) but do not reach the higher values proposed by Ambrose (1990) and Sealy et al. (2014). C and N weight-% concentrations in some of the rejected samples fell out of the ranges established by Ambrose (1990), Sealy et al. (2014) and van Klinken (1999) significantly. For instance, VG 18 has a C concentration of 9.94 % and N of 0.73 % (Supplementary data, T1).

The C:N range of samples was wide: 3.3–24.4. Amongst the accepted samples, the C:N ratios were all within a narrow span of the higher half of the total acceptable range of 2.9–3.6 (Ambrose, 1990), ranging from 3.3 to 3.6. Amongst the 13 rejected samples, only one sample, SH 54, had an acceptable C:N ratio of 3.6 but was removed from the main dataset due to an extremely low collagen yield (0.07 %), clearly lowered C% (16.6 %) and N% (5.4 %) and a $\delta^{13}C$ value (−18.8 ‰) that was noticeably higher than the other samples from the site. All the remaining 12 rejected samples had a C:N ratio higher than 3.6 without exception, varying from 3.6 to 24.4, indicating the presence of carbon contamination or nitrogen loss. The highest C:N ratio were shown by KK 60 (24.4) and VG 18 (15.9) (Supplementary data, T1), which, in addition, had lower $\delta^{13}C$ values (−25.6 ‰ and −23.6 ‰, respectively) and $\delta^{15}N$ values (+5.4 ‰ and +5.6 ‰, respectively) than the rest of the samples.

3.2. $\delta^{13}C$ and $\delta^{15}N$ values

While the range of $\delta^{13}C$ and $\delta^{15}N$ values for the accepted samples was −21.9 ‰ to −19.0 ‰ and from +6.1 to +14.9 ‰, respectively (Table 1), the overall range of $\delta^{13}C$ and $\delta^{15}N$ values for all analysed samples was from −25.6 ‰ to −14.5 ‰ and from +3 to +15 ‰, respectively (Supplementary data, T1). For $\delta^{13}C$, the very wide range of values is a reflection of alteration/contamination effects in poorly preserved samples, while the range for $\delta^{15}N$ is associated with taxon-specific ecological niche. Table 1 presents the $\delta^{13}C$ and $\delta^{15}N$ values of the accepted samples, their site-specific ranges and means and the range and mean for the entire accepted dataset. Given the low accepted sample number for Shestakovo and their statistically similar isotopic values in comparison to Krasnoyarskaya Kurya, as well as the relatively close proximity of these two sample sites, we treat the values from Shestakovo and Krasnoyarskaya Kurya as a single dataset referred to as SH + KK further in the text (averages $\delta^{13}C$: −21.1 ‰ ± 0.6 and $\delta^{15}N$: 8.0 ‰ ± 1.0) for further comparisons with Volchia Griva (averages $\delta^{13}C$: −20.3 ‰ ± 0.5 and $\delta^{15}N$: 13.2 ‰ ± 1.0) and other published records. The average values and standard deviations for the SH + KK dataset do not include the values of SH 53 because it is a horse molar. Originally, we included the horse and deer molars to be consistent with the $\delta^{18}O$ study by Krivokorin et al. (2024), as the set of samples used in that publication is identical to the one we are using in this study. However, in the further text, the results of horse and deer dentine samples are not discussed because the deer sample was excluded from the main dataset due to low collagen yield (see Supplementary data, T1), and the horse from Shestakovo being a singular sample not derived from mammoth in the whole dataset and being very similar to the published isotopic values of horses (e.g. Drucker et al., 2015) would not have contributed much valuable insight into the Discussion.

4. Discussion

4.1. Sample preservation

The generally low yields obtained throughout the studied material imply collagen loss, a common characteristic of subfossil finds. Low collagen yields serve as a sign of general degradation (van Klinken, 1999), when the peptide bonds between amino acids (collagen á-chains) gradually break (Collins et al., 1995). Low yields observed in our samples suggest that the samples from all three sites have been subject to degradation and that the preservation status is less than ideal. For example, microbial heterotrophy implied as potential compromiser of the oxygen isotope integrity of the mineral part of the samples (Krivokorin et al., 2024), could have been a factor contributing to collagen deterioration. Additionally, Volchia Griva's formation conditions, which included periodic shifts between wet and dry phases (Leshchinskiy, 2018) may have created a conducive environment for the physical deterioration of the samples. Notably, low collagen yields do not immediately suggest interactions with exogenous molecules, and degradation itself does not necessarily compromise isotopic integrity (van Klinken, 1999).

According to Guiry and Szpak (2021), samples that have C:N values between 3.3 and 3.6 are all likely to carry minor level carbon contamination: according to their models, the strict induced error is within 0.5–1 ‰ from the measured value. We explored the option of applying stricter collagen quality control criteria, as suggested by Guiry and Szpak (2021). Applying the suggested stricter range of 3.1–3.3 to our dataset would reduce the number of acceptable samples from 13 to four: KK 64, KK 65, VG 16 and VG 34 ("the strict C:N dataset"). The averages in the "strict C:N″ dataset for Krasnoyarskaya Kurya (δ^{15}N +8.8.‰; δ^{13}C −21.3 ‰) and Volchia Griva (δ^{15}N +13.3 ‰; δ^{13}C −20.8 ‰) are similar to the averages for the accepted, wider C:N based Krasnoyarskaya Kurya (δ^{15}N +8.2 ‰; δ^{13}C −21.3 ‰) and Volchia Griva datasets (δ^{15}N +13.2 ‰; δ^{13}C −20.3 ‰). While the suggested strict C:N range can improve data quality (Guiry and Szpak, 2021), applying a narrower C:N range to our dataset does not influence the interpretation of our isotopic values, since the average isotopic values in the "strict C:N″ dataset do not differ from those in the main dataset. Additionally, such a small dataset would not be suitable for meaningful interpretations. Therefore, we continue relying on the C:N criteria outlined in Ambrose (1990); DeNiro (1985); DeNiro and Weiner (1988); Sealy et al. (2014); van Klinken (1999) and use the isotopic values presented in Table 1. For the purposes of this paper, i.e. a broad paleoecological interpretation and comparison to other regions, the added uncertainty level implied by the C:N ratio range 3.3–3.6 in our dataset is acceptable and taken into consideration when comparing datasets.

4.1.1. *Mineral fraction vs organic fraction*

In a study focusing on the δ^{18}O values of the bioapatite phosphate of the same material studied here (Krivokorin et al., 2024), found the mineral fraction of the majority of samples from Shestakovo, Krasnoyarskaya Kurya and Volchia Griva intact. Nevertheless, there were both tusk and even enamel samples that showed signs of post-depositional isotopic and/or chemical (cf. FTIR data) alteration. Many of the tusk specimens from Krasnoyarskaya Kurya and Volchia Griva displayed elevated Infrared Splitting Factor (IRSF) values and associated lower C/P ratios interpreted to reflect carbonate loss and accompanying structural changes (cf. France et al., 2020). The cause of the loss could not be established, as it could be attributed to site-specific conditions, sample pretreatment methods, or a combination of both factors (Krivokorin et al., 2024).

We compared the results of the preservation assessment of the mineral fraction from the article by Krivokorin et al. (2024) and the results of our preservation assessment of organic fraction in this study to see whether we could find a link between the alteration of the mineral and the organic parts of our samples (Supplementary data, T1). Regarding the visual preservation, some of the samples from Table 1 marked as visually "acceptable", i.e. the poorest appearance compared to other samples, yielded reliable oxygen isotope results (Krivokorin et al., 2024). However, it is notable that out of the 13 rejected samples, nine had "acceptable" visually evaluated preservation quality (Supplementary data, T1). In contrast, out of 16 accepted samples, only seven had "acceptable" preservation quality, which implies that the samples rejected based on their collagen quality properties often had worse visual preservation. The remaining accepted samples had either "good" or "very good" preservation quality. Thus, visual appearance is a more relevant clue to the preservation of the organic than the mineral, especially the phosphate component of bioapatite at these sites.

Collagen quality control parameters, including C:N ratios, nitrogen concentration, and collagen yield, did not show any clear relationship with elevated IRSF values (Supplementary data, T1), which is here used as a parameter of the general preservation status of the mineral component. Samples with elevated IRSF values from Shestakovo and Krasnoyarskaya Kurya had acceptable collagen yields, C% and N% values and C:N ratios (Supplementary data, T1).

The samples from Volchia Griva showed more pronounced signs of post-depositional alteration compared to Shestakovo and Krasnoyarskaya Kurya and more congruence between mineral and organic part preservation: regarding the mineral component, eight out of 19 VG samples analysed for phosphate δ^{18}O values showed elevated IRSF values (Supplementary data, T1). Seven out of these eight samples also demonstrated elevated C:N ratios in the organic part. Overall, ten samples from VG were excluded due to elevated C:N ratios and six out of these yielded N concentration values below 3.5 % and C:N ratios >3.6 (Supplementary data, T1), which can be considered an indicator of non-collagenous molecules like lipids and humic acids (Guiry and Szpak, 2021). Overall, it is challenging to make firm conclusions about whether there is a link between the post-depositional alteration of the organic and the mineral fraction of the samples from Shestakovo, Krasnoyarskaya Kurya and Volchia Griva. However, it is notable that three samples from Volchia Griva with elevated C:N ratios are also associated with carbonate-phosphate disequilibrium, which was used to assess the isotopic alteration of skeletal bioapatite (Supplementary data, T1). The fact that the samples with carbonate-phosphate δ^{18}O disequilibrium come exclusively from Volchia Griva further supports the evidence that the mineral and the organic part of samples from Volchia Griva have suffered from post-depositional alteration to a bigger extent than the samples from Shestakovo and Krasnoyarskaya Kurya.

4.2. *Carbon and nitrogen isotope composition*

There is relatively little comparative data for Eurasian mammoths from the LGM time period matching the datings of the sites analysed in this study. Altogether, 13 specimens directly dated to ca. 28-22 ka ago with published δ^{13}C and δ^{15}N isotope values are available from Northern Siberia, specifically Wrangel Island, Bykovsky peninsula, Bolchoy Lyakhovsky island, Lena Delta River and Taymyr Peninsula (Arppe et al., 2019; Iacumin et al., 2010; Szpak et al., 2010) (Fig. 2). However, their mean isotopic values (−21.6 ± 0.5 ‰ for δ^{13}C and 8.7 ± 0.9 ‰ for δ^{15}N) are statistically indistinguishable from those of a much more extensive compilation of North Siberian mammoth data spanning 60-12 ka (Arppe et al., 2019) with δ^{13}C (−21.7 ± 0.6 ‰; n = 82) and δ^{15}N (9.0 ± 1.8 ‰; n = 82), and therefore, we will use the wider dataset as a point of comparison, and refer to it as the Northern Siberian dataset further in the text. A comparison between the δ^{13}C and the δ^{15}N isotopic values of SH + KK, Volchia Griva and Northern Siberian datasets is presented in Fig. 3 (see Supplementary data, T2 for full comparative data), illustrating the elevated isotope values at Volchia Griva clearly standing out from both SH + KK and Northern Siberian mammoth data.

Studies by (van der Merwe, 1982; Ambrose and DeNiro, 1986) show that animals whose diet completely consists of C_3 plants have collagen δ^{13}C values approximately around −21.5 ‰, and the average δ^{13}C values of SH + KK dataset (−21.1 ‰) and the Northern Siberian datasets (−21.7 ‰) (Fig. 3) suggest that the diet of mammoths in both regions consisted predominantly of C_3 plants. However, the SH + KK and Northern Siberian datasets are statistically different for δ^{13}C ($p=0.02696$) and δ^{15}N ($p = 0.01054$). The average δ^{13}C value from the SH + KK dataset is higher than the Northern Siberian dataset by 0.6 ‰, whereas the δ^{15}N average value from the SH + KK dataset is lower than that of the comparative dataset by 1.3 ‰ (see Fig. 3 and Table 1).

Fig. 2. Map showing the general location of Shestakovo, Krasnoyarskaya Kurya and Volchia Griva sites and other mammoth sites discussed in the text. Basemap: Esri, Maxar, Earthstar Geographics, and the GIS User Community.

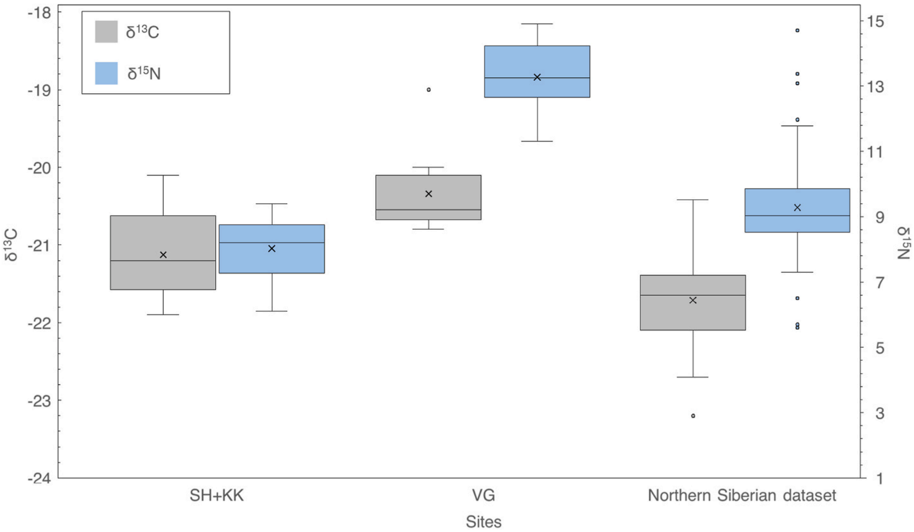

Fig. 3. Comparison between the δ^{13}C and δ^{15}N values between the SH + KK, Volchia Griva and the Northern Siberian Dataset (Arppe et al., 2019; Iacumin et al., 2010; Szpak et al., 2010).

Firstly, the potential carbon contamination in SH + KK samples with C/N ratios >3.3 may introduce a larger error to isotopic analysis results, and thus the difference in δ^{13}C values should be considered tentative, as discussed in the “Sample preservation” section above. In contrast, the difference in δ^{15}N values is unequivocal. Despite complicating factors like season of precipitation, and edaphic conditions such as water storing capacity and rooting depth (e.g. Ehleringer, 2005; Schenk and Jackson, 2002; Farquhar et al., 1989) influencing plant isotopic values on a local scale, on a global scale, temperature, aridity and altitude are the main factors that influence δ^{13}C and δ^{15}N of plants (e.g., Amundson et al., 2003; Bocherens, 2015; Craine et al., 2009; Kohn, 2010; Körner et al., 1991; Männel et al., 2007; Sah and Brumme, 2003; Zech et al., 2011). The potentially lower δ^{13}C values in the Northern Siberian datasets compared to SH + KK can be explained by large-scale latitudinal trends in temperature and precipitation, which influence isotopic baselines at the plant level leading to lower plant δ^{13}C values at higher latitudes (Kohn, 2010; Stuiver and Braziunas, 1987; Van Klinken et al., 1994). The difference between the δ^{13}C values of the mammoths at SH + KK and the Northern Siberian dataset could also be related to differences in the makeup of their diets, with differences in the types and proportions of various plants consumed by these populations from two distant regions. For example, the mammoths in Northern Siberia could supplement their diet with bark, twigs and mosses (Gorlova, 1982; Olivier, 1982; Vereshchagin and Baryshnikov, 1982), suggested by Iacumin et al. (2000) to lower the $\delta^{13}C$ of the mammoths' tissues. During harsh winters, the Northern Siberian mammoths may have relied on fat reserves to survive periods of food scarcity (Kubiak, 1982; Olivier, 1982). Since fat has lower $\delta^{13}C$ values relative to other nutrients, Bocherens (2003) suggested this metabolic strategy could also contribute to the lowered $\delta^{13}C$ values.

The relatively higher $\delta^{13}C$ values and lower $\delta^{15}N$ values for SH + KK site mammoths compared to Northern Siberia mirror the pattern reported by Szpak et al. (2010) for Late Pleistocene woolly mammoths of Eastern Beringia (Alaska and Yukon) in comparison to Western Beringia (i.e. Northern Siberia). The pattern of lower $\delta^{15}N$ combined with a higher $\delta^{13}C$ appears to be in conflict with plant $\delta^{13}C$ and $\delta^{15}N$ values showing parallel correlations to environmental gradients like temperature and moisture: higher $\delta^{13}C$ and $\delta^{15}N$ values are often associated with more arid climatic conditions and higher temperatures (Amundson et al., 2003; Craine et al., 2009; Gröcke et al., 1997; Heaton, 1987; Kohn, 2010; Sealy et al., 1987; Wooller et al., 2021). Szpak et al. (2010) proposed more arid conditions as the main driver of higher $\delta^{15}N$ values in Northern Siberian mammoths and suggested that variations in high arctic $\delta^{13}C$ may be insensitive to moisture differences and rather reflect regional differences in mean annual temperature, i.e. warmer conditions in Eastern Beringia. Indeed, according to recent climate simulations (Extended data in Wang et al., 2021), Eastern Beringia was more wet and had higher mean annual temperature than Western Beringia. This same line of reasoning could also explain the differences between the $\delta^{15}N$ values of SH + KK and Northern Siberian datasets. We propose that environmental threshold points may partially explain the contrasting $\delta^{13}C/\delta^{15}N$ responses. For nitrogen isotopes, Craine et al. (2009) showed that plant $\delta^{15}N$ values stop responding to changing mean annual temperatures (MAT) in a linear way below $-0.5°C$. Considering that mean annual temperatures during LGM in the Northern Siberia were far below zero (Vandenberghe et al., 2014; Wang et al., 2021), it is highly likely that plant $\delta^{15}N$ values were rather insensitive to variations in temperature. However, in the case of carbon isotopes, while the global C_3 plant data analysed by Kohn (2010) showed that the correlation between plant $\delta^{13}C$ and mean annual precipitation (MAP) flattens out in wet environments, the mammoth steppe was generally characterized by aridity with MAPs well below 500 mm/a (Wang et al., 2021) and thus, a hypothesis of 'too wet to register differences in MAP' doesn't seem plausible.

Alternative or complementary factors accounting for the more elevated $\delta^{15}N$ values in the Northern Siberian dataset point to involvement of metabolic strategies for dealing with aridity and/or a diet composed primarily of nutrient-poor, protein-deficient herbaceous and graminoid vegetation, as discussed in Szpak et al. (2010). Graminoid-dominated diet of the Northern Siberia mammoths is also supported by Wang et al. (2021), who showed that vegetation during LGM in Northern Siberia had a larger proportion of graminoids compared to Eastern Beringia. It has been suggested that in arid environments, where plants typically contain lower protein and nitrogen levels, herbivore $\delta^{15}N$ may be elevated due to water saving mechanisms increasing the urea concentration of urine (Ambrose and DeNiro, 1986), or microbial recycling of nitrogen in the digestive tract (Sealy et al., 1987). Overall, despite the conflicting evidence on the influence of animal metabolic processing on tissue $\delta^{15}N$ (e.g. Sponheimer et al., 2003; Ambrose, 2000; Hartman, 2011), it is plausible that the physiology and metabolism of the Northern Siberian mammoths would have additionally influenced bodily isotope levels during the LGM, a period generally thought to represent a very arid and cold time period, which could have resulted in their higher $\delta^{15}N$ values. In summary, we propose that, similarly to what has been reported for West Beringian mammoths (Szpak et al., 2010), regional vegetation, climate, and physiological adaptations all likely contributed to the isotopic differences between mammoth populations in Southeast Western Siberia and Northern Siberia.

4.2.1. *Unusual isotopic values from Volchia Griva*

Leshchinskiy and Burkanova (2022) published $\delta^{13}C$ and $\delta^{15}N$ values for five mammoth bone samples from Volchia Griva (age range – 22.2–23.7 ka cal BP), which are very similar to our results and are here combined with our samples from that site to yield an extended Volchia Griva dataset with mean $\delta^{13}C$ and $\delta^{15}N$ values at -20.3 ‰±0.5 and + 13.3 ‰±0.1, respectively. Mammoths had a low-protein diet and generally tended to have higher $\delta^{15}N$ values than other herbivores like horses or deer (Bocherens et al., 1996), but the mammoths from Volchia Griva occupy an outstanding position among the so far published isotopic records of mammoth sites globally due to their abnormally high $\delta^{15}N$ values. The average $\delta^{15}N$ value from Volchia Griva is 5.3 ‰ higher than the average SH + KK values and 4.3 ‰ higher than the average of the North Siberian dataset ($p < 0.05$). To the authors' knowledge, few woolly mammoth samples to date have yielded $\delta^{15}N$ values in such a high range of 11–15 ‰. For example, in the compilation of East Eurasian and Northwest North American isotope data on mammoths (Arppe et al., 2019) less than 5 % of the >350 listed samples showed $\delta^{15}N$ values ≥ 12 ‰ common for Volchia Griva mammoths, most of them from Northern Siberia (Bocherens et al., 1996; Iacumin et al., 2000; Kirillova et al., 2023; Szpak et al., 2010) and a few from Northern Yukon (Metcalfe et al., 2016). Overall, Volchia Griva potentially has the densest concentration of the highest $\delta^{15}N$ values reported for the Northern Hemisphere.

The fact that Volchia Griva has significantly higher $\delta^{13}C$ and $\delta^{15}N$ values than the SH + KK dataset is unexpected considering the relatively short distance between Shestakovo, Krasnoyarskaya Kurya and Volchia Griva. We propose that potential explanations for such differences in the isotope levels could lie in local characteristics of these sites and potentially also the likely temporal differences between the sites. We consider the elevated isotopic baselines of the Volchia Griva site as a likely relevant cause of the observed elevated $\delta^{15}N$ values, because, in addition to mammoths, for the same period of 22.2–23.7 ka cal BP, Leshchinskiy and Burkanova (2022) published elevated $\delta^{15}N$ values for a single equid (+12.3 ‰) as well as elevated $\delta^{15}N$ values for carnivores such as fox (16.2 ‰) and wolf (17.1 ‰). The other factors discussed further in the text are offered as mechanisms that can further influence the isotopic values.

Mineral salts were the primary factor attracting large herbivores to Volchia Griva (Leshchinskiy, 2018) and Shestakovo (Derevianko et al., 2000), and it also seems conceivable that there might be a connection between the elevated salinity of local soils in these areas and the nitrogen isotopic composition of local plants. High soil pH and salinity decrease NO_3^- uptake by the plants' roots (Aslam et al., 1984) and can elevate the $\delta^{15}N$ values of plants (van Groenigen and van Kessel, 2002). Therefore, it is possible that the salinisation of local soils at Volchia Griva would result in high $\delta^{15}N$ values in local plants and, by extension, in local mammoths' tissues. However, it is also worth noting that while both Shestakovo and Volchia Griva were "beast solonetz", we did not observe a similar pattern of elevated $\delta^{15}N$ values in Shestakovo samples, which may be due to the low number ($n = 2$) of analysed samples or other site-specific differences in soil properties, for which we do not currently hold any detailed information. This is why the high nitrogen values in samples from Volchia Griva are particularly important: there are currently no studies exploring whether such elevated nitrogen values are a general feature of salt licks. This presents a promising direction for future research.

Elevated soil salinity can also influence plant $\delta^{13}C$ values: in a manner comparable to effects of stress induced by aridity, plants tend to close their stomata due to salt stress, which reduces stomatal conductance and the within-cell partial $^{12}CO_2$ pressure. As a result, the salinity-stressed plant assimilates a larger proportion of $^{13}CO_2$, leading to less negative $\delta^{13}C$ values in the newly formed plant tissues (van Groenigen and van Kessel, 2002). In addition, although the $\delta^{13}C$ values from

Volchia Griva suggest a diet primarily composed of C_3 plants, we do not entirely rule out the inclusion of C_4 vegetation. Volchia Griva lies within the present-day native geographical distribution of certain C_4 taxa, such as *Atriplex sibirica and Atriplex tatarica* (Rakhmankulova et al., 2019; Sukhorukov et al., 2022) and these species are not only well adapted to arid climates but also well adapted to saline and ruderal environments (Rakhmankulova et al., 2019; Sukhorukov et al., 2022). The presence of such taxa at Volchia Griva is supported by the pollen analysis from Volchia Griva (Leshchinskiy and Burkanova, 2022) and suggests a minor C_4 component in mammoth diets at Volchia Griva.

As an additional local factor, large animal herds frequenting sites of mineral oases produce a lot of dung. Szpak (2014) showed that using animal dung as a fertiliser can increase plant δ^{15}N values by +2 - +8 ‰ (if cattle manure is used) and even by +10 to +40 ‰ (if pig – an omnivore - manure is used). Although reaching such an effect of elevated nitrogen values generally requires a substantial amount of dung (Bogaard et al., 2013), the presence of mammoth and other large animal populations frequenting Volchia Griva over several millennia could have led to the elevation of local soil δ^{15}N values contributing to the observed values. It is also possible that the mammoths at Volchia Griva practised coprophagy, which would, in turn, result in elevated δ^{15}N values in their tissues (Clementz et al., 2009; Kuitems et al., 2015; van Geel et al., 2008, 2011).

The elevated δ^{13}C and δ^{15}N values at Volchia Griva, compared to both the SH + KK dataset and the Northern Siberian dataset, may also suggest that the mammoths found at Volchia Griva could have subsisted in more arid conditions than their counterparts in Northern Siberia or at Shestakovo and Krasnoyarskaya Kurya, yet a difference in climatic conditions among the SEWS sites seems improbable due to their close mutual proximity. Speculatively, some kind of a permanent geographic separation in the large-scale foraging range areas between the populations frequenting VG and those discovered at SH + KK could be suggested. However, the fact that the layer dates providing the chronological context indicate the sites are not contemporaneous may play a significant role, and the isotopic differences could also reflect temporal changes in the environment. This hypothesis is further supported by the results of palynological analysis from Volchia Griva (Leshchinskiy and Burkanova, 2022), which showed a clear aridisation of the climate since the site's formation.

5. Conclusion

We analysed 29 mammoth molar dentine samples, alongside dentine from one horse and one deer molars from three Late Pleistocene paleontological sites in the southeast of the Western Siberian Plain (SEWS): Shestakovo, Krasnoyarskaya Kurya, and Volchia Griva. We assessed the preservation of these samples using C:N atomic ratios, collagen yields, and elemental carbon and nitrogen content. Our results reveal unusually high δ^{15}N values reported for mammoth remains in the Northern Hemisphere from Volchia Griva. We attribute this isotopic enrichment to the unique local environmental conditions at Volchia Griva, including saline soils and intensive trampling, which may have altered nitrogen cycling at the site. The clear difference in δ^{15}N and δ^{13}C values between Volchia Griva and the other two sites, suggests that the mammoth population represented at Volchia Griva had different foraging areas from those at Shestakovo and Krasnoyarskaya Kurya despite the geographical proximity of the sites. This could be interpreted either as restricted geographic mobility between site areas or, perhaps more likely, a reflection of the likely non-contemporanous nature of the sites, with Shestakovo and Volchia Griva displaying completely non-overlapping age ranges.

Future studies of skeletal materials from these sites should take into consideration the generally poor preservation of the organic component, resulting in low extract yields, and select samples in quantities sufficient to run initial analyses, potential reanalysis, and C14 dating. Quality screening should follow the established protocols; however, we advise considering evaluating the preservation of the samples on an individual basis. Tusks seem to have a higher rejection rate compared to molars; this trend is observed for both the mineral and organic components.

CRediT author statement

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2025.109645.

Data availability

All data and/or code is contained within the submission.

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