Late Pleistocene chronology and environment of woolly rhinoceros (*Coelodonta antiquitatis* (Blumenbach, 1799)) in Beringia

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ABSTRACT

Uncertain chronology and data scarcity have impeded realistic reconstructions of megafauna extinctions in the Late Pleistocene in several key regions of the Northern Hemisphere such as Beringia. This region was a refuge for several plants, animals during the extremely cold period of the Late Pleistocene in high Arctic latitudes. The woolly rhinoceros was one of the most widespread members of the megafauna in the Asiatic part of the region (West Beringia) between ~60 and 14 cal ka BP. This study is based on statistical analyses of 20 newly obtained and 110 previously published radiocarbon dates. We found three large "waves" in the woolly rhinoceros range changes separated between themselves by the cold climatic Heinrich events (H2 and H4). The chronology of the woolly rhinoceros was overlaid on data of environmental changes obtained basing on 504 generalized early published pollen spectra throughout the species range and, separately, outside the range — in the east of the West Beringia realm and in East Beringia. In general, milder environmental conditions of MIS3 (57–29 ka BP) were more favourable for the woolly rhinoceros than the harsh conditions of the Last Glacial Maximum (~29–15 cal ka BP) in MIS2. We have concluded that the feed base was unlikely the main limiting factor in the distribution of woolly rhinoceros in Western Beringia, and other ecological factors (temperature/precipitation) determined the species range and its oscillation over the MIS3–MIS2 stages. Based on summarizing available data and this research, we have proposed that there were sets of different reasons that prevented the woolly rhinoceros migration to the east of Beringia in different periods of the Late Pleistocene. Abrupt woolly rhinoceros extinction in Beringia between 15 and 14 cal ka BP coincided with the Bölling warming and the Older Dryas cooling. The ecological situation just before the extinction, associated with climate warming, moisture increasing and shrub tundra expansion in West Beringia, was qualitatively different from previous cases of the species range degradations in the second half of the Late Pleistocene. This multi-proxy study of woolly rhinoceros chronology provide a new basis for further understanding of its population history, demography, and biology in Beringia before its extinction.

1. Introduction

The woolly rhinoceros *Coelodonta antiquitatis* is one of the largest representations of megaherbivorous mammals of the "*Mammuthus–Coelodonta*" mammalian assemblage in the Late Pleistocene of Eurasia (Kahlke, 2014).

A probable region of origin of the woolly rhinoceros genus is usually placed in the west of the modern Tibetan plateau. In the

Middle Pliocene, of about 3.7 million years ago, an early representative of the genus *C. thibetana* — lived there in a mountainous steppe landscape (Deng et al., 2011). Paleontological evidence of the subsequent expansion of woolly rhinoceros across Asia is preserved in the paleontological records of China, Mongolia, Transbaikalian region and Western Siberia (Teilhard de Chardin, and Piveteau, 1930; Chow and Chow, 1959; Kahlke, 1969; Li, 1984; Zheng and Cai, 1991; Foronova, 1999; Deng et al., 2011). In the Middle Pleistocene (Chibanian stage), of about 460 thousand years ago (MIS 12), rhinos close to *C. tologoijensis* Beliajeva, 1966, appeared in Western Europe (Kahlke and Lacombat, 2008). In Northeast Asia, woolly rhinoceros were probably absent up until

the Middle Pleistocene (Sher, 1971; Lazarev, 2005; Kahlke and Lacombat, 2008). In the Late Pleistocene, this species was widespread in Eurasia (Fig. 1A) from the Iberian Peninsula and the British Isles to Chukotka and the Kamchatka Peninsula (Stuart and Lister, 2012; Markova et al., 2013).

During the majority of the Late Pleistocene (MIS4−MIS2, 71−11.7 ka BP), woolly rhinoceros was an important species in cold adapted mammalian assemblage ("mammoth steppe" fauna) of northern Eurasia. At the end of the Late Pleistocene, the Eurasian range of the species probably disintegrated into several isolates, and then woolly rhinoceros became extinct between 15,000 and 10,000 cal yr BP. According to Stuart and Lister (2012) the species probably became extinct at about 14 cal ka BP, but this process was gradual and asynchronous across its entire range from about 35 cal ka BP (MIS3). The authors believed that "… the dynamics of range change in the woolly rhinoceros, in the millennia leading to its extinction, appear to relate largely to climatic and/or vegetational changes. Final extinction probably correlates with the widespread Late Glacial change to shrubs and trees at the expense of grasses and herbs".

The last optimum for that species in the European part of its range dates back to the Denekamp (= Bryansk) meagainterstadial (MIS3, ~37.4−29 cal ka BP) in Europe. The significant reduction of the range occurred during the Last Glacial Maximum (Greenland Stadial 2, GS2, ~23.2−14.7 cal ka BP) when the environmental conditions were probably particularly unsuitable for the woolly rhinoceros in most parts of Europe. After GS2 the range began to restore partly, but the species practically disappeared from Europe as early as the Bølling and Allerød interstadials (Greenland Interstadial 1, GS1, ~14.7−12.9 cal ka BP) (Markova et al., 2013). The youngest remains of the species were found in: Europe (Wilczyce, median − 13,250, 2σ range −13,540−13,010 cal yr BP, Ua-15720 (Irish et al., 2008)), the Urals (Lobvinskaya cave, 10,820, 11,610−10,190, IERZ=IPAE-92 (Kosintsev, 1995, 2007)), Western
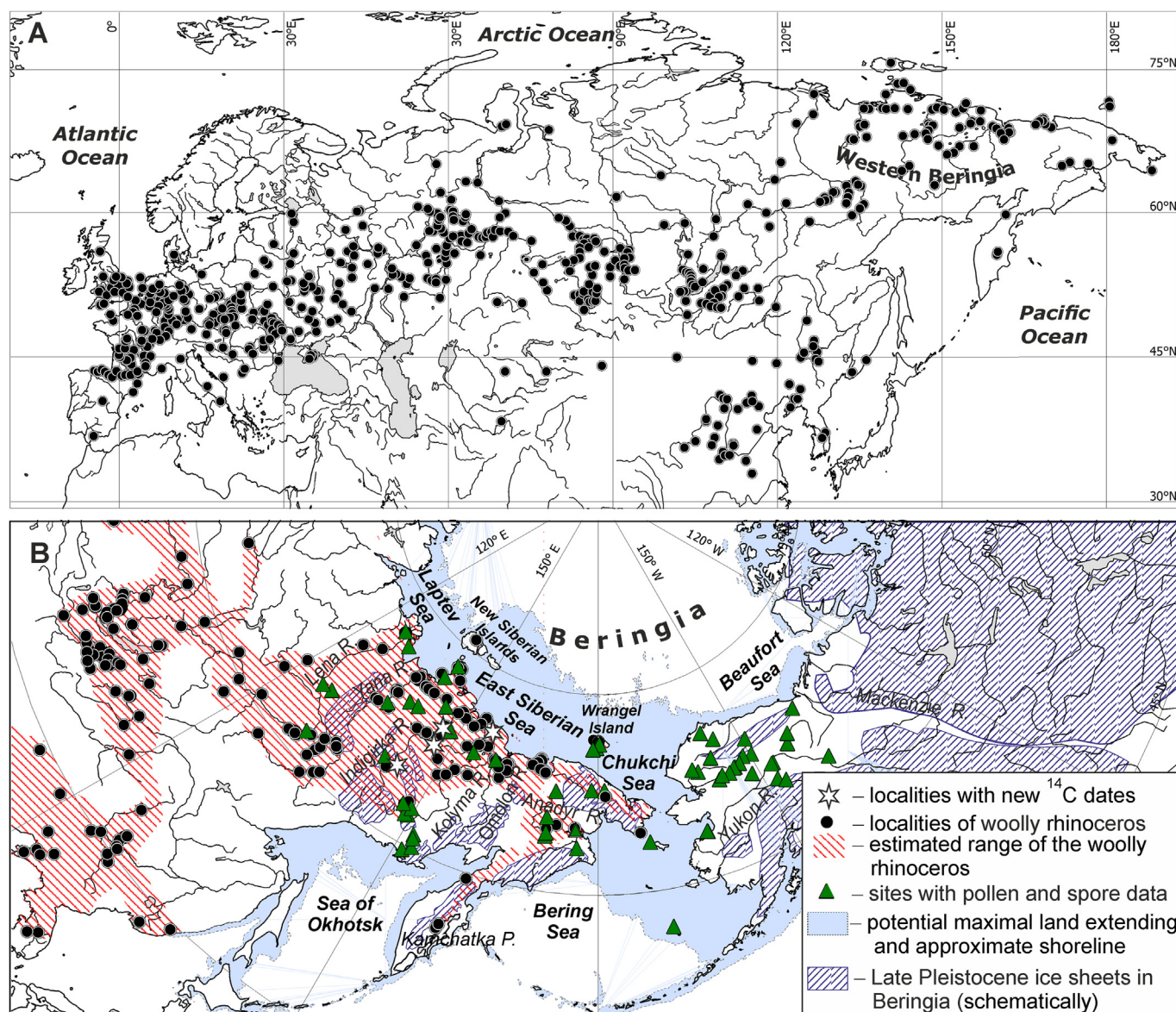

Fig. 1. The Late Pleistocene woolly rhinoceros localities. A − Eurasia, B − North-Eastern Asia, included West Beringia: ★ − localities with new radiocarbon dates. The sites with spore and pollen data used in this work are mapped as green triangles. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Siberia (Lugovskoe, 12,660, 13,182−11,990 cal yr BP, SOAN-4757 (Kuzmin, 2010)), Eastern Siberia (Lena R. − Amga R. interfluve, 14,040, 14,180−13,880 cal yr BP, AAR-11027/OxA-18602 (Stuart and Lister, 2012)).

The Western Beringia region (Fig. 1A) was probably the most stable part of the woolly rhinoceros range in MIS3-MIS2 (Stuart and Lister, 2012). A recent study (Lord et al., 2020) has shown relatively high genomic diversity and most likely stable population size of the woolly rhinoceros from this region prior to extinction. A diversification between mitochondrial clades 1 and 2 was proposed within the wide time range 440−116 ka BP (the Middle Pleistocene − the Early Late Pleistocene), and within clade 1−326−91 ka BP and 86−22 ka BP (MIS4−MIS2).

In our previous study (Puzachenko et al., 2019) of 69 well preserved woolly rhinoceros skulls from the Yana, Indigirka and Kolyma Rivers basins, two size groups were identified based on the result of multivariate morphometric analysis. A statistically significant morphological heterogeneity of the samples of both males and females separately was inferred from specimens variability in a general skull size (length and width); and these differences were not associated with animals' age variations. Based on a few available ^{14}C dates for this selection we assumed its age was mainly within the MIS3 and the beginning of the MIS2 (~50−27 cal ka BP). Notably, the larger skulls usually had a greater age, more often >40 ka BP, than the smaller ones. Contrary to the hypothesis of population stability, these preliminary results suggested the possibility of some dynamics of the woolly rhinoceros numbers in the region in the second half of the Late Pleistocene.

Thus, studying woolly rhinoceros population dynamics in Beringia is of great importance for understanding its population history and its ecological tolerance. In addition, it may shed light on the mystery of the absence of the species in North America (eastern part of Beringia) in the Late Pleistocene in contrast to the other representatives of regional mammals assemblages (woolly mammoth, cave lion, musk ox, wapiti, caribou, saiga antelope and other) (Garutt et al., 1970; Elias and Crocker, 2008; Stuart and Lister, 2012).

In the last decades, many new radiocarbon dates of woolly rhinoceros remains were obtained from the basins of the Yana, Indigirka and Kolyma Rivers and from adjacent territories of Beringia. In addition, rich palynological data throughout Beringia (Fig. 1B) were collected (Ager and Phillips, 2008; Anderson and Lozhkin, 2001, 2015). All these records allow the reconstruction of an outline of palaeoenvironmental conditions for woolly rhinoceros range in Western Beringia and beyond its range in Eastern Beringia (Anderson and Brubaker, 1994; Sher et al., 2005; Zazula et al., 2006a,b; Elias and Crocker, 2008; Blinnikov et al., 2011).

To add to the woolly rhinoceros chronology we have produced a set of 20 radiocarbon dates for skulls and other remains from "National Alliance of Shidlovskiy" collection (Russia). We have also collated 110 previously published direct finite radiocarbon dates of woolly rhinoceros remains from Western Beringia.

2. Regional setting

2.1. Beringia

There are different geographical interpretations of Beringia in a broad sense (Mathis, 1986; Kozhevnikov and Zheleznov-Chukotsky, 1995, 2014, 2014; Buks, 1976; Sher, 1976). According to many authors, Beringia extends from Taymyr Peninsula to Canadian Arctic Archipelago and includes the drained shelves of the Northern Seas east of Taymyr Peninsula. According to Yu.P. Kozhevnikov, to the south Beringia includes the entire territory of Alaska to the lower coastline of the Aleutian Ridge, the Kuril Islands, the Kamchatka Peninsula, up to Lopatka Cape with the adjacent islands, Sakhalin Island, Japan Islands, the Korean Peninsula, Primorye and Khabarovsk regions (the Russia Far East) and even the Baikal Lake region.

In this study, the concept of Beringia is used in a narrow sense. Beringia (*sensu stricto*) is the name (after Russian zoologist P.P. Sushkin (1925) and Swedish botanist E. Hult (1937)) of the geographical region extending approximately between 130°W and 125°E, and from 53°N to 75°N from the Verkhoiansk Ridge (part of Lena River watershed) in eastern Siberia east to the Mackenzie River in north-western Canada (Edwards et al., 2000; Sher et al., 2005; Elias and Brigham-Grette, 2007) (Fig. 1B).

During the periods of low sea level associated with glacial cycles in the Pleistocene, the shallow shelf of the East Siberian Sea, the Chukchi Sea, the Bering Sea, the Bering Strait between Chukotka and Alaska, and the shelf of the Sea of Okhotsk was a part of the Beringia land (Sushkin, 1925; Hopkins, 1973; McManus, Creager, 1984; Elias and Crocker, 2008).

The main modern spatial pattern of zonal vegetation (arctic deserts, tundra, and taiga) in Siberia correlates with variation of precipitation value and sum of positive temperatures during growing season (Ukraintseva, 2020). Both past and modern arctic and subarctic climate and vegetation cover in Beringia vary considerably both in time and from east to west and from north to south (Matthews, 1970; Anderson et al., 1994; Edwards et al., 2000; Elias, 2000; Anderson and Lozhkin, 2001, 2005, 2005; Lozhkin et al., 2001, 2019; Repenning, 2001; Yurtsev, 2001; Walker et al., 2001; Brigham-Grette et al., 2004; Kienast et al., 2005; Zazula et al., 2006a,b; Kurek et al., 2009; Anderson and Lozhkin, 2011; Berman et al., 2011; Blinnikov et al., 2011; Lozhkin and Anderson, 2011; Lorenzen et al., 2011; Kuzmina et al., 2011; Zech et al., 2011; Wooller et al., 2011; Andreev et al., 2012; Rabassa and Ponce, 2013 Willerslev et al., 2014; Binney et al., 2017; Wang et al., 2017; Ashastina et al., 2018).

Summarizing the data from literary sources, we can conclude that long special interest of researchers in the Beringia region arose for several basic reasons.

This region was a refuge of several plants, animals and overall biodiversity during extremely cold period of the Pleistocene in high Arctic latitudes region. Several studies have described the specific variant of the Pleistocene cold- and dry-adapted vegetation cover (mammoth steppe or steppe-tundra/tundra-steppe (Yurtsev, 2001)) in Beringia capable of supporting a high faunal diversity including megaherbivorous (woolly mammoth, woolly rhinoceros, bison, musk ox), carnivores (cave lion, short-faced bear, wolf) and many other large and small vertebrate and invertebrate consumers in a food chain (Ukraintseva, 1981, 2002, 2002; Tomskaya, 2000; Hofreiter and Stewart, 2009; Dale Guthrie, 2001; Sher et al., 2005; Kuzmina et al., 2011; Yeakel et al., 2013; Mann et al., 2013, 2015, 2019, 2015; Haas et al., 2020; Neretina et al., 2020). The unexpected combination of the harsh climate in the Arctic and Subarctic during the late glaciation with paleontological evidence of high diversity of plants and animals was named a "Productivity paradox" (Hopkins et al., 1982; Zhu et al., 2018). Researchers' attention was attracted to the two basic topics: the ecological reasons for high biological diversity and relatively rapid extinction (mainly megafauna) of species in the end of the Late Pleistocene − Early Holocene in Beringia.

Beringia and, in a narrow sense, the Bering Isthmus (bridge) between Asia and North America were an important both refuge and pathway for flora and fauna interchange between the Old World and New World numerous times in the past (Sher, 1999; Campos et al., 2010a, 2010b, 2010b; Stuart and Lister, 2011; Meiri et al., 2014; Lister and Sher, 2015; Ersmark et al., 2015; Graham, 2018; Jiang et al., 2019). Beringia probably played a key role in the dispersal of humans to North America at the end of the Late

Pleistocene (Hoffecker et al., 2016, 2020, 2020; Graf and Buvit, 2017).

And finally, because of this region position at high northern latitudes, the biosphere responses to global climate change, and especially warming, are expected to be significant during the 21st century (Edwards et al., 2005).

2.2. Woolly rhinoceros in Beringia

The woolly rhinoceros was one of the most widespread and prominent members of the Pleistocene megafauna assemblage of Western Beringia (Pereladov end Shpansky, 1997; Garrut, and Boeskorov, 2001; Boeskorov, 2005; Lazarev, 2005; Boeskorov et al., 2011). However, the remains of the species occur less frequently in comparison, for example, with the woolly mammoth. This is not a surprise because if we compare woolly rhinoceros and woolly mammoth, it turns out that the Eurasian range of the first species was smaller (Stuart and Lister, 2012; Markova et al., 2013; Puzachenko et al., 2016). Unlike the woolly mammoth, the woolly rhinoceros was a solitary animal, or formed small family groups (perhaps 10−15 animals by analogy with the African white rhinoceros (*Ceratotherium simum*)), and its population density was lower, respectively (Garrut, 1998).

The timing of the woolly rhinoceros in Beringia is not established reliably (Sher, 1971; Kahlke and Lacombat, 2008). Its continuing presence in the Late Pleistocene was confirmed, at least for isotope stages MIS3−MIS2 (~60−14 cal ka BP) (Boeskorov, 2005; Lazarev, 2005). The majority of woolly rhinoceros remains were found on the Yana−Indigirka− Kolyma lowland (Fig. 1B). The northern border of the species range reached up to ~75.77°N (Kotelny Island, the New Siberian Islands archipelago) (Plotnikov and Mashchenko, 2020). Remains of woolly rhinoceros are extremely rare on the Chukchi Peninsula and the Kamchatka Peninsula. So far, there is no reliable evidence for rhinoceros remains in Eastern Beringia (Alaska). It is most likely that the range of species was limited to the Western Beringia region only.

3. Material and methods

3.1. Radiocarbon analysis

We generated 20 new radiocarbon dates of woolly rhinoceros specimens, of which 19 at the Centre of Accelerator Science at ANSTO, Australia (OZ) and one new date was produced at the Institute of Geography, Russian Academy of Sciences, Russia (IGAN). All samples came from the Yana-Indigirka-Kolyma lowland (Western Beringia). Bone samples were pretreated following the ultrafiltration protocol (Higham et al., 2006; Bronk Ramsey et al., 2004; Brown et al., 1988) to extract clean non-degraded collagen for radiocarbon dating. Before extraction, tests were performed to determine the degree of bone preservation and suitability of the extracted collagen (or gelatine) for dating. These results are presented in the Table 1, and the list of localities − in Supplementary data Table A1.

Collagen yield was determined to be >10% for most samples with only three samples between 10 and 4%, which overall indicates an excellent quality collagen.

C/N ratios of collagen range between 2.9 and 3.5 are usually based on numerous studies (primarily DeNiro (1985)) that have investigated the use of C/N ratios as a tool to detect the contamination of collagen. The C/N ratios of the collagen extracted from studied samples were in the range 3.2−3.4 (Table 1). This indicates that the collagen was well preserved and suitable for dating and that contaminants have been effectively removed. At ANSTO elemental and stable isotopes ratios were determined on EA-IRMS

(Elementar varioMICRO CUBE coupled to a Micromass Isoprime). Isotopic measurements of samples prepared at IGRAS were done on Elementar varioMICRO Cube (Elementar, Germany) coupled to an Isoprime PrecisION IRMS (Isoprime, Switzerland).

Once the collagen had been extracted, the ANSTO samples were processed to graphite in the AMS chemistry laboratories (Hua et al., 2000) and consequently measured for radiocarbon on VEGA AMS installation (Wilcken et al., 2015). At IGRAS Radiocarbon Laboratory graphitization and pressing of the target for ^{14}C AMS were conducted with the automated graphitization system AGE 3 (Wacker et al., 2010). ^{14}C AMS measurement was performed at the Center for Applied Isotope Studies, University of Georgia (Athens, USA) using the CAIS 0.5 MeV accelerator mass spectrometer. The sample ratios at ANSTO were normalized on Ox I standard ratio and at IGRAS on the Oxalic acid II (NBS SRM 4990C) standard measured together with unknowns. Blanks (radiocarbon free samples) were processed together with unknowns, and all measurements were corrected to that.

The quoted uncalibrated dates are given in conventional ^{14}C years before AD 1950 using the ^{14}C half-life of 5568 years. The error is quoted as one standard deviation and reflects both statistical and experimental errors. Calibration in OxCal 4.4 software was made using both the InCal13 and IntCal20 calibration curves (Bronk Ramsey and Lee, 2013; Reimer et al., 2013, 2020). The IntCal13 curve was used in most cases, since about half of the pollen spectra used in this work had only calibrated dates, which were calibrated, used previous calibration curves (IntCal13/IntCal09) and therefore could not be recalculated. The dates calibrated using the new IntCal20 curve are shown separately in the Table 1 and in the Supplementary data Table A2. The correlation between dates calibrated by IntCal13 and IntCal20 is 0.999 for 14,000−45,000 cal yr BP time interval.

3.2. Early published radiocarbon dates

The previously published 110 radiocarbon dates of woolly rhinoceros remains from Western Beringia and adjacent areas are listed in Supplementary data Table A2 (Lazarev and Tirskaya, 1975; Mochanov, 1977; Sulerzhitsky, 1997; Sulerzhitsky and Romanenko, 1997; Orlova et al., 2004; Pitulko et al., 2004, 2014; Sher et al., 2005; Vartanyan et al., 2008; Boeskorov et al., 2011, 2016; Lorenzen et al., 2011; Stuart and Lister, 2012; Kuzmin, 2013; Plotnikov, 2014; Lord et al., 2020).

3.3. Chronology

The woolly rhinoceros remains from the studied selection have no definite associations with any stratigraphic layer in most cases, with the exception of few stratified localities. The sample is mainly represented by scattered finds from various alluvial loose icy sediments of the regional large river basins. Therefore, we were not able to perform Bayesian analysis of radiocarbon dates.

Instead, we considered the following statistical hypotheses about the dates' distribution: 1) dates are distributed according to uniform (rectangular) distribution (null hypothesis), 2) the dates are not distributed uniformly, but the distribution can be reproduced by one or more normal (Gaussian) distributions ("mixture" model) (Gridgeman, 1970). If the null hypothesis is not rejected, it can be assumed that there is no indication of any temporal pattern, or that the chronology is consistent with the genetic model conclusion about population stability (Lord et al., 2020). We tested the null hypothesis using Kolmogorov-Smirnov test. The Anderson-Darling goodness-of-fit test (Anderson and Darling, 1954) was used to compare the sample dates' distribution with the modelled "mixture" distributions.

Table 1
New ^{14}C dating of woolly rhinoceros remains from Western Beringia (collection of F. Shidlovskiy).

##	Lab. code	ID	Material	Collagen %	Atomic C/N ratio	δ(^{13}C) per mil	Modern carbon, % pMC	Conventional ^{14}C age	Mean IntCal13	95.4% IntCal13	Mean IntCal20	95.4% IntCal20
		Skull										
	OZU324	F-39	Petrosum	11.8	3.4	−19.2 ± 0.1	5.34 ± 0.09	23,530 ± 140	27,670 ± 110	27,900−27,440	27,670 ± 140	27,890−27,360
	OZU325	F-41	tooth root	14.6	3.2	−19.9 ± 0.1	0.78 ± 0.03	38,960 ± 260	42,830 ± 200	43,240−42,430	42,620 ± 120	42,870−42,380
	OZU327	F-64	tooth root	11.5	3.4	−19.6 ± 0.1	3.00 ± 0.06	28,160 ± 170	32,010 ± 310	32,620−31,460	32,270 ± 350	32,940−31,720
	OZU328	F-65	petrosum	8.9	3.3	−20.0 ± 0.1	2.45 ± 0.04	29,810 ± 140	33,930 ± 130	34,200−33,660	34,330 ± 130	34,580−34,070
	OZU332	F-377	petrosum	4.7	3.4	−20.4 ± 0.1	0.53 ± 0.02	42,050 ± 380	45,400 ± 350	46,120−447,00	44,810 ± 290	45,440−44,280
	OZU333	F-379	tooth root	14.7	3.2	−20.3 ± 0.1	1.82 ± 0.05	32,200 ± 210	36,090 ± 240	36,550−35,600	36,550 ± 230	37,000−36,140
	OZU334	F-390	tooth root	15.1	3.3	−19.7 ± 0.1	0.48 ± 0.03	42,810 ± 420	46,070 ± 430	46,970−45,240	45,320 ± 360	46,000−44,650
	OZU335	F-391	tooth root	13.1	3.3	−19.8 ± 0.1	0.38 ± 0.03	44,860 ± 580	48,250 ± 720	49,690−46,870	47,200 ± 660	48,450−45,990
	OZU336	F-392	tooth root	13.8	3.2	−19.2 ± 0.1	0.79 ± 0.04	38,850 ± 410	42,790 ± 300	43,400−42,190	42,600 ± 180	42,960−42,260
	OZU337	F-393	tooth root	16.0	3.2	−20.3 ± 0.1	0.43 ± 0.06	43,700 ± 1100	47,240 ± 1120	49,580−45,260	46,470 ± 1160	48,730−44,500
	OZU338	F-531	petrosum	7.7	3.3	−20.6 ± 0.2	0.97 ± 0.03	37,250 ± 240	41,750 ± 200	42,140−41,340	41,960 ± 160	42,250−41,590
	OZU339	F-1084	Zygoma	13.1	3.3	−19.3 ± 0.1	2.32 ± 0.04	30,220 ± 130	34,240 ± 160	34,570−33,940	34,620 ± 170	35,060−34,330
	OZU340	F-2292	zygoma	17.2	3.4	−19.5 ± 0.1	0.52 ± 0.03	42,300 ± 500	45,640 ± 470	46,610−44,720	45,020 ± 380	45,840−44,350
	OZU343	F-3773	tooth root	16.2	3.3	−20.2 ± 0.1	0.36 ± 0.05	45,100 ± 1100	48,320 ± 960	−46,610	47,800 ± 1400	50,760−45,350
		Mandible										
	IGAN6917	F-509	tooth root	14.9	3.3	−19,6 ± 0.2	0,75 ± 0.03	39,500 ± 180	43,190 ± 190	43,580−42,810	42,840 ± 110	43,060−42,610
	OZU329	F-222	bone	13.3	3.2	−20.0 ± 0.1	2.74 ± 0.04	28,900 ± 120	33,110 ± 200	33,520−32,710	33,400 ± 230	33,850−32,990
		Scapula										
	OZU274	F- n/n	bone	−	−	−20.2 ± 0.1	1.16 ± 0.03	35,810 ± 120	40,440 ± 210	40,870−40,040	40,940 ± 140	41,210−40,650
		Keratin derivate of the horn										
	OZU326	F-55	horn	74.3	−	−24.2 ± 0.1	0.76 ± 0.03	39,150 ± 190	42,950 ± 170	43,290−42,610	42,690 ± 100	42,900−42,480
	OZU330	F-371	horn	84.8	−	−34.5 ± 0.1	1.54 ± 0.04	33,530 ± 320	37,810 ± 490	38,660−36,820	38,370 ± 540	39,330−37,350
	OZU331	F-372	horn	86.9	−	−23.8 ± 0.1	0.46 ± 0.02	43,280 ± 420	46,510 ± 480	47,520−45,610	45,680 ± 410	46,570−44,870

We aggregated the sample of 130 dates (14,040−50,094 cal yr BP) within 31 steps of about one thousand years each to present the distribution in a discrete form.

3.4. Palynology

The objectives of this work do not include the reconstruction of vegetation cover in Beringia for the times when woolly rhinoceros lived. We used pollen spectra as a data proxy of changes in the environment that surrounded rhinoceroses and beyond the species range. For this, we aggregated (averaging) data from the set of different sections on the scale close to the time scale adopted for the rhinoceros. In addition, we narrowed consideration only to the most common taxa of plants, which were found in most sections in significant quantities.

Our list includes 504 pollen spectra yielded from 62 sites (Fig. 1B, Supplementary data Table A3). The "Neotoma Paleoecology database" (https://apps.neotomadb.org/explorer/) was the main source of data. The rest of the spectra we took from publications (Matthews, 1970; Andreev et al., 2011; Zazula et al., 2006a,b; Lozhkin et al., 2007, 2019, 2019; Wetterich et al., 2008).

The list of variables for any spectrum includes frequencies of pollen/spores of "trees and shrubs", "herbs", "forbs", "spore", *Pinus* (Western Beringia), *Picea* (Eastern Beringia), *Betula*, *Alnus/Duschekia*, *Salix*, *Artemisia*, Cyperaceae, Poaceae, *Sphagnum*, and *Selaginella*. Arcsine transformation (Sokal and Rohlf, 1995) of the frequencies was used to "normalize" their distribution. In the next step, the variables were standardized to eliminate differences in pollen/spore production among different plant groups. Then, the chord metric was utilised for calculation of pairwise "distances" between all time scale intervals. The chord distance is Euclidean distance between normalized vectors, which is commonly used for abundance data and in particular in pollen analysis (Gavin et al., 2003). The matrix was then processed by non-metric multidimensional scaling (Kruskal, 1964). The modelled multidimensional Euclidean space was used for representation of time intervals, according to their dissimilarity. In each case, an "optimal" dimensionality of the space was estimated using Kruskal's stress values (Kruskal, 1964; Abramov et al., 2012). A good model should well reproduce variations of row variables (relative occurrence of pollen of *Salix*, *Artemisia*, Cyperaceae, etc.) and, also, correlate well with the "generalized" variables − "trees and shrubs", "herbs", "forbs", "spore", which were not included in multivariate analyses. The coordinates of multivariate models calculated for subsets of pollen spectra yielded from woolly rhinoceroses range and out of its range − Asiatic part of Beringia where rhinos were not found, and Eastern Beringia. The coordinates describe, by default, main temporal environmental patterns, which are invariants with respect to any spatial variations of initial data. An optimal dimensionality was three for all three models. Here we labelled spatial invariants as Chord-1, Chord-2, and Chord-3.

3.5. Climatic variables

We used time series of North Greenland Ice Core Project (NGRIP) oxygen isotope data (Andersen et al., 2004; Svensson et al., 2008; Rasmussen et al., 2014) as the reference climatic (temperature) variable. In this work, we attempted a detailed comparison of three time series: the distribution of dates of woolly rhinoceros remains, the spatial invariant Chord-1, and the values of δ^{18}O (‰). The common abbreviations of Greenland Stadials (GS) and Interstadials (GI) were used (Rasmussen et al., 2014). The positions of cold Heinrich events (H5−H1) on the time scale were done according to Hemming (2004). In addition, we considered the reconstruction of insolation variation at 60°N in June (Berger and Loutre, 1991).

The statistical analyses were carried out with STATISTICA v. 8.0 (StatSoft, Tulsa, OK, USA), PAST v. 3.12 (Hammer et al., 2001), and NCSS 12 Statistical Software (ncss.com/software/ncss).

4. Results

4.1. Woolly rhinoceros chronology in Beringia

The statistical tests of hypotheses of distributions type of dates

allowed us to reject confidently the uniform distribution model as well as the mixture models with one or two Gaussian distributions (Table 2). The mixed model with three Gaussian distributions has significant statistical support. Based on this decision, we have identified three main chronological stages in the history of the woolly rhinoceros in Beringia between 51 and 14 cal ka BP (Fig. 2).

The species ranges in stages I–III were approximately equal (Fig. 3). The inter-stage intervals were very short, but well pronounced. The interval between stage I and II is most continuous — about 1800 years. The interval between stage II and III was shorter; it was no more than 1000 years. The very large standard deviation value of the youngest date attributed to stage III (Wrangel Is., 39,829 ± 1266 cal yr BP, LE-5276) does not give a basis for hypothesis about species extinction during cold H4 event. One can only assume a very significant range reduction in Beringia.

4.2. Environmental changes in Beringia

The averaged pollen spectra are characterized by the environmental conditions within the woolly rhinoceros range and beyond. Three multidimensional NMDS models (labelled here as model I, II, and III) describe variations of most plant variables (except frequencies of willows pollen abundances), which directly flow from values of the correlation coefficients between variables and the spatial invariants (Chord-1–3) given in Table 3. The spatial invariants describe the integral variables (trees and shrubs, herbs, forbs, spore) despite the fact that they were not taken into account in the models calculation. This is the expected result, confirming the correctness of the models, since the data on the most abundantly represented taxa were used.

The basic spatial invariant Chord-1 describes the main temporal pattern of trees and shrubs and herbs pollen abundances in all cases (models I–III, Table 3), pollen of forbs out of the woolly rhinoceros range (models II and III), and spores in Eastern Beringia (model III). In addition, Chord-1 correlates with the most variables included in models (Table 3). The Chord-2 correlates with the pollen occurrence of sagebrush, sedges, forbs and grasses (model I), spore and sedges with willows in part (model II), and only sedges in model III (Eastern Beringia). The last invariant Chord-3 shows the correlation with sum of spore, pollen of pine (Siberian dwarf pine (*Pinus pumila*) mostly), *Alnus/Duschekia*, and spores of spikemosses (*Selaginella*) within the rhino's range. In the model II (Table 3), the invariant describes the main temporal variations of spore sum, and in the model III — pollen of spruce.

The invariants of models I–III are shown at the Fig. 4 (A, C, and E) as time series. In general, the models I and II reproduce more complex environmental dynamics in Western Beringia than in its eastern part during the Karga = Middle Wisconsinan (MIS3) and the Sartan = Late Wisconsinan (MIS2).

However, firstly we want to note the asynchronous dynamics of environmental conditions in Western and Eastern Beringia. In the east of the region it is not possible to distinguish periods of warming and subsequent cooling within the interval of 40–23 cal ka BP (MIS3–MIS2). In Western Beringia on the contrary, these

stages and an extremely cold period of maximum cooling (Late Glacial Maximum) are clearly marked by the dynamics of the Chord-1 spatial invariant. Secondly, the steady climate warming in the second half of the Late Wisconsinan time began much earlier (between 25 and 20 cal ka BP) in Eastern Beringia as compared to Western Beringia (20–15 cal ka BP). This is supported by the comparison of averaged spectra of trees and shrubs pollen and spore in Western and Eastern Beringia (Fig. 4B, D, and 4E). The median values of the most palynomorph variables differ significantly between Western and Eastern parts of Beringia (Table 4).

Within the range of rhinoceros, on average, the pollen in the spectra of birches, willows, and *Artemisia* are less, and pollen of *Alnus* is more pronounced than that of East Beringia. In addition, once again, we note the very sporadic occurrence or rather practical absence of spruce pollen in the rhinoceros' range and in Western Beringia overall and the similar almost complete absence of pine pollen in Eastern Beringia.

An estimate of size and, especially, boundaries of the range is highly speculative in cases of extinct species. The remains of woolly rhinoceros have not yet been found in most of the Chukchi Peninsula and in the area adjacent to the Bering Sea and Sea of Okhotsk coasts (Fig. 1). We know about only two sites on the peninsula: undated — 67.65°N, −178.79°E, Rogatyi creek (Ekityki R. basin) (Pereladov end Shpansky, 1997) and with infinite date − ~64.245°N, −73.108°E, Chukotskiy Nos Cape = Chukotskiy Mys (?) (Lorenzen et al., 2011). The conditions in this mountainous area were less favourable for both burial and preservation of large animal remains than on the coastal arctic lowlands. For example, most of the Chukchi Peninsula is occupied by highlands usually up to 1000 m above sea level; however, the Koryak Highlands vary from 600 to 1800 m above sea level. The last factor possibly affecting the likelihood of finding remains is a low human population density in these regions. So far, we only assume that the northeastern edge of Asia and coastal areas were at least unfavourable for the rhinoceros during MIS3–MIS2 stages.

The main temporal patterns (Chord-1 invariants) are approximately the same within the species range and beyond it (Fig. 4A and C). We found significant differences between them in the variations of second and third invariants (Chord-2 and Chord-3). For the woolly rhinoceros range, the Chord-2 invariant describes changes in pollen compositions of *Artemisia*, Poaceae (negative correlation) and Cyperaceae (positive correlation) and, forbs (negative correlation) (Table 3). For example, the proportion of pollen of *Artemisia* and Poaceae decreased, while the proportion of Cyperaceae pollen increased in the interval of ~50–38 cal ka BP. On the contrary, starting from the second half of the Karga interstadial and up to ~16 cal ka BP, the proportions of *Artemisia* and Poaceae pollen increased "steadily". In ecological sense, these trends are adequately interpreted within the context of well-known changes in aridity and mean annual temperature in the second half of the Late Pleistocene.

The Chord-2 spatial invariant is a complex virtual variable, describing the dynamics of changes partly of a proportion of spores, and partly of several other variables (Table 3) in the spectra obtained outside the rhino's range. The dynamics of herbs and forbs pollen occurrences predictably negatively correlates with the proportion of tree and shrub pollen, and it is reproduced by the first invariant of the model, respectively (Table 3).

The dominance of tree and shrub pollen between ~42 and ~32 cal ka BP is clearly distinguished at Fig. 4D. A slight increase in the proportion of tree and shrub pollen occurred approximately within the time interval in the woolly rhinoceros range, but it was much less pronounced. The relative and slight dominance of tree and shrub pollen over herb pollen was a short-term occurrence at the end of the Karginian time (Fig. 4B).

Table 2
Kolmogorov- Smirnov test (d) and Anderson-Darling goodness-of-fit test (A^2) for modelled distributions of 130 direct calibrated dates of woolly rhinoceros remains from Western Beringia.

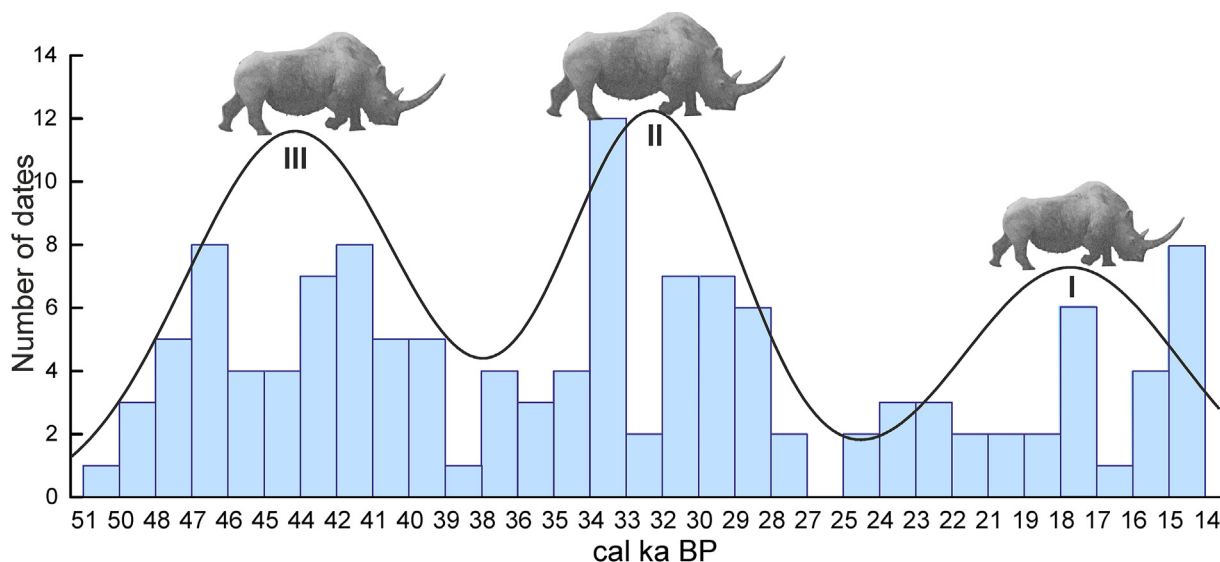| Model of distribution	d	A^2	p	Decision
Uniform	0.14		<0.05	Rejected
Normal		1.979	0.094	Rejected
Gaussian Mixture, 2 mixtures		0.852	0.444	Rejected
Gaussian Mixture, 3 mixtures		0.242	0.974	Accepted

Fig. 2. The distribution of calibrated dates of the woolly rhinoceros remains from Western Beringia. I, II, and III are the modelled Gaussian distributions in the mixture model. The stage I spanned interval from 25 to 14 cal ka BP. Stage II covers the period between 38 and 27 cal ka BP (MIS3, the second part of the Karga or Molotkov (Shilo, 1987) interstadial = Middle Wisconsinan). The oldest stage III is determined ~51−39 cal ka BP (MIS3, the first part of the Karga interstadial (Shilo, 1987) = Middle Wisconsinan).

The Chord-3 invariants in both models I and II correlate with a proportion of spores: within the woolly rhinoceros range (model I) − with the abundance of *Selaginella* spores, and outside the range (model II) − with the abundance of spores of ferns and mosses that we did not include in the model (Table 3).

In model I, an increase in the abundance of spores positively correlates with the abundance of *Pinus* pollen and negatively − with the relative abundance of *Alnus/Duschekia* pollen. Outside of the species range, the occurrence of pollen of Siberian dwarf pine (*P. pumila*) is described by the first spatial invariant of the model II (Table 3). This means that refuge of this species was located in the region of the Sea of Okhotsk during the MIS3−MIS2 period and suggests (more details see in (Andersen and Lozkin, 2010)) the relatively high snow cover and a shorter growing season because of lower summer temperatures in *P. pumila* refuges. Thus, the conditions that were favourable for the survival of the Siberian dwarf pine were obviously not favourable for the relatively short-legged grazer such as woolly rhinoceros.

Statistically significant differences between the medians of the averaged pollen spectra from the rhinoceros range and outside of it in West Beringia is marked with an asterisk in the Table 4. There are relatively high proportions of herb pollen, in general, and, in particular, pollen of sedges and grasses within the species range. Comparatively, the proportion of pine pollen is significantly higher outside the range. No statistically significant differences were found for the rest of the variables.

4.3. The woolly rhinoceros chronology and environmental dynamics in Beringia

The initial data (radiocarbon dates of woolly rhinoceros remains and the spore pollen spectra) do not allow constructing equivalent uniform/homogeneous time scales for both rhinoceros and spatial environmental invariants (Chord-1− Chord-3). The biases are due to uneven distribution of dates within the unit of the scale that we adopted for the rhinoceros (~1000 cal yr). In addition, the standard deviation values of radiocarbon dates themselves grow nonlinearly with age (Puzachenko and Markova, 2019), which can make an additional contribution to the bias. Potentially, the total bias would

be reduced as new data is added in the future. Under these limitations, the visual matching is the most "unbiased" method of coupled analysis of the rhino' dates distribution and the environmental variable (the first spatial invariant − Chord-1, model I) with the reference climate variable of NGRIP series. The result of combining of different time series is shown at Fig. 5.

Phase I of the woolly rhinoceros chronology falls entirely within the coldest climatic stage of the Late Pleistocene, corresponding to MIS2 and the Late Glacial Maximum. The start of the phase I is most likely marked by the H2 event early in the GS-3 stage. The last event is associated with the minimum value of the Chord-1 variable. Thus, in general, the Sartanian time should probably be considered as the least favourable for the woolly rhinoceros in Western Beringia. An increase in the number of dates at the end of MIS2 can be associated with improved environmental conditions, which are also reflected in the environmental variable Chord-1 and, in general, "correlate" with increase of summer time insolation (Fig. 5).

The chronological stage II (~39−27 cal ka BP) falls in the period of gradual cooling at the end of the Karga interstadial (MIS3). Its onset is marked by the H4 event (GS-9, ~39.9−38.2 cal ka BP) most clearly. Within the stage II, the ups/downs of the distribution of dates are plotted against the ups/downs of Chord-1 variable. The increases of Chord-1 correspond to increases of relative proportions of tree and shrub pollen, and to decreases of proportions of herbs pollen, respectively. These fluctuations are associated with the temperature series, but not very accurately (possibly due to bias), except for the most pronounced local decrease, which is marked by the H3 event (GS-6, ~33.4−32.5 cal ka BP). Nevertheless, the general trend of the decrease of relative amount of pollen from trees and shrubs is associated definitely with cooling and an increase in climate aridity in the end of MIS3.

Finally, the third chronological stage shows a good synchronicity between the number of dates and fluctuations in the environmental variable, excluding the very end of this stage. Any speculations about the distribution of dates are characterized by highest uncertainty for this stage due to large confidence intervals of radiocarbon dates. For example, the local minima of the distribution of dates can correspond possibly to both the H5 or H5a events, and the local maxima − to different interstadials (Fig. 5). Therefore,
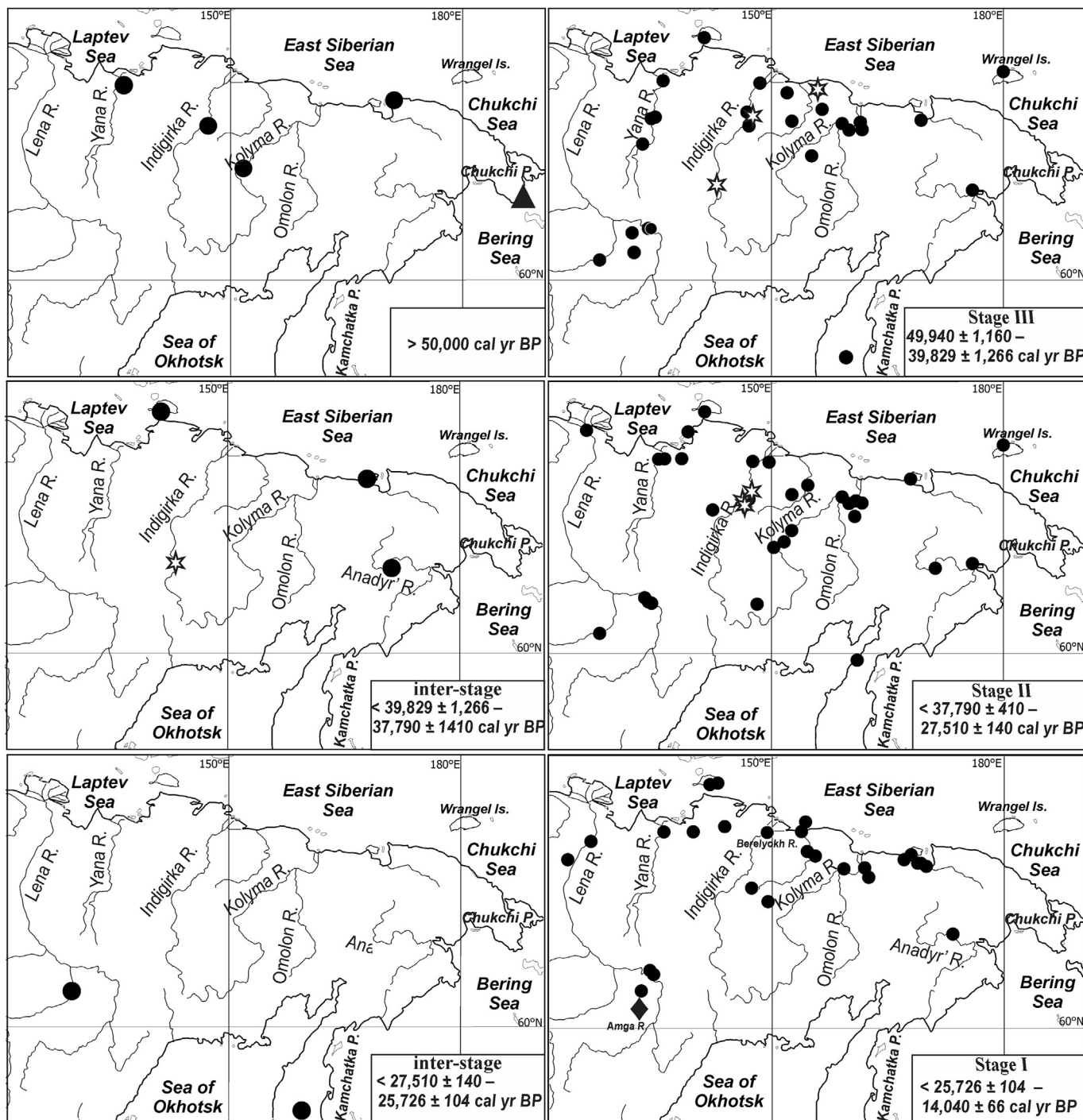
Fig. 3. The mapped woolly rhinoceros localities in Western Beringia belonged to the different chronological stages (I, II, and III) and inter-stages according to Fig. 2: • − localities with published radiocarbon date, ★ − localities with new radiocarbon dates; ▲ − the only dated find on the eastern edge of the Chukchi Peninsula (Chukotskiy Nos Cape = Chukotskiy Mys ?) has just a limit age > 46,000 ^{14}C yr BP, AAR-11046 (Lorenzen et al., 2011); ◆ − the youngest date: Amga R. − 14,040 ± 66 cal yr BP (AAR-11027/OxA-18602) (Stuart and Lister, 2012).

with such an uncertainty, we restrict ourselves with the statement of the correlation between the distribution of dates and the variable Chord-1. Our results indicate that environmental conditions were favourable for the woolly rhinoceros in general during the Karga interstadial (MIS3). However, within MIS3, environmental conditions were not uniform. The first part (~50−40 cal ka BP) that corresponds to chronological phase III is characterized by the higher proportions of herb pollen (Poaceae, Cyperaceae) and forbs in the

pollen spectra (Supplementary data, Fig. A1) in relation to the final part of the interstadial (chronological phase II). In this context, and also taking into account the previous results of our morphometric analysis of rhinoceros skulls (they were on average larger for specimens dated to stage III) (Puzachenko et al., 2019) we may assume more favourable feed base as well as other ecological conditions for the oldest part of chronological stage III.

The good correspondence of the boundaries between

Table 3
Spearman rank correlations for spatial invariants Chord 1–3 and averaged spore-pollen spectra yielded from the sites within woolly rhinoceros range and out of the range in Beringia. The values of the coefficients with statistical significance $p \leq 0.01$ are marked in italics.

Variable	Chord-1	Chord −2	Chord-3
Model I: within woolly rhinoceros range			
Trees and shrubs	*0.96*	0.19	−0.21
Herbs	*−0.96*	−0.12	−0.17
Forbs	−0.18	*−0.46*	0.11
Spore	0.29	−0.12	*0.86*
Pinus	0.28	0.37	*0.47*
Betula	*0.86*	0.22	−0.28
Alnus + Duschekia	*0.69*	−0.12	*−0.52*
Salix	0.11	0.01	−0.07
Artemisia	−0.19	*−0.60*	−0.34
Cyperaceae	*−0.66*	*0.61*	0.06
Poaceae	*−0.67*	*−0.59*	−0.12
Sphagnum	0.35	0.25	0.15
Selaginella	*−0.48*	−0.16	*0.63*
Model II: Western Beringia			
Trees and shrubs	*0.99*	−0.06	−0.11
Herbs	*−0.97*	−0.11	0.09
Forbs	*−0.91*	0.14	0.01
Spore	−0.19	*0.53*	*0.71*
Pinus	*0.87*	0.19	0.01
Betula	*0.84*	−0.36	0.05
Alnus + Duschekia	*0.88*	−0.20	−0.4
Salix	−0.14	−0.43	0.07
Artemisia	*−0.77*	−0.09	−0.37
Cyperaceae	*−0.63*	−0.46	0.27
Poaceae	*−0.93*	0.04	−0.21
Sphagnum	*0.72*	0.04	0.20
Selaginella	*−0.73*	0.37	0.26
Model III: Eastern Beringia			
Trees and shrubs	*0.98*	0.01	0.13
Herbs	*−0.98*	−0.09	−0.17
Forbs	*−0.87*	−0.37	−0.01
Spore	*0.78*	0.04	0.31
Picea	−0.24	0.18	*0.56*
Betula	*0.95*	0.12	0.09
Alnus + Duschekia	−0.37	−0.04	0.14
Salix	0.40	0.24	0.06
Artemisia	*−0.81*	−0.27	0.22
Cyperaceae	0.1	*0.95*	−0.08
Poaceae	*−0.90*	−0.28	−0.15
Sphagnum	0.57	0.07	0.24
Selaginella	−0.1	−0.33	0.04

chronological stages to the cold Heinrich events and some other correspondences between the climatic series and the distribution of dates indicate that temperature changes are the main factor determining the West Beringia availability for the woolly rhinoceros in the Karga interstadial and Sartan stadial.

Most likely, the woolly rhinoceros reacted positively to the Bölling warming (GI-1e, 14,600–14,000 cal yr BP) (Fig. 5). The extinction of the species in Beringia occurred, probably, over the Older Dryas cooling (GI-1d, ~14,100 cal yr BP), that is, quite a while before the Younger Dryas (GS-1) cooling began (~12,800 cal yr BP). The abrupt species extinction was unlikely to be caused by climatic fluctuation only.

The woolly rhinoceros extinction was occurring against the backdrop of very high proportion of tree and shrub pollen and low proportion of herb and forb pollen in the averaged spectra (Table 5; Supplementary Fig. A1). In particular, the average relative proportion of birch and willow pollen reached very high values for the first time within the considered time interval in West Beringia. The low levels of herb pollen was due to a significant decrease in the presence of graminoids and sedges. In addition, a very high proportion of sphagnum mosses spores and a low proportion of spikemosses spores were found. Taken together, the palynological

data mark relatively warm and humid climate conditions.

The estimated environmental parameters based on palynological data at the time of rhinoceros extinction differ markedly from those parameters that are associated with the supposed reductions of species range in Beringia, between chronological stages I–II and II–III (Table 5). Probably different combinations of ecological reasons led to the species range degradation in MIS3 and MIS2.

Summarizing, in our opinion, the most probable key reasons of the woolly rhinoceros range and population size dynamics in Beringia lay in both climate changes and in diversity of vegetation cover time-specific responses to these changes.

5. Discussion

The range of woolly rhinoceros in north-eastern Siberia to the north of 60° latitude, based on the distribution of finds lay from west to east roughly between 120°E (the Lena R. basin) and about 180ᵒE (Pereladov and Shpansky, 1997; Boeskorov, 2005; Kuzmin, 2010; Stuart and Lister, 2012; Markova et al., 2013). R.-K. Kahlke (2014) suggested that the species range might extend further west from the Lena river basin despite the absence of woolly rhinoceros finds on the Central Siberian Plateau.

Stuart and Lister (2012) discussed in detail the dynamics of woolly rhinoceros extinction within its range. The authors drew attention to a number of gaps in the pattern of dates that probably indicate the temporary absence of species in intervals of 40–34 cal ka BP (Central and Eastern Europe and Southern Siberia) and of 27–21 cal ka BP (the Urals). In addition, we can see a gap or a very small number of dates about 25 cal ka BP and about 40 cal ka BP in "E. Yakutia", "Kamchatka", "Chukotka" and "Wrangel Island" (Stuart and Lister, 2012: Fig. 2A and B). Our study provides new evidence for range change in the woolly rhinoceros. In this work, we found at least three "waves" of woolly rhinoceros expansion alternating with two relatively short reductions of the range in Western Beringia before extinction. The temporal boundaries between chronological stages (about 39 and 27 cal ka BP) correspond roughly to the position of the gaps in the pattern of dates described earlier in (Stuart and Lister, 2012).

Here, we also show for the first time a plausible relationship between proposed changes in woolly rhinoceros range with changes in climate (δ^{18}O, NGRIP time series) and its habitat environment (generalized pollen data) on a relatively large time scale with a greater amount of detail.

Previous studies have provided evidence of the important role of temperature changes that influenced the size of the woolly rhinoceros range in the Late Pleistocene of Eurasia (Stuart and Lister, 2012; Markova et al., 2013). It appeared that the woolly rhinoceros was apparently less adapted to the cold conditions of the Last Cold Stage of the Pleistocene in comparison with the woolly mammoth (*Mammuthus primigenius*) (but see Ukkonen et al. (2011) and Nadachowski et al. (2018)) and the muskox (*Ovibos moschatus*) (Markova et al., 2015). This assumption can be indirectly confirmed by both the absence of woolly rhinoceros' finds in the north of central Siberia between the Lena River and Yenisei River basins (the part of the mammoth and muskox ranges (Markova et al., 2015; Puzachenko et al., 2016)), and more southern position of the range boundary in Asia (Fig. 1A).

Lorenzen et al. (2011) suggested the climate change as the main cause of this species extinction based on demographic modelling and assessing a possible human impact. Stuart and Lister (2012) proposed that the dynamics of woolly rhinoceros range variability appear to relate largely to climatic and/or vegetational changes. In this paper on the Fig. 2A and B (Stuart and Lister, 2012: 10), two time gaps are clearly seen in the plots of radiocarbon dates for "E. Yakutia" region and the Lena R. basin. These gaps are approximately
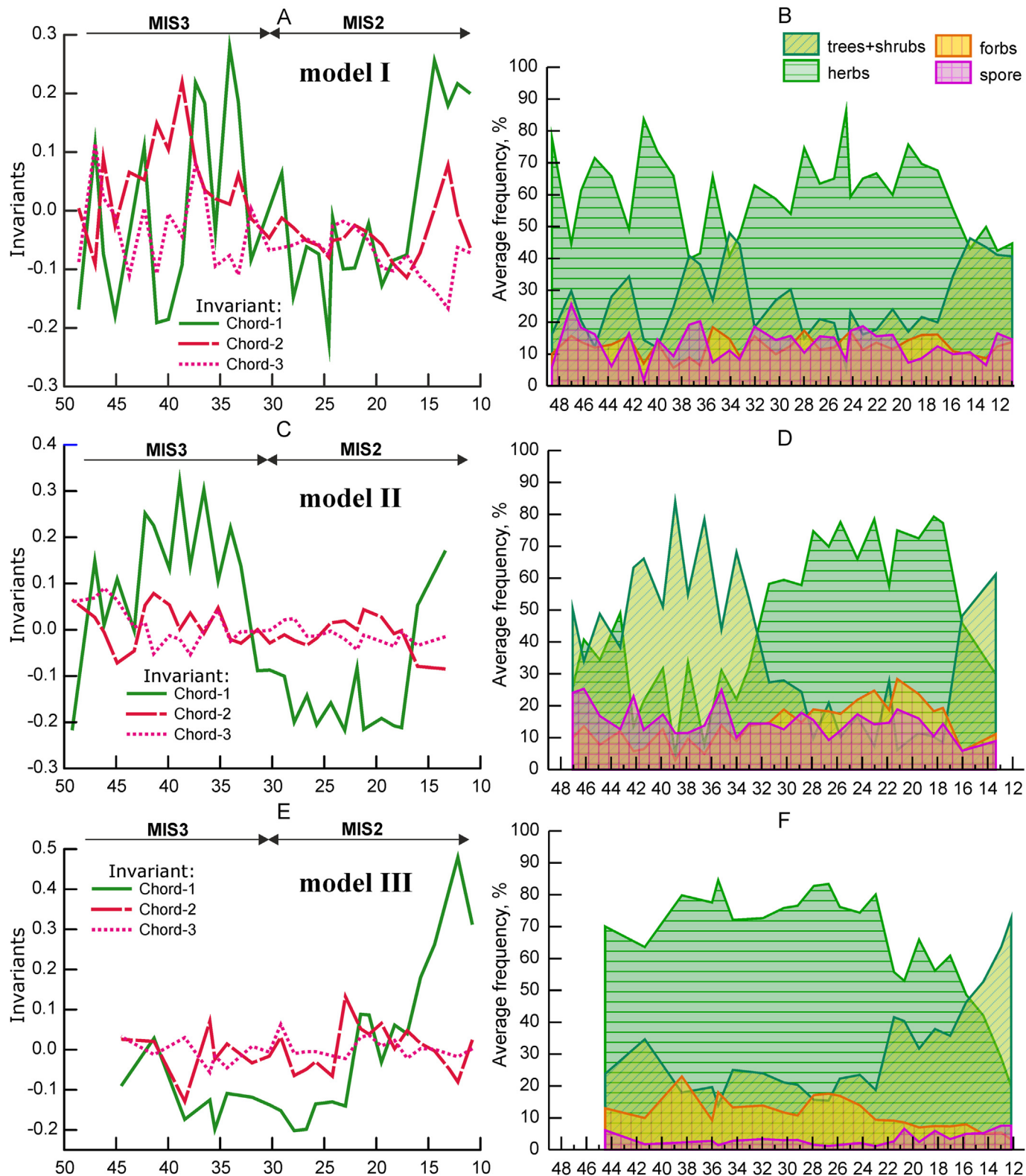
Fig. 4. The models (spatial invariants Chord-1–3, models I–III) of environmental changes and averaged pollen spectra within woolly rhinoceros range (A, B) and out of the range (C–F) in MIS3–MIS2: A, B – model I and pollen spectra within woolly rhinoceros range; C, D – model II and pollen spectra out of the range in the Asiatic part of Beringia; E, F – model III and pollen spectra out of the range in Eastern Beringia.

Table 4

Descriptive statistics of averaged spore-pollen spectra (%) yielded from the sites within the woolly rhinoceros range and out of the range in Beringia between 49 and 14 kyr BP. The median values which show significant statistical differences between the Western and Eastern parts of Beringia (Mann-Whitney test, $p < 0.05$), are underlined and the medians showing significant differences between woolly rhinoceros range and out of the range in Western Beringia are marked with an asterisk.

Variable	Mean	± standard error of mean	Standard deviation	Median	Min	Max
Within the woolly rhinoceros range, Western Beringia						
Trees and shrubs	24.9	1.97	10.8	22.5*	5.6	48.0
Herbs	61.9	2.30	12.6	64.3*	39.9	86.3
Forbs	12.7	0.61	3.3	12.8	5.7	18.4
Spore	13.2	0.96	5.3	14.5	1.9	25.6
Pinus	2.8	0.74	4.1	1.2*	0.0	18.5
Picea	0.06	0.04	0.23	0.0	0.0	1.2
Betula	10.5	0.92	5.0	10.8	1.9	26.5
Alnus + Duschekia	6.4	0.70	3.8	6.0	0.6	16.0
Salix	1.9	0.21	1.1	2.0	0.0	5.1
Artemisia	7.7	0.81	4.4	7.8	1.3	15.9
Cyperaceae	18.7	1.84	10.1	16.6*	7.5	46.7
Poaceae	22.8	1.31	7.2	22.7*	11.7	43.4
Sphagnum	1.6	0.28	1.6	1.0	0.0	6.6
Selaginella	4.8	0.61	3.3	4.3	1.1	17.9
Outside the range, Western Beringia						
Trees and shrubs	35.5	4.50	23.8	31.0*	3.9	83.9
Herbs	48.8	4.47	23.6	53.3*	4.7	79.3
Forbs	14.5	1.24	6.6	14.3	2.9	28.4
Spore	15.7	1.01	5.4	14.4	5.9	28.5
Pinus	9.5	1.93	10.2	5.7*	0.0	37.1
Picea	0.01	0.01	0.1	0.0	0.0	0.3
Betula	11.7	1.45	7.7	11.7	0.7	26.8
Alnus + Duschekia	8.1	1.20	6.3	6.9	0.8	23.5
Salix	2.3	0.30	1.6	2.1	0.0	7.6
Artemisia	6.6	0.92	4.9	6.4	0.0	16.6
Cyperaceae	12.4	1.41	7.5	13.4*	0.6	27.4
Poaceae	15.3	1.72	9.1	14.1*	1.2	30.1
Sphagnum	1.9	0.41	2.2	1.0	0.0	8.0
Selaginella	7.0	0.95	5.0	5.5	1.0	24.1
Eastern Beringia						
Trees and shrubs	27.7	2.42	11.1	23.8	14.0	52.6
Herbs	69.1	2.67	12.2	72.7	42.2	84.5
Forbs	11.9	1.00	4.6	10.8	5.0	23.0
Spore	3.1	0.37	1.7	2.8	1.2	6.6
Pinus	—	—	—	—	0.0	0.003
Picea	3.04	0.50	2.2	2.7	0.0	9.1
Betula	14.9	2.06	9.4	12.1	3.5	39.3
Alnus + Duschekia	2.4	0.48	2.2	1.9	0.0	10.5
Salix	6.3	0.66	3.0	5.8	1.2	13.0
Artemisia	10.5	1.10	5.1	10.8	3.5	23.8
Cyperaceae	21.2	1.67	7.6	20.9	4.5	41.1
Poaceae	25.6	1.73	7.9	26.1	11.5	38.0
Sphagnum	1.2	0.19	0.9	1.1	0.0	2.9
Selaginella	0.1	0.04	0.2	0.0	0.0	0.5

correspondent to the gaps described in our study. Our results agree with Stuart and Lister (2012) in relation to the climate influence on the woolly rhinoceros population dynamic. We propose that the cold Heinrich events H2 (GS-3) and H4 (GS-9) were the basic cause of the most pronounced degradation of the range in Beringia. It is very possible that the Heinrich events H3 (GS-6, 33.36−32.5 ka BP) also led to depression in the Beringian population of woolly rhinoceros (Fig. 5), but to a lesser extent.

Published data indicate that climatic fluctuations in the second half of the Late Pleistocene could have affected some other large mammals in West Beringia in a similar way. The time gaps in a chronology, which were observed in cave lion (*Panthera spelaea*) in "Siberia" region (Ersmark et al., 2015: Fig. 4b), are very close to the chronological gaps in the woolly rhinoceros. It is likely that the wapiti (*Cervus elaphus canadensis*) population that had inhabited the Kolyma R., Indigirka R. and Aldan R. lowlands was depressed at about the same time as the woolly rhinoceros population, based on published dates (Meiri et al., 2014).

The variations in climatic condition could have influenced the morphology of woolly rhinoceros in Beringia in particular the general size of a skull. Earlier we tested this hypothesis combining the results of preliminary research (Puzachenko et al., 2019) with the new set of radiocarbon dates from the current study, as some of the newly dated skulls were also involved in morphometric study. The Kruskal-Wallis test of medians confirmed ($H = 8.35$, $p = 0.004$, $N = 20$) the difference in age of groups of woolly rhinoceros with "large" and "small" skulls for joint male−female sample. For the group with "small" skulls, the median age 39.0 cal ka BP (46.07−27.67 cal ka BP) was obtained and in the group with the "large" the median was 48.2 cal ka BP (50.1−32.0 cal ka BP). It is problematic to expect that these intervals would coincide well with the chronological "waves", since not all the skulls in morphological study were dated (hence significant biases are possible for the group medians). Also, there is always a dispersion of skull' sizes in population under all environmental conditions. Nevertheless, the median age for woolly rhinoceroses with conventionally "small" skulls falls within the period of the species range degradation with unfavourable environmental conditions in Beringia (GS-9 = H4, Fig. 5). The second median falls into the first half of the chronological stage III, i.e. into a period, as proposed, with conditions that

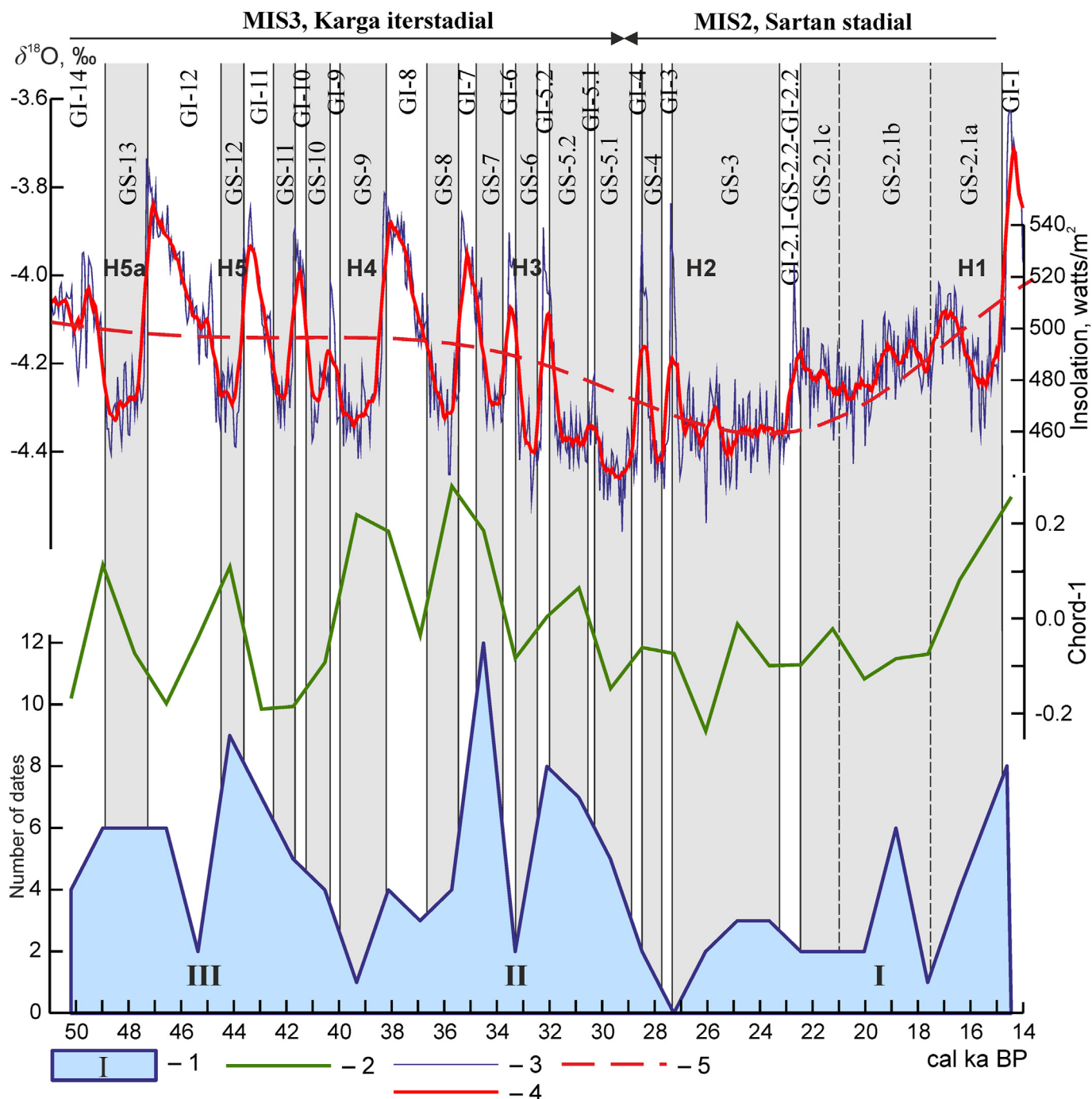**Fig. 5.** The comparison of time series: the distribution of woolly rhinoceros remains (1; I–III - the chronological stages) in Western Beringia; "environmental variable" – the first spatial invariant Chord-1 (2); $\delta^{18}O$ – NGRIP series (3) and NGRIP smoothed series (4); Insolation – the incoming solar radiation values at 60°N in June (5) (Berger and Loutre, 1991). GI, GS – Greenland interstadials and stadials (Andersen et al., 2004; Rasmussen et al., 2014), H5a–H1 – Heinrich events (Hemming, 2004).

were more favourable for the woolly rhinoceros. Thus, our hypothesis for a future research is that changes in a phenotypic (general size of skull) temporal pattern and chronology should be in phase shift up to antiphase, relative to each other.

The spatial and temporal diversity of the vegetation cover in Beringia was very high, as follows from the reconstructions proposed by the palynologists. According to Elias and Brigham-Grette (2007), during the second part of MIS3 in the Western Beringia region the temperature conditions were close to the present-day level, and the northern boundary of forest–tundra subzone was

near its contemporary position (approximately between ~70°N in the north-east and 60°N in the south-west of the region) (Tishkov et al., 2020). Anderson and Lozhkin (2001) proposed larch–birch forests in the Yana–Indigirka–Kolyma Lowland in about 48–34 cal ka BP (probably the most favourable part of the woolly rhinoceros range). At the same time (45–39 cal ka BP), a shrub tundra with limited larch forests and later (33–30 cal ka BP) herb/shrub birch tundra were proposed in upper reaches of the Kolyma R. and the Indigirka R. The pollen and spore spectra, derived from sediment embedded in the skin of the mummified woolly

Table 5
Average proportions (%) of pollen or spore which correlate with the boundaries between chronological stages I−II, II−III, and the estimated time of woolly rhinoceros extinction (~14,400 cal yr BP) in Western Beringia. Percentile boundaries for the distributions of variables: < 20% − very low, 20−40% − low, 40−60% − moderate, 60−80% − high, >80% − very high.

Variable	"Extinction"		I−II		II−III	
	%	Level	%	Level	%	Level
Trees and shrubs	46.3	Very High	19.8	Low	24.7	Moderate
Herbs	43.1	Very low	65.1	High	66.0	Very High
Forbs	9.8	Low	12.1	Moderate	5.7	Very low
Spore	10.6	Low	15.2	Moderate	9.4	Low
Pinus	0.97	Moderate	0.26	Very low	6.8	Very High
Betula	26.5	Very High	9.2	Low	7.9	Low
Alnus + Duschekia	12.0	Very High	7.1	Moderate	4.6	Low
Salix	5.1	Very low	1.5	Low	1.95	Moderate
Artemisia	8.7	Moderate	11.4	Very High	2.2	Very low
Cyperaceae	9.4	Very low	14.1	Low	46.7	Very High
Poaceae	15.8	Low	27.6	Very High	12.4	Very low
Sphagnum	4.4	Very High	0.35	Very low	0.93	Moderate
Selaginella	1.9	Very low	3.89	Moderate	4.30	Moderate

rhinoceros (Boeskorov et al., 2011), enabled the assemblage of steppe, meadow-steppe and meadow plant communities to be reconstructed in the Lower Kolyma R. in the middle of the Karga interstadial (43,650−42,390 cal yr BP, OxA-18755, GI11). Grass and prostrate shrubs pollen dominates the assemblage (61.0%), especially grass pollen (23.9%).

For the Chukchi Peninsula, there was willow/birch high shrub tundra, willow−herb tundra and tundra steppe in different parts of the region (Anderson and Lozhkin, 2001). These plant cover reconstructions at a large scale do not contradict, in general, with our small-scale generalized models of environmental conditions within the woolly rhinoceros range in MIS3 (mostly) and MIS2.

Garutt et al. (1970) argued a point of view that the main factor determining the ecology of woolly rhinoceros over all the range was not so much low temperatures as climate aridity/humidity (Vangenheim, 1961). Garutt and others (Garutt et al., 1970; Boeskorov et al., 2011) tried to explain the woolly rhinoceros absence in North America and combined the arguments of various researchers. According to them, there was lack of suitable food base in north-eastern Siberia (Beringia) at times of the Bering Land Bridge. The species became extinct by the time of mammal's second wave migration into North America at the end of MIS2 (Meiri et al., 2014).

Stuart and Lister (2012) also discussed different causes of absence of woolly rhinoceros in North America based on numerous literary sources and concluded that this species possibly had relatively narrow ecological tolerances in comparison with, for example, woolly mammoth. In particular, the elevated humidity in the area of the Beringia isthmus and snow cover reconstructed by different proxy records were considered as a barrier that the short−legged woolly rhinoceros could not pass (Elias and Crocker, 2008).

According to our result, there was relatively low pollen proportions of Cyperaceae and Poaceae reconstructed (Table 5), and, indirectly, a high snow cover with probably short vegetation period beyond the woolly rhinoceros range in MIS3 (see Andersen and Lozkin (2010)). However, we incline to consider these evidences as markers of both unfavourable food base for woolly rhinoceros and high snow cover at the eastern edge of Western Beringia.

The current explanations in literature for the absence of woolly rhinoceros in North America (Eastern Beringia) cannot be taken as conclusive (Guthrie, 2001; Kuz'mina et al., 2010; Stuart and Lister, 2012). The reconstruction of sea level indicates that the Bering Land Bridge existed between 50 and 11 ka BP (Jakobsson et al.,

2017). In this work, we have demonstrated significant differences in the evolution of vegetation cover between Western and Eastern Beringia within that time interval. So, we can assume that the ecological conditions in the east of the West Beringia realm and East Beringia were unfavourable for the woolly rhinoceros during MIS3−MIS2.

Elias et al. (1996) proposed mesic birch−heath−graminoid tundra with little or no steppe elements for the Middle Wisconsinan time, and birch−graminoid tundra with small ponds choked with aquatic plants without steppe−tundra vegetation at the central and northern sectors of the Beringia isthmus for the Late Wisconsinan. A little to the East, on the modern coast of Alaska, graminoid herb tundra with birch shrubs (in various proportions) were distributed in the Middle−Late Wisconsinan (Ager and Philips, 2008). Guthrie (2001) hypothesized an impact of regional cloud cover (moist maritime air masses influence from the north and south of the Bering isthmus) on ecological conditions and plant cover in the Beringia resulting in the Bering isthmus having had mesic ecological conditions ("mesic tundra belt"), which were unfavourable for arid−adapted species (plants and animals) of the "Mammoth steppe" community. Elias and Crocker (2008) proposed that it was biological filter (mesic shrub tundra) that blocked the movements of some steppe−tundra plants and animals across the in the Bering isthmus. In numerous studies, it has been established that the dominant ecosystem in Western Beringia and the interior regions of Eastern Beringia was steppe−tundra, with herbaceous plant communities and arid climate. Our crude but robust result of multivariate statistical analyses of pollen spectra shows the striking differences between steppe−tundra of Western and Eastern Beringia in pollen spectra composition and especially on proportions of Artemisia, Cyperaceae and Poaceae pollen. In addition, we observed evidence that the evolutionary process, which can be called "mesicification", began in the east of Beringia much earlier than in its western, Asiatic part.

In Western Beringia, the main fodder for woolly rhinoceros probably comprised of herbaceous plants, as well as dwarf willows and similar plants. According to Boeskorov et al. (2011), the pollen spectra from the stomach contents of the well-preserved frozen mummy of woolly rhinoceros (Kolyma R. basin), mentioned above, were dominated by herbaceous plants (98.88%) including Poaceae (46.07%) and Compositae (41.46%, sagebrush predominated). The relative stability of this type of diet during the MIS3−MIS2 (including LGM) was supported by genetic analysis of woolly rhinoceros gut/coprolite samples (Willerslev et al., 2014). In addition, the woolly rhinoceros diet could have somewhat varied with seasons (Tiunov and Kirillova, 2010) and in different parts of its range (Khubanova et al., 2016; Geel et al., 2019; Ma et al., in press). In different geographical parts of the range, the woolly rhinoceros also could switch to branch feeding, similar to the more specialized representatives of the genus Stephanorhinus (Asperen and Kahlke, 2015; Geel et al., 2019). Numerous studies of stable isotope (^{15}N, ^{13}C) composition in bone remains from different regions of Eurasia allow us to consider woolly rhinoceros, like the modern white rhinoceros (Ceratotherium simum), as a typical megaherbivore grazer (Garutt et al., 1970; Lazarev and Tirskaya, 1975). In general, its food niche was close to the niches of caballoid horses (Equus ferus) and (less) to niches of the steppe bison (Bison priscus) (Bocherens, 2003; Bocherens et al., 2011; Pushkina et al., 2014; Gröcke et al., 2017; Rivals and Álvarez-Lao, 2018; Schwartz-Narbonne et al., 2019). In the Late Pleistocene (excluding the Late Glacial Transition time) of Eurasia, food niches of woolly rhinoceros and woolly mammoths were usually partitioned in terms of values of $\delta^{15}N$ (in favour of the latter species) and $\delta^{13}C$ (in favour of the first species) in bone collagen.

Summarizing, we conclude that the feed base was unlikely the

main direct limiting factor in the distribution of woolly rhinoceros in Western Beringia, and rather other ecological factors (temperature/precipitation) determined the species range and its variation over the MIS3−MIS2 stages. One of the probable hypotheses is the assumption that the population of woolly rhinoceroses was reduced during the most favourable periods for passing the Bering Land Bridge (the coldest and driest events of MIS3 and MIS2). In addition, for the woolly rhinoceros, the eastern mountainous edge of West Beringia could be a significant physical barrier to its potential route to North America. Moreover, perhaps, if the woolly rhinoceros reached up the Alaska Peninsula, it would hardly had found favourable ecological conditions, since the local steppe−tundra differed significantly from the steppe−tundra of Western Beringia.

The Late Pleistocene chronology of many species from the both sides of the Bering Strait has not yet been studied in detail. The additional dating of woolly rhinoceros remains and a comparative studies of the chronology of such species as woolly mammoth, horses (*Equus* sp.), muskox, reindeer (*Rangifer tarandus*), cave lion, saiga antelope (*Saiga tatarica*) and others in Beringia at the end of the Late Pleistocene are required. However, Lorenzen et al. (2011) proposed that each species responds differently (species-specific) to the effects of climatic changes in the Late Pleistocene. Consequently, no common cause of species migrations across the Bering Land Bridge might be found and every case could be regarded as unique.

The Late Pleistocene was a time of frequent climatic fluctuations with significant amplitude (Fig. 5). These climate variations created highly temporally dynamic and unstable ecological conditions for both vegetation and animals in the steppe-tundra biome. Ecological changes led to range fluctuations and population dynamics; local population extinctions with subsequent recolonization from refugia (Mann et al., 2015).

The spatiotemporal instability of environment did not contribute to insurmountable (zonal) barriers formation and supported free migration. Thus, the spatiotemporal environmental diversity supported the steady ecosystem biological diversity in mammoth steppe in the small-timescale during glacial cycle in the Late Pleistocene. The transition to the Holocene was quite different from climatic fluctuations usual for the Pleistocene. Man et al. (2019) proposed the transition from spatial mosaic to spatial zonal environment ("the plaid-to-stripes transition"), which might lead to extinction of many megafaunal species on the planetary scale. The last hypothesis can explain partly a rapid widespread extinction of the woolly rhinoceros in Beringia not later than 14 cal ka BP or even a little earlier, i.e. before the collapse of the mammoth fauna began (Fiedel, 2009). We assume that the extinction occurred almost "simultaneously" across the entire range of the species in Beringia, since the latest date (14,040 ± 66 cal yr BP, Amga R.) of those included in the study was obtained for locality out of Beringia (*sensu stricto*) (Fig. 3). It is possible that ecological conditions, such as the expansion of mesic shrub (birches, willows) tundra, the decrease in forbs and grasses participation in plant communities, and an increase in moisture (waterlogging and paludification) (Rabanus-Wallace et al., 2017) contributed to reduction and/or forage base quality decrease within the woolly rhinoceros range just before its extinction. However, before that, most probably there was a partition of the species range, and/or the environmental barriers (waterlogged territories and wetlands) were created for intra-range migrations.

One of the main results of our study is the demonstrated fluctuations in population size of the woolly rhinoceros in Beringia during the second half of the Late Pleistocene. Chronological data allow substantiating at least three main large "waves" of growth/decline in the species range in this region. It is possible that there

were other smaller "waves" on a larger time scale. Thus, our result does not support the hypothesis of the effective population size stability in this species at the end of the Late Pleistocene in Beringia, based on new, yet scarce palaeogenomic data (Lord et al., 2020). Regardless of ecological reasons, which determined the changes both in the range size and population density, the reconstruction of the woolly rhinoceros population history suggests a significant contribution of migrations from outside of Beringia to maintain the relatively high genomic diversity observed in MIS2 before the species extinction (as in many other Pleistocene species (Hofreiter and Stewart, 2009: Cooper et al., 2015)). In addition, we do not exclude the possibility that some part of the Beringian population could have survived in regional refugia during an unfavourable climatic period. As a result, the different genetic lines, representatives of different clades, could be preserved.

The role of human activity in the woolly rhinoceros extinction in Beringia is not obvious. Archaeological evidences point to modern human habitation in Western Beringia during MIS3-MIS2 near the mouth of the Yana R., Lena R. and Kolyma R. (about 10 sites), but these Palaeolithic people did not reach Chukchi Peninsula and the Bering Land Bridge *per se* until the end of MIS2 (Pitulko and Nikolskiy, 2012; Nikolskiy and Pitulko, 2013; Hoffecker et al., 2016; Kuzmin and Keates, 2018; Sikora et al., 2019).

However, the human population density was low for such a large region and therefore it is almost improbable that hunting would cause fluctuations in woolly rhinoceros population (as well as the woolly mammoths (Pitulko and Nikolskiy, 2012)) and its extinction. The woolly rhinoceros meat was found in a stomach of a dog puppy whose mummy was recently found near the Tumat settlement (Syalakh R., Yakutia). These remains belong to the period of species extinction in Beringia (14,655−14,130 cal yr BP, ETH-99775 (Lord et al., 2020)). Therefore, an additional negative impact of hunting during the period of the species extinction cannot be ruled out, although the origin of the meat found in the stomach of the puppy is not clear.

Notably, the early movement of humans to Alaska dated after 15 cal ka BP (Potter et al., 2017), before Younger Dryas cooling, which approximately coincides with the millennia of extinction of the woolly rhinoceros in Beringia. Therefore, firstly, it can be proposed that the same complex of ecological events in West Beringia was the cause of both the woolly rhinoceros extinction and the "motive" of people moving to the East of Beringia. Further, in a very general sense, we can speculate that it was a significant decrease in the productivity of the steppe−tundra biome at the end of the Late Pleistocene in Western Beringia. It caused decrease in the ranges and population density of the species − the main objects of human hunting (but it was unlikely that the woolly rhinoceros was included in this hypothetical list). The degradation of the food supply in West Beringia could be the main reason for the migration of people in North America. Another hypothesis ("Beringian Standstill") postulates people were isolated in refugia during the Late Glacial Maximum before dispersal to the Americas, they only left when ecological conditions changed and the climate began to warm in Eastern Beringia at the end of the Late Glacial Transition (Tamm et al., 2007). One more hypotheses based on recent complex palaeogenetic data can be proposed, claiming that the West Beringian people are related to ancestral Native Americans and "Ancient Paleosiberians" were largely replaced by another group of peoples with ancestry from East Asia between 11 and 4 cal ka (Sikora et al., 2019). It is possible that the migration of the latter was caused by all the same climatic changes, which led to the extinction or population density decrease of megafauna in West Beringia. Therefore, the expansion of an alien people directly but gradually motivated a migration of indigenous population to the east of Beringia, from West Beringia or from a hypothetical refugium in the

southern part of the Bering Land Bridge (Sikora et al., 2019; Hoffecker et al., 2020). Therefore, the extinction of the woolly rhinoceros and the beginning of people migrating to America could have coincided in response to several indirect or independent reasons.

6. Conclusion

Compared to previous studies our investigation of the woolly rhinoceros chronology provides new information and a more detailed analysis that presents evidence of probable changes in the size of the rhinoceros range and, indirectly, in the population size in an important region of northeast Asia (West Beringia) at the end of the Pleistocene from 50 to 14 cal ka BP.

Firstly, the observance of three large "population waves", which were most likely caused by (Heinrich events H2 and H4) of the Late Pleistocene, indicate the limits in cold tolerance of this species from the "*Mammuthus − Coelodonta*" faunal assemblage. In general, milder environmental conditions of the Karga interstadial (MIS3) in Western Beringia that were reconstructed on both the numerous palynological data and δ^{18}O NGRIP time series, were more favourable for the woolly rhinoceros than the harsh conditions of the Sartanian time (MIS2).

Secondly, the observed changes in the distribution of calibrated radiocarbon dates (not only those that marked boundaries between the chronological stages) largely correlate with both the general changes in plant communities within the species range and with the global temperature dynamics. However, we could not clearly determine which specific changes in environmental conditions (vegetation cover) of Beringia, most probably caused by climate change, were the direct drivers of the woolly rhinoceros range evolution in different cases. We have no evidence that the same ecological conditions (according to palynological data), excluding some obvious consequences of climate cooling, were the cases of maximum degradation of the species range, between chronological stages I, II, and III.

Thirdly, the ecological situation just before the woolly rhinoceros extinction about 14 cal ka BP, associated with a composition of climate warming, moisture increasing and shrub tundra expansion in West Beringia, was qualitatively different from previous cases of the species range degradations in MIS3 and MIS2. The population of woolly rhinoceros reacted positively at the Bölling warming. The abrupt extinction of the species coincided with, most probably, cooling of the Older Dryas, that is, before Alleröd warming and even before the Younger Dryas cooling. A hunting of woolly rhinoceros by humans could have affected population size at time of its rapid decline before extinction. However, most likely, it appears that both the degradation of the Late Pleistocene "tundra-steppe" biome and the decreasing in quality of food potential, associated with the onset of warming and rainfall increasing, were the primary drivers of the woolly rhinoceros' extinction.

Fourthly, the specific reason for the lack of evidence of the woolly rhinoceros migration activity in the direction of North America is still not certain. Most plausibly, the population of rhinoceroses was reduced along the periods that were best for overcoming the Beringia isthmus (the coldest events of MIS3 and MIS2). More research is needed to address this issue. However, it is likely, that no single cause would be found, there could be sets of different reasons that prevented the woolly rhinoceros migration to the east of Beringia.

This study confirms that dated palaeontological findings which are not associated with any stratigraphic units (typical for Arctic and Subarctic Asia regions) can furnish suitable material for statistical analysis of palaechronology. The chronology provides basis for understanding the population history, demography, and biology of extinct representatives of the "*Mammuthus−Coelodonta*" faunal assemblage to develop better understanding of causalities, timing and rate of megafauna extinction during the Late Quaternary. The palynological information generalized for a small geographic scale using multivariate analysis methods is useful for interpreting the chronology of megafauna population.

Author statement

All of the authors contributed to the interpretation of data in the paper and the writing of the manuscript.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2021.106994.

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