



The Paleolithic diet of Siberia and Eastern Europe: evidence based on stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in hominin and animal bone collagen

Yaroslav V. Kuzmin¹ · Aleksei A. Bondarev² · Pavel A. Kosintsev³ · Elya P. Zazovskaya⁴

Received: 10 March 2021 / Accepted: 2 September 2021 / Published online: 2 October 2021
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2021

Abstract

We present an analysis and interpretation of current knowledge on Paleolithic diet in Siberia and Eastern Europe, based on C and N stable isotope ratios in bone collagen of the pre-Last Glacial Maximum (LGM) and LGM hominins: three Neanderthals; one possible Denisovan; a Neanderthal/Denisovan hybrid; and 13 early anatomically modern humans (AMH). We used animal stable isotope information for Siberia obtained previously to establish the baselines for hominins; this is supplemented by stable isotope values for large mammals from the central West Siberian Lowland which were the probable sources of protein for Paleolithic humans in this region (first of all, the oldest directly radiocarbon-dated Ust'-Ishim AMH in Asia). A comparison of results on Paleolithic hominin diet from Siberia and Eastern Europe with Central Europe was also undertaken. The Neanderthal diet in Siberia was based on the consumption of terrestrial animal protein. As for the Neanderthal/Denisovan hybrid from Denisova Cave (Altai Mountains, southern Siberia), the contribution of aquatic food like freshwater fish can be preliminarily suggested. Overall, Paleolithic AMHs in Siberia and Eastern Europe procured mainly terrestrial herbivores—in particular, reindeer, horse, and bison. It is possible that some of the oldest AMH individuals—like Kostenki 1—supplemented their diet with a certain amount of aquatic food (freshwater fish).

Keywords Paleodiet · Stable isotopes · Paleolithic · Denisovans · Neanderthals · Anatomically modern humans · Siberia · Eastern Europe

Introduction

In the 1990s–early 2000s, studies of Paleolithic diet in Eurasia based on carbon and nitrogen stable isotope ratios, often accompanied by direct radiocarbon (^{14}C) dating of human remains (see review: Kuzmin and Keates 2014), were initiated (Bocherens et al. 1991, 1999; Richards et al. 2000,

2001). They were concentrated mainly in Western and Central Europe with numerous finds of Neanderthals and early anatomically modern humans (AMHs) (see summaries: Richards 2009; Richards and Trinkaus 2009; Trinkaus et al. 2009; Wißing et al. 2016, 2019). Later on, some research was conducted in Eastern Europe and Siberia (Prat et al. 2011; Dobrovolskaya et al. 2012; Dobrovolskaya and Tiunov 2013; Fu et al. 2014; Drucker et al. 2017). However, the small amount of analyzed contemporaneous animals in Eastern and Central Europe to some extent hampers the interpretation of the results obtained.

In this paper, we present all the available data on stable isotopes for Paleolithic hominins and Late Pleistocene mammals in Siberia and Eastern Europe, and compare it to information collected from Central Europe and neighboring regions. Although zooarchaeological data for the Middle and Upper Paleolithic of Siberia and Eastern Europe exist (see, for example, Hoffecker 2002; Vasil'ev 2003; Kuzmin 2011; Turner et al. 2013), they are less relevant to the issue of which mammals were the dominant objects of hunting

✉ Yaroslav V. Kuzmin
kuzmin_yv@igm.nsc.ru; kuzmin@fulbrightmail.org

¹ Sobolev Institute of Geology and Mineralogy, Siberian Branch of the Russian Academy of Sciences, Novosibirsk, Russia
² Omsk Branch of the Russian Geographical Society, Omsk, Russia
³ Institute of Plant and Animal Ecology, Urals Branch of the Russian Academy of Science, Yekaterinburg, Russia
⁴ Institute of Geography, Russian Academy of Sciences, Moscow, Russia

for ancient populations due to incomplete survival of the remains of prey bones at Paleolithic sites. The carbon and nitrogen stable isotope values provide the best evidence known to date on the protein sources of prehistoric people (e.g., Richards 2019).

Material and methods

The number of Paleolithic hominin remains analyzed for composition of C and N stable isotopes in both Siberia and Eastern Europe is relatively small (Fig. 1; Table 1). For Siberia and the Russian Far East, only eight individuals have stable isotope values, namely, those from the sites of Denisova and Okladnikov caves, Ust'-Ishim, Maly Log 2, and Malta. In Eastern Europe, there are five sites—Kostenki 1, 8, and 14; and Buran-Kaya III and Sungir—with ten AMH individuals for which the stable isotope values were measured. Basic data on these sites can be found in Hoffecker (2002, 2017), Gerasimova et al. (2007), Mednikova (2011), Fu et al. (2014), Zubova et al. (2016), and Douka et al. (2019). For comparison of data available for Siberian and East European Paleolithic hominins, information generated for the Central European finds of AMH derived from pre-Last Glacial Maximum (LGM) times was used (Table 1).

The overall number of Paleolithic hominin remains in Eastern Europe and Siberia is not large compared to Central and Western Europe. For example, in a catalog compiled by Gerasimova et al. (2007), 49 fossil hominin localities in Eastern Europe and nine in Siberia are mentioned. Turner

et al. (2013: 386–390) discussed the very small number of Paleolithic hominin remains in Siberia—keeping in mind the enormous size of this region, ca. 14,000,000 km²—and arrived at eight possible suggestions, none of which can explain this phenomenon.

The analysis of stable isotopes' ratios for carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in bone collagen of the Paleolithic hominins was carried out according to standard procedures (e.g., Richards 2019). Unfortunately, not all hominin samples from Siberia, Eastern Europe, and Central Europe have the whole set of parameters to evaluate the reliability of results obtained (van Klinken 1999; Brock et al. 2012). Nevertheless, for most of them (81% of the total dataset), the crucial value of C:N_{atom} ratio, which should be within the interval of 2.9–3.6 (DeNiro 1985; Ambrose 1990), is available (Table 1). This gives us confidence that the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data on Paleolithic hominins considered in this paper are reliable. Many C:N_{atom} values are close to “optimal” $\text{C:N}_{\text{atom}} = 3.243$ as suggested by Schwarcz and Nahal (2021). All of them (except the Předmostí 1 site) are less than what was recently suggested as the upper limit for this kind of collagen— $\text{C:N}_{\text{atom}} = 3.45\text{--}3.50$ (Guiry and Szpach 2021).

The stable isotope data for pre-LGM mammals from the Altai Mountains of southern Siberia are presented in Table 2. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for Late Pleistocene mammals from the Ust'-Ishim area of Western Siberia are based on samples collected by us (Table 3). These bones have come from alluvial deposits of the lower course of the Irtysh River that were formed during the Marine Isotope

Fig. 1 Location of Paleolithic sites with stable isotope values in Siberia and Eastern Europe, and main geographic regions mentioned in this paper

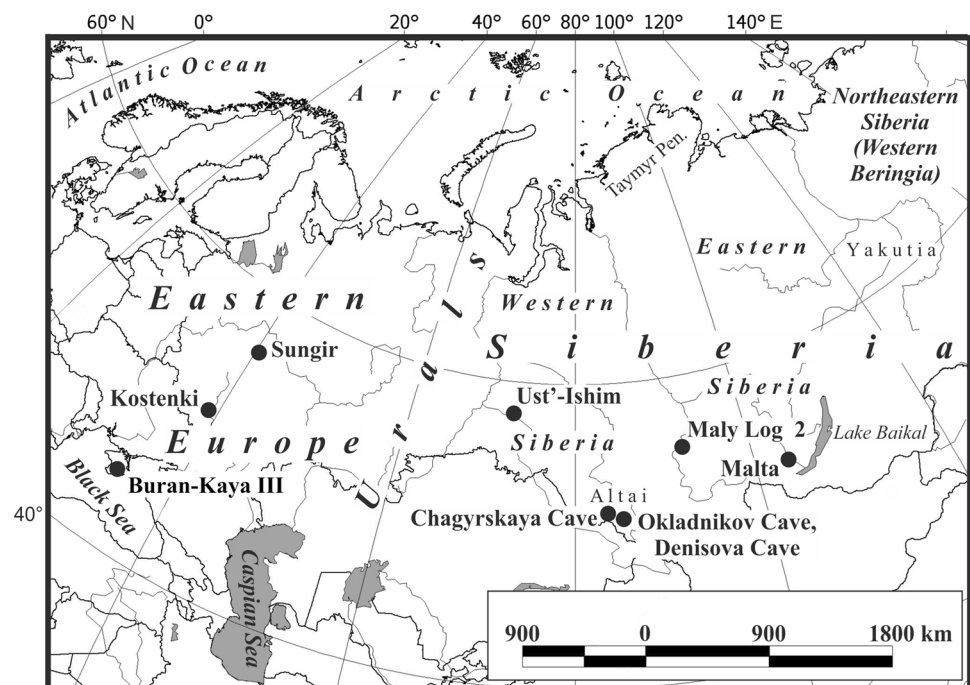


Table 1 Stable isotope values and ^{14}C dates for the pre-LGM and LGM hominins from Siberia, and Eastern and Central Europe (AMHs, unless otherwise indicated)

Site, hominin, layer	C:N _{atom} ratio	$\delta^{13}\text{C}$, ‰	$\delta^{15}\text{N}$, ‰	Collagen yield, %	^{14}C date, BP	Calendar age (cal BP), median value ^a	References
Siberia							
Denisova Cave ^b	3.2	-18.9	16.0	—	—	—	Dobrovolskaya and Tiunov (2011)
Denisova Cave ^c	3.3	-17.4	16.4	4.6	> 49,900	—	Douka et al. (2019)
Denisova Cave ^d	3.2	-18.6	12.7	9.1	> 50,200	—	Douka et al. (2019)
Chagyrskaya Cave ^e	3.3	-19.2	13.8	—	ca. > 49,000 ^f	—	Salazar-García et al. (2021); Kolobova et al. (2020)
Okladnikov Cave ^g	—	-18.9	13.8	—	ca. > 45,000	—	Dobrovolskaya and Tiunov (2013); Higham (2019)
Ust'-Ishim	3.2	-19.0	14.2	7.7	41,400 ± 1300	ca. 44,330	Fu et al. (2014)
Maly Log 2	3.3	-18.4	10.4	6.7	27,740 ± 150	ca. 31,610	Akimova et al. (2010)
Malta	—	-18.4	12.2	—	19,880 ± 160	ca. 23,840	Richards et al. (2001)
Eastern Europe							
Kostenki 14	—	-19.5	13.5	—	33,250 ± 500	ca. 37,840	Dobrovolskaya and Tiunov (2011); Marom et al. (2012)
Buran-Kaya III (Layer 6.2)	3.2	-18.8	15.8	—	32,450 ± 240	ca. 36,800	Drucker et al. (2017)
Kostenki 1 ^h	3.1	-18.3	15.3	6.6	32,070 ± 190	ca. 36,470	Richards et al. (2001); Higham et al. (2006)
Buran-Kaya III (Layer 6.1)	3.3	-19.4	15.4	—	31,900 ± 230	ca. 36,250	Péan et al. (2013); Drucker et al. (2017)
Buran-Kaya III (Layer 6.1)	3.2	-18.9	16.8	—	—	—	Drucker et al. (2017)
Sungir, S-1	3.1	-19.5	10.7	—	27,050 ± 210	ca. 31,230	Dobrovolskaya et al. (2012)
Sungir, S-2	3.1	-19.9	11.1	5.4	26,190 ± 120	ca. 30,470	Kuzmin et al. (2014)
Sungir, S-3	3.5	-19.6	11.0	—	26,000 ± 410	ca. 30,190	Dobrovolskaya et al. (2012)
Sungir, S-5	3.4	-17.9	12.9	1.2	26,040 ± 180	ca. 30,400	Sikora et al. (2017)
Kostenki 8	—	-18.3	10.9	—	23,020 ± 320	ca. 27,130	Dobrovolskaya and Tiunov (2011); Anikovich et al. (2008)
Central Europe							
Peștera cu Oase 1	3.3	-18.7	13.3	4.0	34,950 + 990 / - 890	ca. 39,650	Trinkaus et al. (2003, 2009)
Peștera Muierii 1	3.4	-19.3	12.3	13.3	29,930 ± 170	ca. 34,400	Soficaru et al. (2006); Trinkaus et al. (2009)
Peștera Muierii 2	3.3	-19.1	12.4	11.2	29,110 ± 190	ca. 33,660	Soficaru et al. (2006); Trinkaus et al. (2009)
Peștera Cioclovina Uscată 1	3.4	-19.6	12.7	5.9	28,510 ± 170	ca. 32,650	Soficaru et al. (2007); Trinkaus et al. (2009)
Dolní Věstonice II, DV16	3.3	-19.7	12.5	13.9	27,220 ± 110	ca. 31,300	Fewlass et al. (2019)
Dolní Věstonice II, DV43	3.3	-19.6	12.6	10.2	27,070 ± 110	ca. 31,160	Fewlass et al. (2019)
Dolní Věstonice II, DV13	3.2	-19.3	12.9	13.5	27,040 ± 100	ca. 31,140	Fewlass et al. (2019)
Dolní Věstonice II, DV42	3.4	-19.8	12.7	9.0	26,880 ± 110	ca. 31,070	Fewlass et al. (2019)
Dolní Věstonice II, DV14	3.5	-20.2	13.3	9.5	26,760 ± 100	ca. 31,010	Fewlass et al. (2019)
Dolní Věstonice II, DV15	3.2	-19.4	12.6	8.0	26,680 ± 70	ca. 30,960	Fewlass et al. (2019)
Pavlov, Pav 1	3.4	-19.5	13.6	9.3	25,490 ± 90	ca. 29,690	Fewlass et al. (2019)
Brno-Francouzská 2	—	-19.0	12.3	—	23,680 ± 200	ca. 27,870	Richards et al. (2001)
Dolní Věstonice 35	—	-18.8	12.3	—	22,840 ± 200	ca. 27,030	Richards et al. (2001)
Předmostí 1	3.6	-19.4	12.6	2.6	—	—	Bocherens et al. (2015)

^aThe IntCal20 dataset and Calib Rev 8.1.0 software (available at: <http://calib.org/calib/>) were used

^bThe species is unclear; in the same Layer 11 (see Dobrovolskaya and Tiunov 2011: 86), the *Denisova 3* fossil (see Douka et al. 2019, Supplementary Information, p. 28) was found, and its DNA was identified as Denisovan (see Reich et al. 2010)

^cNeanderthal/Denisovan hybrid (Denisova 11 individual) (see Douka et al. 2019)

^dNeanderthal (Denisova 15 individual) (see Douka et al. 2019)

^eNeanderthal

^fAge estimate is based on a ^{14}C date of animal bones from the same layer (see Kolobova et al. 2020)

^gNeanderthal, average values of sub-adult humerus (see Dobrovolskaya and Tiunov 2013)

^hAverage values (see Richards et al. 2001; Higham et al. 2006)

Table 2 Composition of stable isotopes for the pre-LGM mammals from the Denisova and Chagyrskaya caves, Altai Mountains, southern Siberia

Species	No. of samples	$\delta^{13}\text{C}$, ‰		$\delta^{15}\text{N}$, ‰		Source ¹
		Average	s.d	Average	s.d	
Herbivores						
Pleistocene bison (<i>Bison</i> sp.)	8	-19.5	0.4	7.4	1.1	1
Pleistocene bison (<i>Bison/Bos</i> sp.)	5	-19.7	0.6	5.4	1.3	2
Ovodov horse (<i>Equus ovodovi</i>)	4	-20.1	0.5	6.6	1.2	1
Horse (<i>Equus</i> cf. <i>hydruntinus</i>)	4	-20.3	0.4	7.3	2.4	2
Deer (<i>Cervus</i> sp.)	3	-19.2	0.2	8.3	1.5	2
Elk (<i>Alces alces</i>)	2	-19.3	0.4	7.0	0.4	2
Ibex (<i>Capra sibirica</i>)	4	-18.7	0.5	5.9	0.5	1
Ibex (<i>Capra</i> sp., <i>Capra sibirica</i>)	3	-18.9	0.3	5.6	0.3	2
Wild sheep/ibex (<i>Ovis/Capra</i>)	4	-18.6	0.3	5.9	0.4	2
Carnivores						
Cave hyena (<i>Crocota spelaea</i>)	2	-19.1	0.5	8.3	2.7	1
Cave hyena (<i>C. spelaea</i>)	1	-17.7	-	10.1	-	2
Gray wolf (<i>Canis lupus</i>)	2	-18.6	0.1	10.6	0.7	1
Red fox (<i>Vulpes vulpes</i>)	2	-20.2	0.7	7.0	0.8	1

¹Source: 1, Salazar-García et al. (2021); 2, Douka et al. (2019)

Stage 3 interstadial, with ¹⁴C dates on wood in the range of ca. 24,500–46,600 BP (Krivonogov 1988). There are a number of ¹⁴C dates from this region run on animal bones of woolly rhinoceros, Pleistocene bison and horse, red deer, and musk ox, in the range from ca. 24,600 BP to more than 48,120 BP (see Stuart and Lister 2012; Soubrier et al. 2016; Rabanus-Wallace et al. 2017; Doan et al. 2021). Some of our samples with stable isotope values are directly ¹⁴C-dated from ca. 22,460 BP to more than 48,120 BP (Table S1).

The measurements of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for West Siberian samples (Table 3) were conducted at the Laboratory of Radiocarbon Dating and Electronic Microscopy, Institute of Geography, Russian Academy of Sciences (Moscow, Russia). Collagen extraction was performed by slow dissolution of the mineral part of the bone in 0.2 M solution of HCl,

rinsing, treatment with 0.1 M NaOH, rinsing again, dissolution of the extract in weak HCl at 80° C, and centrifuging. The material obtained was dried and used for analysis. The measurements of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were conducted on an Isoprime PrecisION IRMS coupled on an Elementar varioIsotope Cube (Elementar, Germany and UK), against IAEA-600, B2155, and B2159 (Elemental Microanalysis Ltd.) standards. The analytical precision is 0.2‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. The C:N_{atom} ratios for all animal collagen samples are within the range of 2.9–3.6 (Table S1).

For comparison of hominin stable isotope values with baseline data on the pre-LGM animals, we used the latest summary publications (Rey-Iglesia et al. 2019, 2021; Raghavan et al. 2014; see also Szpak et al. 2010; Kirillova et al. 2015), mainly for Siberia and to a lesser degree for Eastern Europe and the Urals (Table 4). Only samples with

Table 3 Composition of stable isotopes for the pre-LGM mammals from the Ust'-Ishim area and neighboring regions of Western Siberia (this study; see complete records in Table S1)

Species	No. of samples	$\delta^{13}\text{C}$, ‰		$\delta^{15}\text{N}$, ‰	
		Average	s.d	Average	s.d
Herbivores					
Woolly mammoth (<i>Mammuthus primigenius</i>)	2	-20.8	0.1	6.6	0.3
Woolly rhinoceros (<i>Coelodonta antiquitatis</i>)	1	-19.6	-	2.6	-
Pleistocene bison (<i>Bison priscus</i>)	2	-19.0	0.1	5.8	0.7
Pleistocene horse (<i>Equus ferus</i>)	2	-20.0	0.2	7.3	2.3
Musk ox (<i>Ovibos moschatus</i>)	5	-19.8	0.7	5.6	1.4
Reindeer (<i>Rangifer tarandus</i>)	1	-18.8	-	3.4	-
Elk (<i>Alces alces</i>)	1	-19.2	-	1.4	-
Saiga antelope (<i>Saiga tatarica</i>)	1	-18.0	-	6.7	-
Omnivores					
Cave bear (<i>Ursus spelaeus</i>)	1	-19.4	-	10.7	-

direct ^{14}C dates older than ca. 24,000 BP are included into the dataset.

The ^{14}C dating of most Paleolithic hominins mentioned in this study was performed using different protocols of collagen extraction, namely, bulk collagen (Longin 1971; Arslanov and Svezhentsev 1993), ultrafiltered collagen (Higham et al. 2006; Douka et al. 2019), and individual amino acids (mainly hydroxyproline) (Marom et al. 2012). Details can be found in references indicated in Table 1. Uncalibrated ^{14}C ages are given as “BP,” and calendar dates are presented as “cal BP” (mainly as the median values of calibrated age intervals).

The relatively stable composition of isotopic values for mammoths in various parts of northern Asia throughout the last ca. 50,000 years (Kuitens et al. 2019; Rey-Iglesia et al. 2019) allows us to assume that data from these areas are comparable to each other (see also Table 4). We are fully aware that comparison of stable isotope data for hominins and animals from Siberia and Eastern Europe is to some extent limited due to the vast geographic area where the samples were collected. On the other hand, the Paleolithic way of life and the natural environment for these regions in the second part of the Late Pleistocene were similar (e.g., Allen et al. 2010; Velichko et al. 2017: 518), and this allowed us to use the available information.

Table 4 Composition of stable isotopes for the ^{14}C -dated pre-LGM mammals from Western Beringia (a.k.a. Northeastern Siberia and Yakutia), Eastern Siberia (a.k.a. South/Central Siberia), and Eastern Europe/Urals (see Fig. 4)

Species, regions	No. of samples	$\delta^{13}\text{C}$, ‰		$\delta^{15}\text{N}$, ‰		Source ¹
		Average	s.d.	Average	s.d.	
Herbivores						
Woolly mammoth, Yakutia	8	-22.1	0.6	9.3	1.0	1
Woolly mammoth, Western Beringia	14	-21.8	0.4	9.5	1.1	2
Woolly mammoth, Northeastern Siberia	66	-21.8	0.5	9.5	1.2	3
Woolly mammoth, Western Beringia	33	-22.0	0.4	9.1	1.2	4
<i>Average for woolly mammoth</i>		-21.9		9.4		
Woolly rhinoceros, Northeastern Siberia	65	-20.6	0.5	6.7	1.9	3
Woolly rhinoceros, South/Central Siberia	24	-19.6	0.6	6.0	1.5	3
Woolly rhinoceros, Eastern Europe/Urals	35	-19.4	0.5	5.4	1.7	3
<i>Average for woolly rhinoceros</i>		-19.9		6.0		
Pleistocene bison, Yakutia	1	-19.3	-	6.3	-	1
Pleistocene bison, Western Beringia	3	-20.8	0.6	7.5	1.9	4
<i>Average for Pleistocene bison</i>		-20.1		6.9		
Pleistocene horse, Yakutia	2	-21.9	0.8	5.6	1.2	1
Pleistocene horse, Western Beringia	2	-21.0	0.2	4.4	0.1	4
<i>Average for Pleistocene horse</i>		-21.5		5.0		
Musk ox, Yakutia	1	-19.9	-	5.8	-	1
Musk ox, Arctic Yakutia	31	-20.7	0.6	6.7	1.5	5
Musk ox, Taymyr Peninsula	11	-20.8	0.3	5.5	1.1	5
Musk ox, Urals	6	-20.1	0.3	5.7	1.5	5
<i>Average for musk ox</i>		-20.4		5.9		
Saiga antelope, Siberia	3	-17.9	0.5	8.7	1.4	3
Saiga antelope, Eastern Europe	7	-17.0	1.1	9.1	1.4	3
<i>Average for saiga antelope</i>		-17.5		8.9		
Carnivores and omnivores						
Cave lion, Yakutia	1	-19.6	-	9.8	-	1
Cave lion, Western Beringia	6	-19.6	0.4	11.9	1.1	4
<i>Average for cave lion</i>		-19.6		10.9		
Gray wolf, Yakutia	1	-20.1	-	12.0	-	1
Brown bear, Yakutia	2	-19.3	0.1	11.4	0.1	6
Brown bear, Western Beringia	3	-20.4	0.8	10.7	1.0	4
<i>Average for brown bear</i>		>-19.9		11.1		

¹Source: 1, Bocherens et al. (1996); 2, Szpak et al. (2010); 3, Rey-Iglesia et al. (2021); 4, Rey-Iglesia et al. (2019); 5, Raghavan et al. (2014); 6, Krylovich et al. (2020)

Results and discussion

Siberia

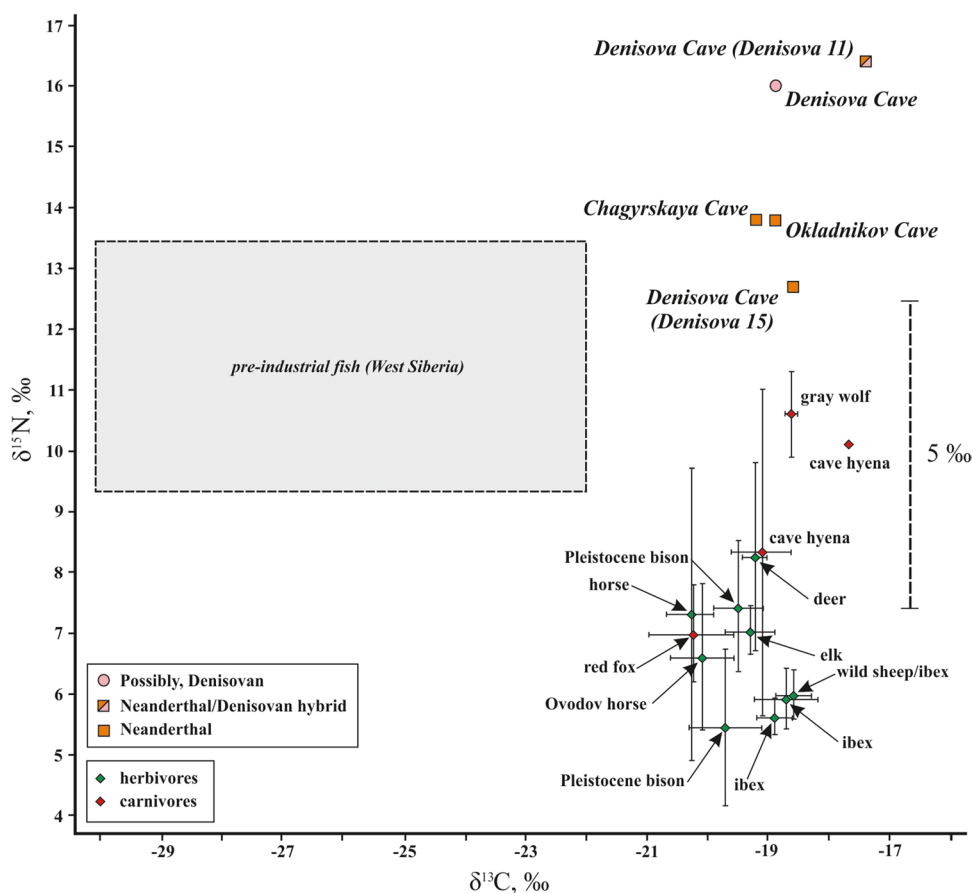
One sample of presumably pre-modern hominins, called Denisovans, was studied by Dobrovolskaya and Tiunov (2011) (see Table 1). It is not clear, however, if it belongs to a Denisovan because this cranial vault fragment (see Dobrovolskaya and Tiunov 2011: 82) is not listed in the catalog of hominin fossils from Denisova Cave (Douka et al. 2019, Supplementary Information, pp. 27–34). It is possible that this is the non-human parietal fragment from Layer 11 (the Denisova 7 find, according to Douka et al. 2019), identified as a cave bear, although its $\delta^{15}N$ value (16.0‰) is too high for this mammal. Therefore, we can only tentatively assume that this sample represents a Denisovan individual. Using the $\delta^{15}N$ value, it is possible that a certain amount of aquatic food (freshwater fish) supplemented the terrestrial animals as a source of protein (Fig. 2).

One specimen belongs to the Neanderthal/Denisovan hybrid (the Denisova 11 find, according to Douka et al. 2019) discovered in Denisova Cave (Douka et al. 2019) (Table 1). Its $\delta^{15}N$ value is very high (16.4‰), and the consumption of

some aquatic food can be suggested (Fig. 2). Unfortunately, we do not have any stable isotope data for Late Pleistocene fish from Western Siberia, and only data on the seventeenth century AD (i.e., pre-industrial) fish from the northern West Siberian Plain is available (Kuzmin et al. 2020; see Fig. 2). The upper end of its $\delta^{15}N$ interval is 12.8‰, and we suggest that this individual supplemented its terrestrial animal diet with freshwater fish. Abundant fish bones (non-identified to species) were found in Okladnikov Cave (Derevianko and Markin 1992: 207) located not far from Denisova Cave. The role of the arid environment in the creation of a relatively high $\delta^{15}N$ level for the Altai mammals should also be taken into account for both Denisova 11 and the possible hominin from Layer 11 of Denisova Cave.

More stable isotope data is now available for Siberian Neanderthals from the Denisova and Okladnikov caves in the Altai Mountains (Figs. 1–2; Table 1). The sub-adult humerus from Okladnikov Cave with Neanderthal DNA (see Kuzmin and Keates 2020) was originally ^{14}C -dated to ca. 34,190 BP (Krause et al. 2007), but recently, it was found that “... the true age of these bones is beyond the radiocarbon age limit ...” (Higham 2019: 1073), and we assume that its age is more than ca. 45,000 BP (Table 1). When we compare the stable isotope values for three Neanderthals and

Fig. 2 $\delta^{13}C$ vs. $\delta^{15}N$ plot for possible Denisovan, Neanderthal/Denisovan hybrid, and Neanderthals from the Altai Mountains (see Table 1), on the background of animal stable isotope values (see Table 2) (with ± 1 sigma)

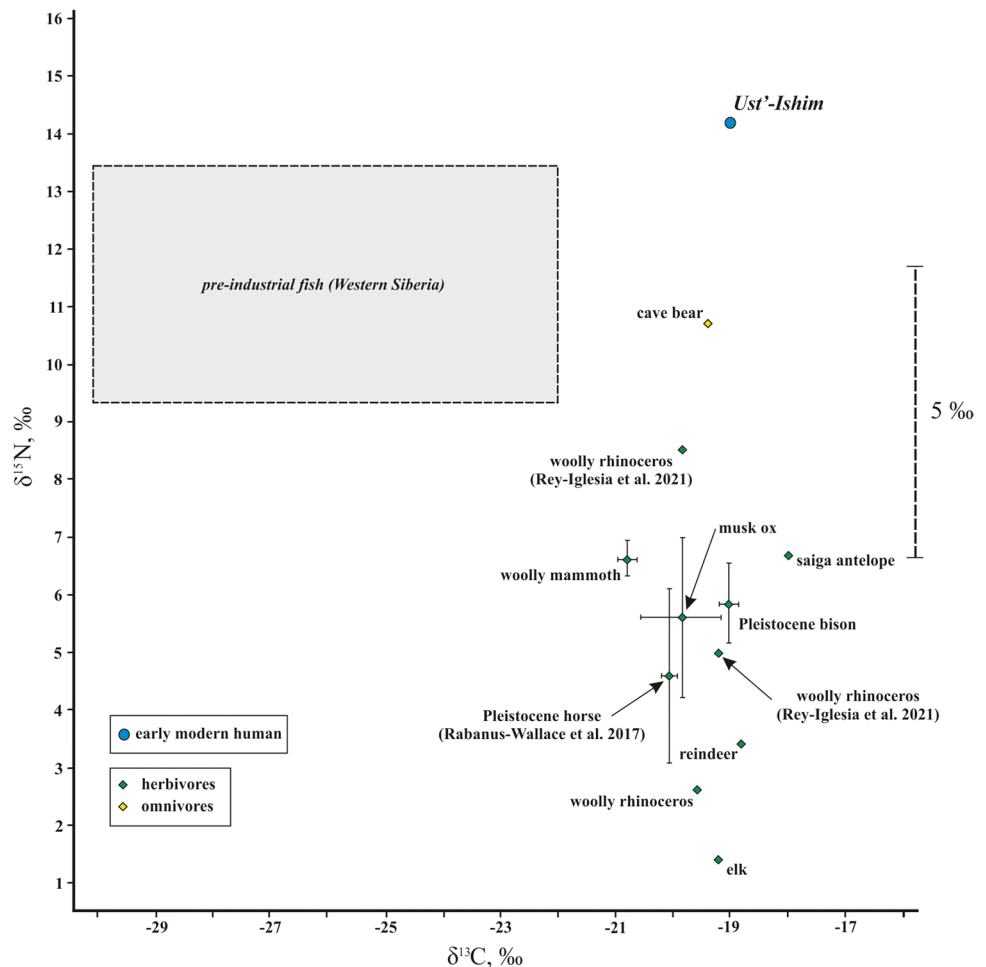


animals from Denisova and Chagyrskaya caves (Tables 1–2; Fig. 2), it is clear that the hominin diet was based on terrestrial mammals as was recently concluded by Salazar-García et al. (2021) for the Chagyrskaya Cave individual. It is evident that if we assume a 5‰ increase in the $\delta^{15}N$ level from herbivores to carnivores (including Neanderthals) (Bocherens and Drucker 2003; Drucker and Bocherens 2004; Hedges and Reynard 2007), it is possible to interpret the $\delta^{15}N$ values (12.7–13.8‰) for the Altai Neanderthals in this way (Fig. 2). The variation of $\delta^{15}N$ values for carnivores, from 7.0 to 10.6‰ (Fig. 2; Table 2), is noteworthy. For the oldest directly ^{14}C -dated AMH in Asia, Ust'-Ishim (Fu et al. 2014) (Table 1), we used the stable isotope values for pre-LGM mammals in central Western Siberia (Fig. 3; Table 3). Judging from this limited baseline dataset, the elevated $\delta^{15}N$ value (14.2‰) for the Ust'-Ishim individual is hard to explain by the consumption of terrestrial protein only (Fig. 3). Also, hunting of the largest representatives of Late Pleistocene megafauna—woolly mammoth and woolly rhinoceros—is less likely. Currently, we have an extremely limited amount of information about the direct procurement of these species by Paleolithic hominins (Zenin 2002;

Kuzmin 2008, 2011; see also Stuart 2021: 48, 63). The main prey of Paleolithic people in Siberia, judging from zooarchaeological data, were reindeer, bison, horse, and mountain sheep (Vasil'ev 2003; Stuart 2021: 63). However, when we take into account the overall data on stable isotopes for the pre-LGM mammals from Siberia and Eastern Europe based on published sources (Table 4; Fig. 4), the major contribution of protein for the Ust'-Ishim individual from terrestrial mammals is evident. The consumption of aquatic food for Ust'-Ishim was previously suggested by Fu et al. (2014) without knowledge of the stable isotope composition for the regional fauna (mammals and fish). It is now clear that it is not necessary to take into account freshwater fish as one of the protein sources for this AMH.

For two other AMHs from Siberia, Maly Log 2 and Malta (Table 1), a diet based on terrestrial herbivores can be estimated. The $\delta^{15}N$ values for these individuals are similar to those for carnivores and omnivores—gray wolf, brown bear, and cave lion (Fig. 4; Table 4). The $\delta^{15}N$ value for Malta (12.2‰), which was previously used by Richards et al. (2001) to assume the consumption of aquatic foods,

Fig. 3 $\delta^{13}C$ vs. $\delta^{15}N$ plot for the Ust'-Ishim AMH (see Table 1) on the background of major food sources from Western Siberia (see Table 3) (with ± 1 sigma)



can now be explained by the contribution of protein from terrestrial sources only.

Eastern Europe

The stable isotope values for the early AMHs from Eastern Europe are quite variable (Table 1; Fig. 4). Some of them—Sungir 1, 2, and 3; and Kostenki 8—are similar to Siberian AMHs from Malta and Maly Log 2; for them, a diet based on terrestrial herbivores can be established (see also Drucker et al. 2021: 9–10). Unfortunately, very little information exists about the stable isotope composition for the pre-LGM mammals of Eastern Europe (Iacumin et al. 2000; Drucker et al. 2017). For the Sungir site, values on reindeer ($\delta^{13}\text{C} = -19.1 \pm 0.3\text{‰}$; $\delta^{15}\text{N} = 5.7 \pm 0.1\text{‰}$) (Trinkaus et al. 2014) are within one trophic level of $\delta^{15}\text{N}$ enrichment for hominins (ca. 3–5‰) who consumed reindeer protein. The values on gray wolf from Sungir are $\delta^{13}\text{C} = -19.8\text{‰}$;

$\delta^{15}\text{N} = 9.8\text{‰}$ (Trinkaus et al. 2014). Comparison with stable isotope data for Siberian mammals demonstrates that the Sungir 1, 2, and 3 individuals are similar to carnivores like cave lion and gray wolf, and to an omnivore like the brown bear (Fig. 4). Zooarchaeological data show that most of the animal bones from Sungir belong to reindeer, Arctic fox, and horse; woolly mammoth and gray wolf are also frequently present (Alekseeva 1998).

The Sungir 5 individual has a higher $\delta^{15}\text{N}$ value (12.9‰). Available parameters for amino acids used for measurements of stable isotopes and ^{14}C age are within a reasonable range; for example, $\text{C:N}_{\text{atom}} = 3.4$ (Sikora et al. 2017, Supplementary Materials, Table S10). Because the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for Sungir 5 were not measured on proper collagen but on amino acids (Sikora et al. 2017, Supplementary Materials, sections S3.1.2 and S3.2.2), data for this individual should be treated as preliminary.

Four AMHs from Eastern Europe—Buran-Kaya III (three individuals) and Kostenki 1—have the highest $\delta^{15}\text{N}$ levels (15.3–16.8‰) known for the entire inland of Eurasia. The compound-specific (phenylalanine and glutamic acid) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the Buran-Kaya III humans (Drucker et al. 2017) indicate the consumption of mainly mammoth (40–70% of total diet) and saiga (10–25%) proteins (see Wißing et al. 2019). Therefore, the AMHs from Buran-Kaya III exhibit a purely terrestrial diet without any contribution of aquatic resources. The elevated $\delta^{15}\text{N}$ levels for mammals and plants from Buran-Kaya III can be explained by the high aridity of the Crimean landscape, compared with northwest Europe (Drucker et al. 2017), during human occupation at ca. 36,300–36,800 cal BP.

Richards et al. (2001) previously suggested a large contribution of aquatic resources (50% and more of total protein) to the diet of the Kostenki 1 individual. However, the lack of data on the stable isotopes for animals from Kostenki in particular, and Eastern Europe in general, to some extent hampers this conclusion. Some information about the landscape around the Kostenki 1 site at ca. 36,500 cal BP (direct ^{14}C date of the Kostenki 1 individual; see Table 1) is available. According to the summary publications (Spiridonova 1991; Hoffecker 2002: 31–32; Hoffecker et al. 2008), the climate at that time was oscillating between colder and warmer conditions, reflected in the amounts of pollen of arboreal (trees and shrubs) and grass species. The Kostenki 1 individual correlates with the cold GS-8 stadial (see Kuzmin 2019); pollen spectra of cultural layer 3 with the human burial show a gradual change of the vegetation from grass-dominated semi-open landscapes to dense spruce forests of the taiga type (Spiridonova 1991: 48–49). The AMH from Kostenki 1 most probably corresponds to the early part of layer 3, and the relatively dry and cold climate can to some extent account for the elevated $\delta^{15}\text{N}$ value of this individual. This, however, does not completely exclude the consumption of

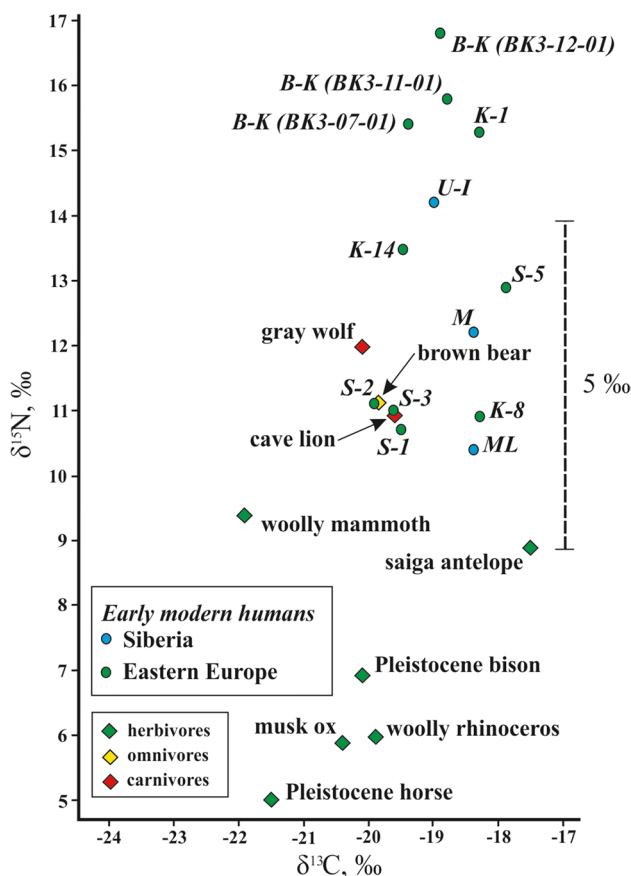


Fig. 4 $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ plot for the AMHs from Siberia and Eastern Europe (see Table 1) on the background of major food sources from Siberia and Eastern Europe/Urals (see Table 4) (with ± 1 sigma). Abbreviations: BK – Buran-Kaya III; K-1 – Kostenki 1; U-I – Ust'-Ishim; K-14 – Kostenki 14; S-5 – Sungir, S-5; M – Malta; K-8 – Kostenki 8; S-1 – Sungir, S-1; S-2 – Sungir, S-2; S-3 – Sungir, S-3; ML – Maly Log 2

aquatic food (Richards 2009). More work is still needed to determine the diet of the Kostenki 1 individual using compound-specific $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for its bone collagen (Naito et al. 2016).

Comparison with Central Europe and neighboring regions, and other issues

The stable isotope values for three Siberian Neanderthals are similar to those for Western Europe (e.g., Wißing et al. 2016, 2019; Salazar-García et al. 2021). The only difference is the slightly elevated $\delta^{15}\text{N}$ level for Siberian individuals, but this can be explained by the arid environment during their existence.

The stable isotope values for early AMHs in Siberia and Eastern Europe are quite variable compared to Central Europe (Figs. 4–5), consistent with previous studies (Richards and Trinkaus 2009). For some Central European individuals, like Peștera cu Oase 1 (Fig. 5), the consumption of freshwater food was suggested, although with some reservations related to the small amount of faunal stable isotope values available (see Bocherens, 2019). Similar conclusions were made for Kostenki 1 (Richards 2009) and Ust'-Ishim (Fu et al. 2014). It is now clear that the Ust'-Ishim individual consumed mainly terrestrial animals. The wide variations of the $\delta^{15}\text{N}$ value for AMHs from Eastern and Central Europe without considering possible variations of the faunal isotopic baseline led to the suggestion of an increase of the food spectrum compared to Neanderthals (Richards and Trinkaus 2009; Trinkaus et al. 2009), although for Western Europe, it was found that the diets of Neanderthals and AMHs were similar (Wißing et al. 2019).

As for the question of woolly mammoth protein as one of the possible main food sources for AMHs in Siberia and Eastern Europe, it can be suggested that these people could have consumed mammoth meat, although evidence for it is non-existent. At some sites, like Malta and Sungir, reindeer is the most abundant species (Aleksееva 1998; Kuzmin 2008). At Kostenki 1 (layer 3), the dominant species are Arctic fox, horse, reindeer, and wolf (Praslov and Rogachev 1982). Because direct hunting of woolly mammoths was uncommon (see above), in the presence of plentiful prey like horse, bison, and reindeer, it is less likely that Upper Paleolithic AMHs in Siberia and Eastern Europe (first of all, Ust'-Ishim and Kostenki 14 individuals) regularly practiced scavenging of meat from recently dead woolly mammoths. It is clear that more research is needed for Eastern Europe, especially for the Kostenki site cluster, to collect data on the stable isotope composition for animal bone collagen as regional and local baselines.

Information about aquatic food consumption could have implications with respect to estimating the freshwater reservoir

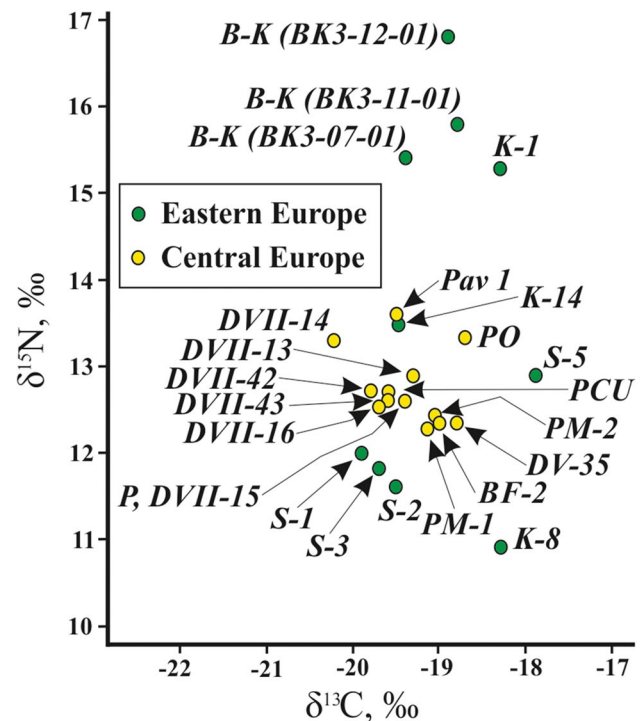


Fig. 5 Comparison of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from AMHs in Siberia, Eastern Europe, and Central Europe (see Table 1). Abbreviations: PO – Peștera cu Oase 1; PCU – Peștera Cioclovina Uscată 1; P – Předmostí 1; PM-1 – Peștera Muierii 1; PM-2 – Peștera Muierii 2; BF-2 – Brno-Francouzská 2; DV-35 – Dolní Věstonice 35; Pav – Pavlov; DVII13–43 – Dolní Věstonice II (different individuals); for other abbreviations, see Fig. 4

effect (FRE) when hominin bones are ^{14}C -dated. According to currently available data about pre-industrial fish in Western Siberia, the FRE is up to ca. 2000 ^{14}C years (Kuzmin et al. 2020).

Conclusions

The analysis of stable isotope values for the majority of pre-LGM hominins from Siberia and Eastern Europe (Neanderthals and AMHs) allows us to suggest that terrestrial food resources (especially, herbivores like reindeer, horse, and bison) were the main suppliers of protein. Some of the oldest AMH individuals like Kostenki 1 with a very high $\delta^{15}\text{N}$ value could have possibly consumed a certain amount of aquatic food, most probably freshwater fish from nearby rivers. The very high level of $\delta^{15}\text{N}$ for the Neanderthal/Denisovan hybrid from Denisova Cave in Siberia may testify to the consumption of aquatic food.

Overall, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for pre-LGM hominins from Siberia and Eastern Europe vary greatly, and this reflects the wide range of protein sources used by Paleolithic hunter-fisher-gatherers. More data on the stable isotope composition from contemporaneous fauna is still needed for these regions

of northern Eurasia for a better understanding of the patterns of hominin diet.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12520-021-01439-5>.

Acknowledgements We are grateful to the Museum of the Institute of Plant and Animal Ecology (Urals Branch of the Russian Academy of Science, Yekaterinburg), Mr. Aleksander S. Golubev (Ust'-Ishim, Omsk Province) and Mr. Nikolai V. Peristov (Omsk) for providing some of the samples used in this paper. We also thank two anonymous reviewers and an Associated Editor for useful comments and notes related to the previous version of this paper.

Author contribution YV Kuzmin: conceptualization, formal analysis, investigation, methodology, writing-original draft, writing review and editing. AA Bondarev: investigation, formal analysis, methodology, writing-original draft. PA Kosintsev: investigation, formal analysis, methodology, writing-original draft. EP Zazovskaya: investigation, formal analysis, providing lab equipment and materials, writing-original draft.

Funding The study was funded by a grant from the Russian Science Foundation (RNF), Project No. 20–17–00033.

Declarations

Competing interests The authors declare no competing interests.

References

- Akimova E, Higham T, Stasyuk I, Buzhilova A, Dobrovolskaya M, Mednikova M (2010) A new direct radiocarbon AMS date for an Upper Palaeolithic human bone from Siberia. *Archaeometry* 52:1122–1130
- Alekseeva LI (1998) Hunting fauna at the Sungir site. In: Bader NO, Lavrushin YA (eds) *Upper Palaeolithic Site Sungir (Graves and Environment)*. Nauchnyi Mir Press, Moscow, pp 240–257 (in Russian with English title)
- Allen JRM, Hickler T, Singarayer JS, Sykes MT, Valdes PJ, Huntley B (2010) Last glacial vegetation of northern Eurasia. *Quat Sci Rev* 29:2604–2618
- Ambrose SH (1990) Preparation and characterization of bone and tooth collagen for isotopic analysis. *J Archaeol Sci* 17:431–451
- Anikovich MV, Popov VV, Platonova NI (2008) *Paleolithic of Kostenki-Borschevo region in the context of Upper Paleolithic of Europe*. Nestor-Istoriya Press, St. Petersburg (in Russian with English title)
- Arslanov KA, Svezhentsev YS (1993) An improved method for radiocarbon dating fossil bones. *Radiocarbon* 35:387–391
- Bocherens H (2019) Isotopic insights on cave bear palaeodiet. *Hist Biol* 31:410–421
- Bocherens H, Drucker D (2003) Trophic level isotopic enrichments for carbon and nitrogen in collagen: case studies from recent and ancient terrestrial ecosystems. *Int J Osteoarchaeol* 13:46–53
- Bocherens H, Fizet M, Mariotti A, Lange-Badre B, Vandermeersch B, Borel JP, Bellon G (1991) Isotopic biogeochemistry (^{13}C , ^{15}N) of fossil vertebrate collagen: implications for the study of fossil food web including Neandertal Man. *J Hum Evol* 20:481–492
- Bocherens H, Pacaud G, Lazarev P, Mariotti A (1996) Stable isotope abundances (^{13}C , ^{15}N) in collagen and soft tissues from Pleistocene mammals from Yakutia. Implications for the paleobiology of the mammoth steppe. *Palaeogeogr Palaeoclimatol Palaeoecol* 126:31–44
- Bocherens H, Billiou D, Patou-Mathis M, Otte M, Bonjean D, Toussaint M, Mariotti A (1999) Palaeoenvironmental and palaeodietary implications of isotopic biogeochemistry of late interglacial Neandertal and mammal bones in Sceldina Cave (Belgium). *J Archaeol Sci* 26:599–607
- Bocherens H, Drucker DG, Germonpré M, Lázníčková-Galetová M, Naito YI, Wissing C, Brůžek J, Oliva M (2015) Reconstruction of the Gravettian food-web at Předmostí I using multi-isotopic tracking (^{13}C , ^{15}N , ^{34}S) of bone collagen. *Quat Int* 359–360:211–228
- Brock F, Wood R, Higham TFG, Ditchfield P, Bayliss A, Bronk Ramsey C (2012) Reliability of nitrogen content (%N) and carbon:nitrogen atomic ratios (C:N) as indicators of collagen preservation suitable for radiocarbon dating. *Radiocarbon* 54:879–886
- DeNiro M (1985) Postmortem preservation and alteration of *in vivo* bone collagen isotope ratios in relation to palaeodietary reconstruction. *Nature* 317:806–809
- Derevianko AP, Markin SV (1992) *Mustie Gornogo Altaya (The Moustertian of the Mountainous Altai)*. Nauka Publ, Novosibirsk (in Russian)
- Doan K, Niedziałkowska M, Stefaniak K, Sykut M, Jędrzejewska B, Ratajczak-Skrzatek U, Piotrowska N, Ridush B, Zachos FE, Popović D, Baca M, Mackiewicz P, Kosintsev P, Makowiecki D, Charniauski M, Boeskorov G, Bondarev AA, Danila G, Kusak J, Rannamäe E, Saarma U, Arakelyan M, Manaseryan N, Krasnodębski D, Titov V, Hulva P, Bălăşescu A, Trantalidou K, Dimitrijević V, Shpansky A, Kovalchuk O, Klementiev AM, Foronova I, Malikov DG, Juras A, Nikolskiy P, Grigoriev SE, Cheprasov MY, Novgorodov GP, Sorokin AD, Wilczyński J, Protopopov AV, Lipecki G, Stanković A (2021) Phylogenetics and phylogeography of red deer mtDNA lineages during the last 50 000 years in Eurasia. *Zoological Journal of the Linnean Society* (in press); doi: <https://doi.org/10.1093/zoolinlean/zlab025>.
- Dobrovolskaya MV, Tiunov AV (2011) Stable isotope ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$) evidence for Late Pleistocene hominides' palaeodiet in Gorny Altai. In: Derevianko AP, Shunkov MV (eds) *Characteristic features of the Middle to Upper Paleolithic transition in Eurasia*. Institute of Archaeology and Ethnography Press, Novosibirsk, pp 81–89
- Dobrovolskaya MV, Tiunov AV (2013) The Neanderthals of Okladnikov Cave, Altai: environment and diet based on isotopic analysis. *Archaeol Ethnol Anthropol Eurasia* 41(1):78–88
- Dobrovolskaya M, Richards MP, Trinkaus E (2012) Direct radiocarbon dates for the mid Upper Paleolithic (eastern Gravettian) burials from Sunghir, Russia. *Bull Mém Soc D'anthropol Paris* 24:96–102
- Douka K, Slon V, Jacobs Z, Bronk Ramsey C, Shunkov MV, Derevianko AP, Mafessoni F, Kozlikin MB, Li B, Grün R, Comeskey D, Devièse T, Brown S, Viola B, Kinsley L, Buckley M, Meyer M, Roberts RG, Pääbo S, Kelso J, Higham T (2019) Age estimate for hominin fossils and the onset of the Upper Palaeolithic at Denisova Cave. *Nature* 565:640–644
- Drucker D, Bocherens H (2004) Carbon and nitrogen stable isotopes as tracers of change in diet breadth during Middle and Upper Palaeolithic in Europe. *Int J Osteoarchaeol* 14:162–177
- Drucker DG, Naito YI, Péan S, Prat S, Crépin L, Chikaraishi Y, Ohkouchi N, Puaud S, Lázníčková-Galetová M, Patou-Mathis M, Yanevich A, Bocherens H (2017) Isotopic analyses suggest mammoth and plant in the diet of the oldest anatomically modern humans from far southeast Europe. *Sci Rep* 7:6833
- Drucker DG, Naito YI, Coromina N, Ruff I, Soler N, Soler J (2021) Stable isotope evidence of human diet in Mediterranean context during the Last Glacial Maximum. *J. Hum Evol* 154:102967

- Fewlass H, Talamo S, Kromer B, Bard E, Tuna T, Fagault Y, Sponheimer M, Ryder C, Hublin J-J, Perri A, Sázalová S, Svoboda J (2019) Direct radiocarbon dates of mid Upper Palaeolithic human remains from Dolní Věstonice II and Pavlov I Czech Republic. *J Archaeol Sci Rep* 27:102000
- Fu Q, Li H, Moorjani P, Jay F, Slepchenko SM, Bondarev AA, Johnson PLF, Petri AA, Prüfer K, de Filippo C, Meyer M, Zwyns N, Salazar-García DC, Kuzmin YV, Keates SG, Kosintsev PA, Razhev DI, Richards MP, Peristov NV, Lachmann M, Douka K, Higham TFG, Slatkin M, Hublin J-J, Reich D, Kelso J, Viola TB, Pääbo S (2014) The genome sequence of a 45,000-year-old modern human from Western Siberia. *Nature* 514:445–450
- Gerasimova MM, Astakhov SN, Velichko AA (2007) Palaeolithic man, its material culture and environment (illustrated catalogue of Pleistocene hominids discovered at Russia and adjacent regions). Nestor-Istoriya Press, St. Petersburg (in Russian with English title)
- Guiry EJ, Szpak P (2021) Improved quality control criteria for stable carbon and nitrogen isotope measurements of ancient bone collagen. *J Archaeol Sci* 132:105416
- Hedges REM, Reynard LM (2007) Nitrogen isotopes and the trophic level of humans in archaeology. *J Archaeol Sci* 34:1240–1251
- Higham TFG (2019) Removing contaminants: a restatement of the value of isolating single compounds for AMS dating. *Antiquity* 93:1072–1075
- Higham TFG, Jacobi RM, Bronk Ramsey C (2006) AMS radiocarbon dating of ancient bone using ultrafiltration. *Radiocarbon* 48:179–195
- Hoffecker JF (2002) *Desolate landscapes: Ice-Age settlement in Eastern Europe*. Rutgers University Press, New Brunswick, NJ & London
- Hoffecker JF (2017) *Modern humans: their African origin and global dispersal*. Columbia University Press, New York
- Hoffecker JF, Holliday VT, Anikovich MV, Sinitsyn AA, Popov VV, Lisitsyn SN, Levkovskaya GM, Pospelova GA, Forman SL, Giacchio B (2008) From the Bay of Naples to the River Don: the Campanian Ignimbrite eruption and the Middle to Upper Paleolithic transition in Eastern Europe. *J Hum Evol* 55:858–870
- Iacumin P, Nikolaev V, Ramigni M (2000) C and N stable isotope measurements on Eurasian fossil mammals, 40 000 to 10 000 years BP: herbivore physiologies and palaeoenvironmental reconstruction. *Palaeogeogr Palaeoclimatol Palaeoecol* 163:33–47
- Kirillova IV, Tiunov AV, Levchenko VA, Chernova OF, Yudin VG, Bertuch F, Shidlovskiy FK (2015) On the discovery of a cave lion from the Malyi Anyui River (Chukotka, Russia). *Quat Sci Rev* 117:135–151
- Kolobova KA, Roberts RG, Chabai VP, Jacobs Z, Krajcarz MT, Shalagina AV, Krivoshapkin AI, Li B, Uthmeier T, Markin SV, Morley MW, O’Gorman K, Rudaya NA, Talamo S, Viola B, Derevianko AP (2020) Archaeological evidence for two separate dispersals of Neanderthals into southern Siberia. *Proc Natl Acad Sci USA* 117:2879–2885
- Krause J, Orlando L, Serre D, Viola B, Prüfer K, Richards MP, Hublin J-J, Hänni C, Derevianko AP, Pääbo S (2007) Neanderthals in Central Asia and Siberia. *Nature* 449:902–904
- Krivosnogov SK (1988) *Stratigrafiya i paleogeografiya nizhnego Priirtyshya v epokhu poslednego oledeneniya (Stratigraphy and paleogeography of the lower Irtysh River valley in the last glaciation)*. Nauka Publ, Novosibirsk (in Russian)
- Krylovich OA, Boeskorov GG, Shchelchkova MV, Savinetsky AB (2020) The trophic position of Pleistocene and modern brown bears (*Ursus arctos*) of Yakutia based on stable isotope analyses. *Biol Bull* 47:1013–1021
- Kuitemans M, van Kolfschoten T, Tikhonov AN, van der Plicht J (2019) Woolly mammoth $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values remained amazingly stable throughout the last ~50,000 years in north-eastern Siberia. *Quat Int* 500:120–127
- Kuzmin YV (2008) Siberia at the Last Glacial Maximum: environment and archaeology. *J Arch Res* 16:163–221
- Kuzmin YV (2011) Mammalian fauna from Palaeolithic sites in the upper Yenisei River basin (southern Siberia): review of the current zooarchaeological evidence. *Int J Osteoarchaeol* 21:218–228
- Kuzmin YV (2019) The older, the better? On the radiocarbon dating of Upper Palaeolithic burials in Northern Eurasia and beyond. *Antiquity* 93:1061–1071
- Kuzmin YV, Keates SG (2014) Direct radiocarbon dating of Late Pleistocene hominids in Eurasia: current status, problems, and perspectives. *Radiocarbon* 56:753–766
- Kuzmin YV, Keates SG (2020) The chronology of hominin fossils from the Altai Mountains, Siberia: an alternative view. *J Hum Evol* 146:102834
- Kuzmin YV, van der Plicht J, Sulerzhitsky LD (2014) Puzzling radiocarbon dates for the Upper Paleolithic site of Sungir (central Russian Plain). *Radiocarbon* 56:451–459
- Kuzmin YV, Kosintsev PA, Boudin M, Zazovskaya EP (2020) The freshwater reservoir effect in northern West Siberia: ^{14}C and stable isotope data for fish from the late medieval town of Mangazeya. *Quat Geochron* 60:101109
- Longin R (1971) New method of collagen extraction for radiocarbon dating. *Nature* 230:241–242
- Marom A, McCullagh J, Higham T, Sinitsyn A, Hedges R (2012) Single amino acid radiocarbon dating of Upper Palaeolithic modern humans. *Proc Natl Acad Sci USA* 109:6878–6881
- Mednikova MB (2011) Postcranial morphology and taxonomy of genus *Homo* representatives from Okladnikov Cave in Altai. Institute of Archaeology & Ethnography Press, Novosibirsk (in Russian with English summary)
- Naito YI, Bocherens H, Chikaraishi Y, Drucker DG, Wißing C, Yoneda M, Ohkouchi N (2016) An overview of methods used for the detection of aquatic resource consumption by humans: compound-specific delta N-15 analysis of amino acids in archaeological materials. *J Archaeol Sci: Rep* 6:720–732
- Péan S, Puaud S, Crépin L, Prat S, Quiles A, van der Plicht J, Valladas H, Stuart AJ, Drucker DG, Patou-Mathis M, Lanoë F, Yanevich A (2013) The Middle to Upper Paleolithic sequence of Buran-Kaya III (Crimea, Ukraine): new stratigraphic, paleoenvironmental, and chronological results. *Radiocarbon* 55:1454–1469
- Praslov ND, Rogachev AN (eds) (1982) *Palaeolithic of the Kostenki-Borshchevo area on the River Don 1879–1979: results of field investigations*. Nauka Publ, Leningrad (in Russian with English abstract)
- Prat S, Péan SC, Crépin L, Drucker DG, Puaud SJ, Valladas H, Lázničková-Galetová M, van der Plicht J, Yanevich A (2011) The oldest anatomically modern humans from far southeast Europe: direct dating, culture and behavior. *PLoS ONE* 6:e20834
- Rabanus-Wallace MT, Wooller MJ, Zazula GD, Shute E, Jahren AH, Kosintsev P, Breen BJA, J, Llamas B, Cooper A, (2017) Megafaunal isotopes reveal role of increased moisture on rangeland during late Pleistocene extinctions. *Nature Ecol Evol* 1:0125
- Raghavan M, Espregueira Themudo G, Smith CI, Zazula G, Campos PF (2014) Musk ox (*Ovibos moschatus*) of the mammoth steppe: tracing palaeodietary and palaeoenvironmental changes over the last 50,000 years using carbon and nitrogen isotopic analysis. *Quat Sci Rev* 102:192–201
- Reich D, Green RE, Kircher M, Krause J, Patterson N, Durand EY, Viola B, Briggs AW, Stenze U, Johnson PLF, Maricic T, Good JM, Marques-Bonet T, Alkan C, Fu Q, Mallick S, Li H, Meyer M, Eichler EE, Stoneking M, Richards M, Talamo S, Shunkov MV, Derevianko AP, Hublin J-J, Kelso J, Slatkin M, Pääbo S (2010) Genetic history of an archaic hominin group from Denisova Cave in Siberia. *Nature* 468:1053–1060

- Rey-Iglesia A, García-Vázquez A, Treadaway EC, van der Plicht J, Baryshnikov GF, Szpak P, Bocherens H, Boeskorov GG, Lorenzen ED (2019) Evolutionary history and palaeoecology of brown bear in North-East Siberia re-examined using ancient DNA and stable isotopes from skeletal remains. *Sci Rep* 9:4462
- Rey-Iglesia A, Lister AM, Stuart AJ, Bocherens H, Szpak P, Willerslev E, Lorenzen ED (2021) Late Pleistocene palaeoecology and phylogeography of woolly rhinoceroses. *Quat Sci Rev* 263:106993
- Richards MP (2009) Stable isotope evidence for European Upper Paleolithic human diets. In: Hublin J-J, Richards MP (eds) *The evolution of hominin diet: integrating approaches to the study of Palaeolithic subsistence*. Springer, Dordrecht, pp 251–257
- Richards MP (2019) Isotope analysis for diet studies. In: Richards MP, Britton K (eds) *Archaeological science: an introduction*. Cambridge University Press, Cambridge, pp 125–143
- Richards MP, Trinkaus E (2009) Isotopic evidence for the diets of European Neanderthals and early modern humans. *Proc Natl Acad Sci USA* 106:16034–16039
- Richards MP, Pettitt PB, Trinkaus E, Smith FH, Paunović M, Karvanić I (2000) Neanderthal diet at Vindija and Neanderthal predation: The evidence from stable isotopes. *Proc Natl Acad Sci USA* 97:7663–7666
- Richards MP, Pettitt PB, Stiner MC, Trinkaus E (2001) Stable isotope evidence for increasing dietary breadth in the European Mid-Upper Paleolithic. *Proc Natl Acad Sci USA* 98:6528–6532
- Salazar-García DC, Power RC, Rudaya N, Kolobova K, Markin S, Krivoshapkin A, Henry AG, Richards MP, Viola B (2021) Dietary evidence from Central Asian Neanderthals: a combined isotope and plant microremains approach at Chagyrskaya Cave (Altai, Russia). *J Hum Evol* 156:102985
- Szwarcz HP, Nahal H (2021) Theoretical and observed C/N ratios in human bone collagen. *J Archaeol Sci* 131:105396
- Sikora M, Seguin-Orlando A, Sousa VC, Albrechtsen A, Korneliusen T, Ko A, Rasmussen S, Dupanloup I, Nigst PR, Bosch MD, Renaud G, Allentoft ME, Margaryan A, Vasilyev SV, Veselovskaya EV, Borutskaya SB, Deviese T, Comeskey D, Higham T, Manica A, Foley R, Meltzer DJ, Nielsen R, Excoffier L, Lahr MM, Orlando L, Willerslev E (2017) Ancient genomes show social and reproductive behavior of early Upper Paleolithic foragers. *Science* 358:659–662
- Soficaru A, Doboş A, Trinkaus E (2006) Early modern humans from the Peştera Muierii, Baia de Fier, Romania. *Proc Natl Acad Sci USA* 103:17196–17201
- Soficaru A, Petrea C, Doboş A, Trinkaus E (2007) The human cranium from the Peştera Cioclovina Uscată, Romania. *Curr Anthropol* 48:611–619
- Spiridonova EA (1991) The vegetation evolution of the Don drainage-basin in the Late Pleistocene and Holocene (Upper Paleolithic – Bronze Age). *Nauka Publ, Moscow* (in Russian with English abstract)
- Szpak P, Gröcke DR, Debruyne R, MacPhee RDE, Guthrie RD, Froese D, Zazula GD, Patterson WP, Poinar HN (2010) Regional differences in bone collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of Pleistocene mammoths: implications for paleoecology of the mammoth steppe. *Palaeogeogr Palaeoclimatol Palaeoecol* 286:88–96
- Soubrier J, Gower G, Chen K, Richards SM, Llamas B, Mitchell KJ, Ho SYW, Kosintsev P, Lee MSY, Baryshnikov G, Bollongino R, Bover P, Burger J, Chivall D, Crégut-Bonnouire E, Decker JE, Doronichev VB, Douka K, Fordham DA, Fontana F, Fritz C, Glimmerveen J, Golovanova LV, Groves C, Guerreschi A, Haak W, Higham T, Hofman-Kamińska E, Immel A, Julien M-A, Krause J, Krotova O, Langbein F, Larson G, Rohrlach A, Scheu A, Schnabel RD, Taylor JF, Tokarska M, Tosello G, van der Plicht J, van Loenen A, Vigne J-D, Wooley O, Orlando L, Kowalczyk R, Shapiro B, Cooper A (2016) Early cave art and ancient DNA record the origin of European bison. *Nature Comm* 7:13158
- Stuart AJ (2021) *Vanished giants: the lost world of the Ice Age*. The Chicago University Press, Chicago & London
- Stuart AJ, Lister AM (2012) Extinction chronology of the woolly rhinoceros *Coelodonta antiquitatis* in the context of late Quaternary megafaunal extinctions in northern Eurasia. *Quat Sci Rev* 51:1–17
- Trinkaus E, Moldovan O, Milota Ş, Bîlgăr A, Sarcina L, Athreya S, Bailey SE, Rodrigo R, Mircea G, Higham T, Bronk Ramsey C, van der Plicht J (2003) An early modern human from the Peştera cu Oase, Romania. *Proc Natl Acad Sci USA* 100:11231–11236
- Trinkaus E, Soficaru A, Doboş A, Constantin S, Zilhão J, Richards M (2009) Stable isotope evidence for early modern human diet in Southeastern Europe: Peştera cu Oase, Peştera Muierii and Peştera Cioclovina Uscată. *Mater Cercet Arheol (ser nouă)* V:5–14
- Trinkaus E, Buzhilova AP, Mednikova MB, Dobrovolskaya MV (eds) (2014) *The people of Sungir: burials, bodies, and behavior in the earlier Upper Paleolithic*. Oxford University Press, New York
- Turner CG II, Ovodov ND, Pavlova OV (2013) *Animal teeth and human tools: a taphonomic odyssey in Ice Age Siberia*. Cambridge University Press, Cambridge
- van Klinken GJ (1999) Bone collagen quality indicators for palaeodietary and radiocarbon measurements. *J Arch Sci* 26:687–695
- Vasil'ev SA, (2003) Faunal exploitation, subsistence practices and Pleistocene extinctions in Paleolithic Siberia. *Deinsea* 9:513–556
- Velichko AA, Vasil'ev SA, Gribchenko YN, Kurenkova EI (2017) Stages of the initial human colonization of Arctic and Subarctic. In: Kotlyakov VM, Velichko AA, Vasil'ev SA (eds) *Human colonization of the Arctic: the interaction between early migration and the paleoenvironment*. Academic Press, London, pp. 507–530
- Wißing C, Rougier H, Crevecoeur I, Germonpré M, Naito YI, Semal P, Bocherens H (2016) Isotopic evidence for dietary ecology of late Neandertals in North-Western Europe. *Quat Int* 411:327–345
- Wißing C, Rougier H, Baumann C, Comeyene A, Crevecoeur I, Drucker DG, Gaudzinski-Windheuser S, Germonpré M, Gómez-Olivencia A, Krause J, Matthies T, Naito YI, Posth C, Semal P, Street M, Bocherens H (2019) Stable isotopes reveal patterns of diet and mobility in the last Neandertals and first modern humans in Europe. *Sci Rep* 9:4433
- Zenin VN (2002) Major stages in the human occupation of West Siberian Plain during the Paleolithic. *Archaeol Ethnol Anthropol Eurasia* 3(4):22–44
- Zubova AV, Stepanov AD, Kuzmin YV (2016) Comparative analysis of a Stone Age human tooth fragment from Khaiyrgas Cave on the Middle Lena (Yakutia, Russian Federation). *Anthrop Sci* 124:135–143

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.