



Extinction of the woolly mammoth (*Mammuthus primigenius*) and woolly rhinoceros (*Coelodonta antiquitatis*) in Eurasia: Review of chronological and environmental issues

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The current evidence for date and environmental preferences of the extinction of two middle–late Pleistocene megafaunal species, the woolly mammoth (*Mammuthus primigenius* Blum.) and woolly rhinoceros (*Coelodonta antiquitatis* Blum.), is presented in this review. It is suggested that extinction of these large herbivores in Eurasia was closely related to landscape changes near the Pleistocene–Holocene boundary (c. 12 000–9000 uncalibrated radiocarbon years ago, yr BP), mainly involving the widespread forest formations in the temperate and arctic regions of northern Eurasia and the loss of grasslands crucial to the existence of woolly mammoth and rhinoceros. However, some woolly mammoth populations survived well into the Holocene (up to c. 3700 yr BP), showing that the process of final extinction was fairly complex, with delays in some regions of up to several millennia. The possible role of Palaeolithic humans in the extinction of Late Pleistocene megafauna is also considered.

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The late–final Pleistocene mammalian extinctions are the subject of continuous debate, judging by several recent monographs, overviews and book reviews (Brook & Bowman 2002, 2004; Barnosky *et al.* 2004; Martin 2005; Koch 2006; Koch & Barnosky 2006; Shabel 2006; Kuzmin & Tikhonov 2007; Stuart & Lister 2007; Gillespie 2008; Lister & Stuart 2008; Webb 2008; Pacher & Stuart 2009). This article is an overview of the latest progress in identifying the final extinction patterns of two middle–late Pleistocene herbivores, the woolly mammoth (*Mammuthus primigenius* Blum.; hereafter mammoth) and woolly rhinoceros (*Coelodonta antiquitatis* Blum.; henceforth rhinoceros). These herbivores were so typical of the Late Pleistocene ‘bestiary’ (Anderson 1984) in Eurasia that the *Mammuthus–Coelodonta* faunal complex was established and named after them (e.g. Kahlke 1999). At the modern stage of research, only for a few mammalian species is there enough chronometric evidence for reconstruction of their spatiotemporal patterns of disappearance in a true hemispheric scale, such as mammoth, rhinoceros and bison (e.g. Orlova *et al.* 2004a); others, like the giant deer, cave lion, musk ox and horse, still do not have extensive ¹⁴C data sets (e.g. Orlova *et al.* 2004a; Stuart & Lister 2007). Reviews of the chronological aspect of the extinction of mammoth and rhinoceros in northern Asia have recently been given in abridged form (Kuzmin 2008; Orlova *et al.* 2008) and are now discussed in more detail.

Study area

The region under consideration includes northern Eurasia within the habitats of the mammoth and rhinoceros: practically all western and central Europe; eastern Europe north of the Caucasus; western Siberia and northern Kazakhstan; eastern and northeastern Siberia; northern Mongolia; northeastern and northern China; and Hokkaido Island (Fig. 1). The southernmost ¹⁴C-dated mammoths are in the south of the Iberian Peninsula in the extreme west of Eurasia and near the Shandong Peninsula on the eastern edge of the Eurasian supercontinent (Takahashi *et al.* 2007). Data on the presence of mammoth on the Korean Peninsula (Park 1988: p. 79) remain to be proved in additional studies. Major attention in this review is given to the northern part of Eurasia, namely northeastern Europe (European Russia and Baltic states) and central and northern parts of Siberia, where the latest mammoths and rhinoceroses existed. The insular territories neighbouring northeastern Siberia, Wrangel Island and Saint-Paul Island (Pribilof Islands) are considered separately because of the specific conditions of mammoth existence in these two regions during the early–middle Holocene (Guthrie 2004; Vartanyan *et al.* 2008; Veltre *et al.* 2008). As for rhinoceros, its habitat was similar to that of the mammoth, besides most of Fennoscandia and some regions in the Arctic (Kola, Yamal, Gydan and Taymyr peninsulas, and the surrounding territories of northeastern Europe, western and central Siberia) (Kahlke 1999;

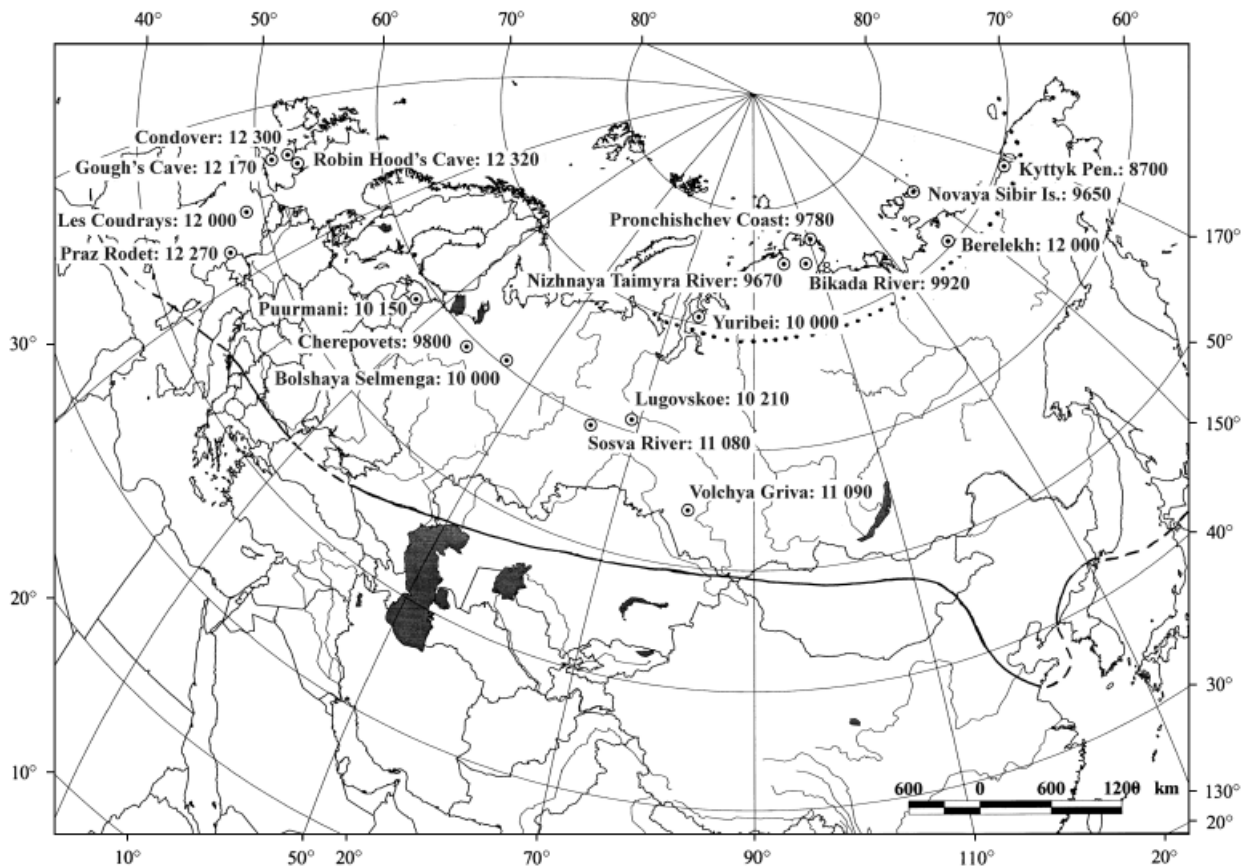


Fig. 1. Distribution of the latest woolly mammoths in Eurasia and the southern limit of their habitat (after Vasil'chuk *et al.* 1997, modified). The dotted line is the southern limit of the mammoth habitat after c. 12 000 BP (after Sher 1997).

Garutt & Boeskorov 2001: p. 159) (Fig. 2). There is published information about the presence of rhinoceros in Korea (Park 1988: p. 78), but it needs to be ratified, although the existence of rhinoceros on the Korean Peninsula is possible because it is known in neighbouring northeast China (Garutt & Boeskorov 2001).

Methods

As done previously (Stuart 1991, 2005; Vasil'chuk *et al.* 1997; Kuzmin & Orlova 2004), only ^{14}C -dated localities of mammoth and rhinoceros are considered, because only for these localities is there the strict chronological control necessary for our purpose in this review. Uncalibrated ^{14}C dates are used (in ^{14}C years ago, hereafter – yr BP; otherwise indicated). Details on the sample pretreatments for ^{14}C dating may be found in Vasil'chuk *et al.* (2000), Kuzmin & Orlova (2004: p. 144), Higham *et al.* (2006) and Brock *et al.* (2007). Mapping of the localities with the youngest ^{14}C dates was conducted with the help of ArcView 3.2 software. Critical analysis of the ^{14}C dates was by comparing problematic dates against general patterns of the extinction of the two species under consideration. Particular attention was given to the possibility of an

independent check of the reliability of some ^{14}C dates, by running the same sample in different laboratories, and general resemblance of ^{14}C dates produced on the same samples, e.g. TIRI and FIRI intercomparisons (e.g. Scott 2003).

In order to correlate ^{14}C records and climatic events in the Lateglacial, calibrated dates were compared with the records of the Greenland ice cores (Rasmussen *et al.* 2006; Lowe *et al.* 2008). The environmental component of the extinction process is considered on the basis of summaries on post-20 000 yr BP Eurasian landscapes published in the past decade (Velichko 2002; Velichko *et al.* 2002; Wright *et al.* 2005; Borisova 2008; Markova & van Kolfschoten 2008), and the approach follows Graham *et al.* (1996: 1601–1602).

Previous studies and their major results

Since the early 1990s, large radiocarbon (hereafter ^{14}C) data sets of mammoths in the Northern Hemisphere have been published, and it has become possible to understand the spatiotemporal patterns of their existence and extinction. Stuart (1991) compiled the first comprehensive review and established the main patterns of the mammoth extinction in Europe and Siberia. Sulerzhitsky (1997), Sulerzhitsky & Romanenko (1999),

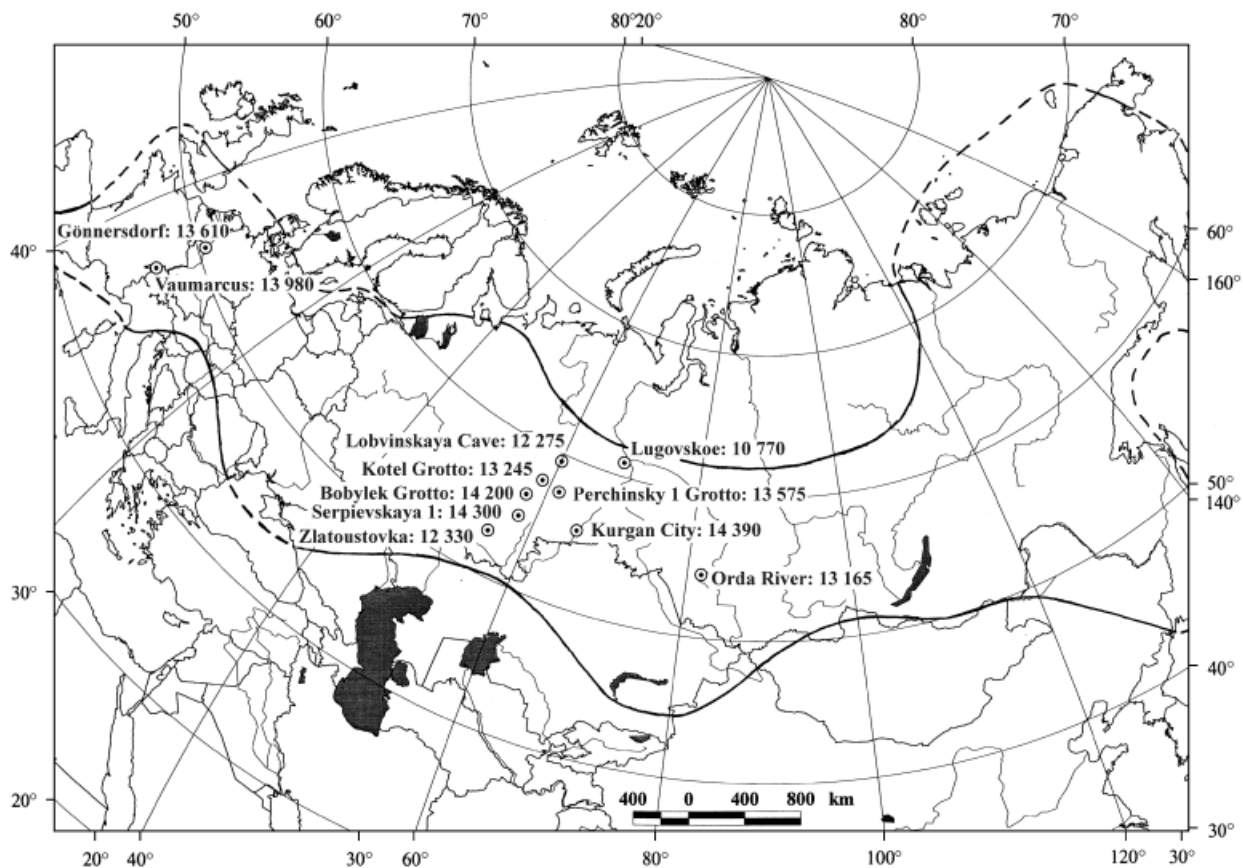


Fig. 2. Distribution of the latest woolly rhinoceroses in Eurasia and their habitat (after Garutt & Boeskorov 2001, modified).

Vasil'chuk *et al.* (1997), Kuzmin *et al.* (2000) and Orlova *et al.* (2003) have published their lists of mammoth ^{14}C dates and interpretations. Sher (1997) created a model of the mammoth extinction which the present author calls, for brevity, 'retreat to the north' ('retreat to the North of extinction model'; Sher 1997: p. 324), and it has a relation to the environmental changes at the Pleistocene–Holocene boundary. It was suggested that after *c.* 12 000 yr BP mammoths existed only in the Siberian High Arctic, north of the Arctic Circle (Taymyr, Gydan and Yamal peninsulas and the Severnaya Zemlya Islands, Fig. 1; see Sher 1997: 323–327).

Stuart (1999, 2005) and Stuart *et al.* (2002) considered the then current situation with age of the latest mammoths in Eurasia, and concluded that in western, central and eastern parts of Europe mammoths had become extinct mainly by *c.* 12 000 yr BP, except at Puurmani in Estonia and Cherepovets in northeastern Europe; in Siberia, mammoths survived on the mainland until *c.* 9700 yr BP. On Wrangel Island in the Siberian Arctic, small mammoths existed until *c.* 3700 yr BP (e.g. Vartanyan *et al.* 1995). Stuart *et al.* (2004: p. 687) suggested that the formation of forests in Europe after *c.* 12 000 BP pushed mammoths to the northernmost part of Eurasia, i.e. the arctic regions of Siberia. They also suggested that 'marked shifts in the distribu-

tions of both species (giant deer and woolly mammoth – Y.K.) were driven by the climate acting through vegetational changes' (Stuart *et al.* 2004: p. 688). Orlova *et al.* (2002, 2003) have provided an overview of the Siberian natural environment during the Lateglacial period (*c.* 15 000–10 000 yr BP) in connection with habitat conditions of the latest mammoths in Siberia.

The possible existence of Lateglacial (*c.* 12 000–10 000 yr BP) mammoth refugia beyond the arctic regions on northern Eurasia was first suggested by Stuart *et al.* (2002: p. 1567) upon receiving post-12 000 yr BP ages of several mammoths in temperate Europe (Lõugas *et al.* 2002; Stuart *et al.* 2002: pp. 1564–5) and Western Siberia (Orlova *et al.* 2000, 2003; Stuart *et al.* 2002: 1565–1566). This was later confirmed by Kuzmin & Orlova (2004) and by Orlova *et al.* (2004a, b).

As for the rhinoceros, the amount of research on the timing of its extinction through ^{14}C dating is less well documented compared to that for the mammoth; only a handful of reviews have been released (Stuart 1991: pp. 500–2; Sulerzhitsky & Romanenko 1999; Boeskorov 2001; Garutt & Boeskorov 2001; Orlova *et al.* 2004a). It has been suggested that the rhinoceros became extinct in Eurasia at *c.* 13 000–12 000 yr BP (Vereshchagin & Baryshnikov 1984: p. 498; Stuart 1991: p. 502; Garutt & Boeskorov 2001).

Results and discussion

Spatiotemporal patterns of the extinction of woolly mammoth in Eurasia: recent research

Based on current evidence (e.g. Kuzmin 2008), until *c.* 12 000 yr BP mammoths were widely distributed in northern Eurasia; in the final Lateglacial (*c.* 12 000–10 000 yr BP) and onset of the Holocene (*c.* 10 000–9500 yr BP) they occupied mainly arctic regions (Table 1). However, some mammoths survived outside the Arctic and existed in temperate (by modern standards) regions of eastern Europe and Siberia (Fig. 1; Table 1). After *c.* 9000–8700 yr BP, mammoths lived only on some isolated islands (Vartanyan *et al.* 2008; Veltre *et al.* 2008).

Stuart (2005: p. 172) and Stuart & Lister (2007: p. 290) have pointed out that the sudden disappearance of mammoths from Europe and most of northern Asia after *c.* 12 000 yr BP was not related to warming and spread of shrub-grassland vegetation, but coincided with the major loss of open biomes at the beginning of the Allerød. Following Sher (1997), they accepted that the extinction of mammoths correlated well with the loss of open tundra-steppe formations and spread of forests in mid-latitudes and peat bogs and tundra in the Arctic (Stuart & Lister 2007: p. 290). Lister & Stuart (2008) put forward the 'extinction lag' feature, which is the delay in final extinction of some megafaunal species (at least mammoth and giant deer) upon loss of most of its habitat; they see extinction as 'an extended process of net range reduction over thousands or tens of thousands of years' (Lister & Stuart 2008: p. 619). The existence of small refugia for megafauna during the process of final habitat contraction is highlighted (Lister & Stuart 2008: p. 619).

Stuart (2005: p. 173) has suggested that mammoths that retreated to the Taymyr Peninsula of the Siberian Arctic after *c.* 12 000 yr BP re-expanded at *c.* 10 500–9800 yr BP into neighbouring parts of Siberia (the Yamal and Gydan peninsulas) and further west to northeastern Europe (Fig. 1). Although this is a possible scenario, more dates are needed, perhaps with the help of strontium isotope analysis of mammoth remains (Barbieri *et al.* 2008). It is also assumed that this re-expansion may be connected with the Younger Dryas cold episode with the return of open steppe-tundra vegetation (Stuart 2005: p. 173).

As for an understanding of the spatiotemporal patterns of mammoth extinction, in the early-mid 2000s it became clear that Sher's (1997) 'retreat to the north' model was no longer valid and had to be replaced. The post-12 000 yr BP mammoths in the central West Siberian Plain, the Urals and eastern Europe show that some populations in extra-Arctic regions had not become extinct after *c.* 12 000 yr BP and survived until almost the end of the Pleistocene. Among them, there

are mammoths in the following localities: Puurmani, *c.* 10 100 yr BP; Cherepovets, *c.* 9800 yr BP; Lugovskoe, *c.* 10 200 yr BP; Volchya Griva and Sosva River, *c.* 11 100 yr BP (see Table 1 and Fig. 1) (Lõugas *et al.* 2002; Stuart *et al.* 2002; Orlova *et al.* 2004a, b; Kosintsev 2007: p. 115; Kuzmin 2008; Leshchinsky *et al.* 2008). For example, at the Volchya Griva locality in western Siberia, where post-12 000 yr BP mammoths were detected in 2000 (Orlova *et al.* 2000), a new ¹⁴C date of *c.* 11 800 yr BP confirms this (Leshchinsky *et al.* 2008).

It has to be borne in mind that, 400 km east–northeast of the Cherepovets locality, the new find of mammoth remains at Bolshaya Selmenga village on the Sukhona River has provided ¹⁴C dates of *c.* 10 000 yr BP (Kosintsev 2008: p. 265) (see Table 1). This might mean that the Lateglacial mammoths in the north of eastern Europe were more numerous than was previously thought. A quite 'late' ¹⁴C date of *c.* 12 600 BP is known from the vicinity of Cherepovets (Stuart *et al.* 2002: p. 1654; Yashina 2006).

As for the famous 'mammoth cemetery' of Berelekh in northeastern Siberia, its youngest ¹⁴C date of *c.* 10 370 yr BP (e.g. Orlova *et al.* 2004a: p. 309) seems erroneous, judging from more recent data. New research (Barnes *et al.* 2007; Debruyne *et al.* 2008) does not confirm such a late age, and it may be concluded that most of the ¹⁴C values for the Berelekh fall within the time interval *c.* 12 350–12 000 yr BP (Kuzmin & Orlova 2004; Barnes *et al.* 2007; Debruyne *et al.* 2008). Thus, the suggestion that the *c.* 10 370 yr BP value from Berelekh is an outlier (Stuart *et al.* 2002: p. 1566) turns out to be correct.

Boeskorov (2004: p. 453) considered the dubious ¹⁴C date of 3730±50 yr BP on mammoth bone from the lower stream of the Lena River (northeastern Siberia) as evidence that 'some mammoth populations existed in Holocene on the mainland part of the north of Eastern Siberia'. This particular ¹⁴C age determination was published without provenance detail and even without a laboratory number, and therefore cannot be accepted at face value as confirmation of middle Holocene mammoth populations in continental eastern Siberia.

With the exception of Wrangel Island, the 'youngest' mammoths in Eurasia until 2005 were known in two regions of the mainland Siberian Arctic: the Taymyr Peninsula (*c.* 9670 BP; Stuart *et al.* 2002) and Novaya Sibir Island (*c.* 9650 yr BP; Anisimov *et al.* 2005) in the modern Laptev Sea, which was part of dry land before *c.* 7000 yr BP (e.g. Bauch *et al.* 2001). It should be noted that an extensive search and ¹⁴C dating of mammoths on the Taymyr Peninsula in recent years (MacPhee *et al.* 2002; Mol *et al.* 2006) has not resulted in new finds of post-9900 yr BP individuals, which perhaps means that the latest mammoths from the Taymyr are not significantly younger than *c.* 9670 yr BP.

Table 1. The latest ^{14}C dates for woolly mammoths in Eurasia.¹

Region, site	Latitude, N	Longitude, E/W	^{14}C date (yr BP)	Lab. no.	Calibrated date (cal. yr BP ²)	Climatic event	Reference
Western/central Europe							
Les Coudrays, Etoilles	48°37'	02°28' E	12 000±220	Ly-1351	14 630–13 360	Boëlling	Evin <i>et al.</i> (1979); Stuart <i>et al.</i> (2002)
Gough's Cave	51°17'	02°46' W	12 170±130	OxA-1890	14 610–13 750	Boëlling	Stuart <i>et al.</i> (2002)
Praz Rodet	46°34'	06°11' E	12 270±210	Ly-877	14 980–13 750	Boëlling	Stuart <i>et al.</i> (2002)
Condover	52°38'	02°44' W	12 300±180	OxA-1316	14 940–13 820	Boëlling	Stuart <i>et al.</i> (2002)
Condover			12 330±120	OxA-1456	14 880–13 960	Boëlling	Stuart <i>et al.</i> (2002)
Robin Hood's Cave ³	53°21'	01°11' W	12 320±120	OxA-1462	14 870–13 940	Boëlling	Stuart <i>et al.</i> (2002)
Pin Hole Cave ³	53°21'	01°11' W	12 460±160	OxA-1204	15 070–14 030	Boëlling	Stuart <i>et al.</i> (2002)
Eastern Europe							
Cherepovets	59°09'	37°44' E	9760±40 ⁴	GIN-8885c	11 240–11 130	Early Holocene	Stuart <i>et al.</i> (2002)
Cherepovets			9810±100 ⁴	GIN-8676a	11 610–10 790	Early Holocene	Stuart <i>et al.</i> (2002)
Cherepovets			9840±50 ⁴	GIN-8885b	11 390–11 180	Early Holocene	Stuart <i>et al.</i> (2002)
Bolshaya Selmenga	60°27'	44°27' E	10 000±800	LE-5521	13 380–9490	Younger Dryas (?)	Kosintsev (2008)
Puurmani ⁵	58°29'	26°13' E	10 100±100	Hela-423	12 050–11 290	Younger Dryas	Lõugas <i>et al.</i> (2002)
Puurmani			10 200±200	Hela-425	12 620–11 250	Younger Dryas	Lõugas <i>et al.</i> (2002)
Western Siberia and Urals							
Yuribei	68°55'	71°00' E	10 000±70	LU-1153	11 770–11 250	Early Holocene	Arslanov <i>et al.</i> (1982)
Lugovskoe	60°57'	68°32' E	10 210±135	SOAN-4752	12 560–11 320	Younger Dryas	Kuzmin & Orlova (2004)
Lugovskoe			11 310±380	SOAN-4755	14 030–12 390	Allerød	Kuzmin & Orlova (2004)
Lugovskoe			11 840±95	SOAN-4753	13 900–13 450	Allerød	Kuzmin & Orlova (2004)
Sosva River (OLP)	59°23'	62°20' E	11 080±160	SOAN-4842	13 260–12 820	Allerød	Kosintsev <i>et al.</i> (2005)
Volehya Griva	54°40'	80°21' E	11 090±120	SOAN-4291	13 210–12 860	Allerød	Kuzmin & Orlova (2004)
Volehya Griva			11 815±90	AA-60771	13 850–13 430	Allerød	Leshchinsky <i>et al.</i> (2008)
Taymyr Peninsula							
Nizhnaya Taymyra River	75°15'	99°44' E	9670±60	GIN-1828	11 220–10 780	Early Holocene	Sulerzhitsky (1997)
Nizhnaya Taymyra River			9860±50	GIN-1495	11 390–11 200	Early Holocene	Sulerzhitsky (1997)
Pronchishev Coast	76°45'	110°30' E	9780±40	GIN-8256	11 250–11 160	Early Holocene	Sulerzhitsky & Romanenko (1999)
Bikada River	74°55'	106°35' E	9920±60	GrA-17350	11 610–11 210	Early Holocene	MacPhee <i>et al.</i> (2002)
Novosibirskiy Islands							
Novaya Sibir Island ⁷	75°00'	149°00' E	9650±60	GIN-11245	11 200–10 780	Early Holocene	Anisimov <i>et al.</i> (2005)
North-eastern Siberia							
Kyrtiyk Peninsula ⁷	69°30'	167°30' E	8700±?	N.a. ⁶	—	Early Holocene	Vartanyan <i>et al.</i> (2005) ⁸
Kyrtiyk Peninsula			9000±?	N.a. ⁶	—	Early Holocene	Vartanyan <i>et al.</i> (2005) ⁸
Berelekh	70°24'	143°57' E	12 000±130	LU-149	14 160–13 570	Allerød	Arslanov <i>et al.</i> (1980)

¹For Wrangel Island, see Vartanyan *et al.* (2008); for St. Paul Island, see Veltre *et al.* (2008).²Calib 5.1.0 software is used (with±2 sigma, all intervals combined).³Sites are situated in the vicinity of each other in Creswell Crags region of Derbyshire (UK).⁴Multiple ^{14}C dates on the same individual.⁵Probably the same individual was dated (see Stuart *et al.* 2002: p. 1564).⁶N.a. = not available.⁷Coordinates are approximate.⁸Dates are produced at the Institute of Geology and Mineralogy, Siberian Branch of the Russian Academy of Sciences, Novosibirsk (laboratory code SOAN).

The most recent discovery of Holocene mammoths in the extreme Northeast Siberian mainland, the Kyttyk (*Karchuk* in *The Times Atlas of the World* (1989), plate 39, grid H2) Peninsula of western Chukotka with ^{14}C dates of *c.* 9000–8700 yr BP (*Vartanyan et al.* 2005) (see Table 1), raises the issue of multiple Holocene mammoth refugia (e.g. *Kuzmin* 2008). This is in excellent accord with *Stuart's* (2005: p. 173) prediction: 'Given the vastness of the region it is possible that other Holocene mammoth refugia will be found elsewhere in Siberia.' Thus, in mainland Siberia there are currently two early Holocene refugia.

Another Holocene refugium of the mammoth (almost of 'normal' size) is known at St. Paul Island of the former Beringian landmass (*Guthrie* 2004; *Veltre et al.* 2008), where they existed at *c.* 7980–5700 yr BP. The environment at that time was represented by lush coastal grasslands (e.g. *Veltre et al.* 2008: p. 47) which seem to have sustained a mammoth population on this already isolated island. This highlights the need for open grasslands for mammoth survival (see details below).

Environmental situation at the time of mammoth extinction in Eurasia

The environmental background of the final mammoth extinction in Eurasia has been studied only in a general fashion, taking into account the vastness of the European and Siberian Arctic and adjacent regions; nevertheless, some reviews are available. In western and central Europe, the latest mammoths are assigned to the Bølling event *c.* 12 500–12 000 yr BP (Table 1). In the northern part of eastern Europe, the Taymyr Peninsula and Novosibirskiye Islands, the latest mammoths existed in post-Younger Dryas times, the early Holocene: at *c.* 9800–9700 yr BP in northeastern Europe and Taymyr, and approximately at 9700 yr BP on the Novosibirskiye Islands (see Table 1). Using the available palaeoenvironmental records reveals the general picture of the environment at the time of the latest mammoth populations.

The vegetation of western and central parts of Europe in the Bølling was mainly periglacial forest steppe and tundra-steppe (the last one is a non-analogous association; e.g. *Kienast* 2007) and periglacial pine-birch woodlands (*Simakova & Puzachenko* 2008a: 392–393). Some mammoths existed in northeastern Europe in the Younger Dryas (*Puurmani*) (Table 1) in an environment of pine-birch open woodland combined with steppe communities (*Muratova et al.* 1993: p. 114; *Bohncke* 2008: 412–413).

In the northern part of eastern Europe, the main vegetation type in the early Holocene was conifer forests with some forest steppe and tundra formations (*Simakova & Puzachenko* 2008b: 442–443). The presence of pine and birch forests at *c.* 11 000 cal. yr BP (or *c.* 9600 yr BP, see *Reimer et al.* 2004) is confirmed by stu-

dies of lake sediments in the Rostov–Yaroslavl region (*Wohlfarth et al.* 2007). In the more northern region of eastern Russian Karelia, open forests with birch and poplar existed at the onset of the Holocene after *c.* 11 500 cal. yr BP (or *c.* 10 000 yr BP) (*Wohlfarth et al.* 2007). Pollen records from Lake Galichskoye, about 270 km east of the Cherepovets mammoth locality, show that in the Younger Dryas (*c.* 11 000–10 300 yr BP) vegetation was represented by periglacial steppe formations, while in the early Holocene (*c.* 10 000–8000 yr BP) forests expanded and occupied the region (*Velichko et al.* 2001).

The general trend in vegetational change from the Last Glacial Maximum (LGM) toward the early Holocene in eastern Europe was a gradual decrease of open landscapes with a prevalence of grasses and an increase of tree-dominated formations, mainly conifer forests in the north and mixed conifer-broadleaved forests in the south (*Wohlfarth et al.* 2007; *Simakova* 2008). In northeastern Europe (between 55° and 60°N), the mosaic landscapes of pine-birch forests and shrub tundra existed in the Bølling–Allerød phase, turning to forest tundra in the Younger Dryas and, finally, to pine-birch forests with patches of tundra (*Simakova* 2008).

In central western Siberia and the Urals, the latest mammoths belong to the Allerød and Younger Dryas (*Lugovskoe*) (Table 1). The Allerød vegetation of these regions comprised a combination of open landscapes (with graminoids, wormwood and chenopods) and birch–larch woodlands (*Volkova* 2005: p. 83). In the Younger Dryas, the central part of the West Siberian Plain where the *Lugovskoe* site is situated was covered by open woodland with larch (*Muratova et al.* 1993: p. 114). The Younger Dryas vegetation of western Siberia was mostly treeless, with some shrubs growing along the river valleys (e.g. *Blyakharchuk & Sulerzhitsky* 1999; *Volkova* 2005).

The 'youngest' mammoth in western Siberia is known from the Yuribei locality on Gydan Peninsula (Fig. 1). It existed at the onset of the Holocene, *c.* 10 000 yr BP (or *c.* 11 500 cal. yr BP) (Table 1, Fig. 3). The vegetation at that time was sedge communities, peat bogs and shrubs (e.g. *Ukrainitseva et al.* 1996: p. 134). This was a time of transition from open dry tundra-steppe landscapes to the emergence of forest-tundra and peat bogs. Larch and birch began to penetrate the Polar Urals and northern parts of western Siberia at *c.* 9800 yr BP (*Andreev et al.* 2001; *Forman et al.* 2002; *Jankovská et al.* 2006). Peat accumulation in the arctic region of West Siberia started at *c.* 11 600–10 700 yr BP, while it intensified in the early Holocene, *c.* 9500 yr BP (*Peteet et al.* 1998: p. 122).

In the southern Taymyr Peninsula, vegetation in the early Holocene, *c.* 10 000–9500 yr BP, comprised herbaceous species along with shrub birch and willow (*Andreev et al.* 2004a). In northern Taymyr, dwarf birch and Ericaceae dominated directly after

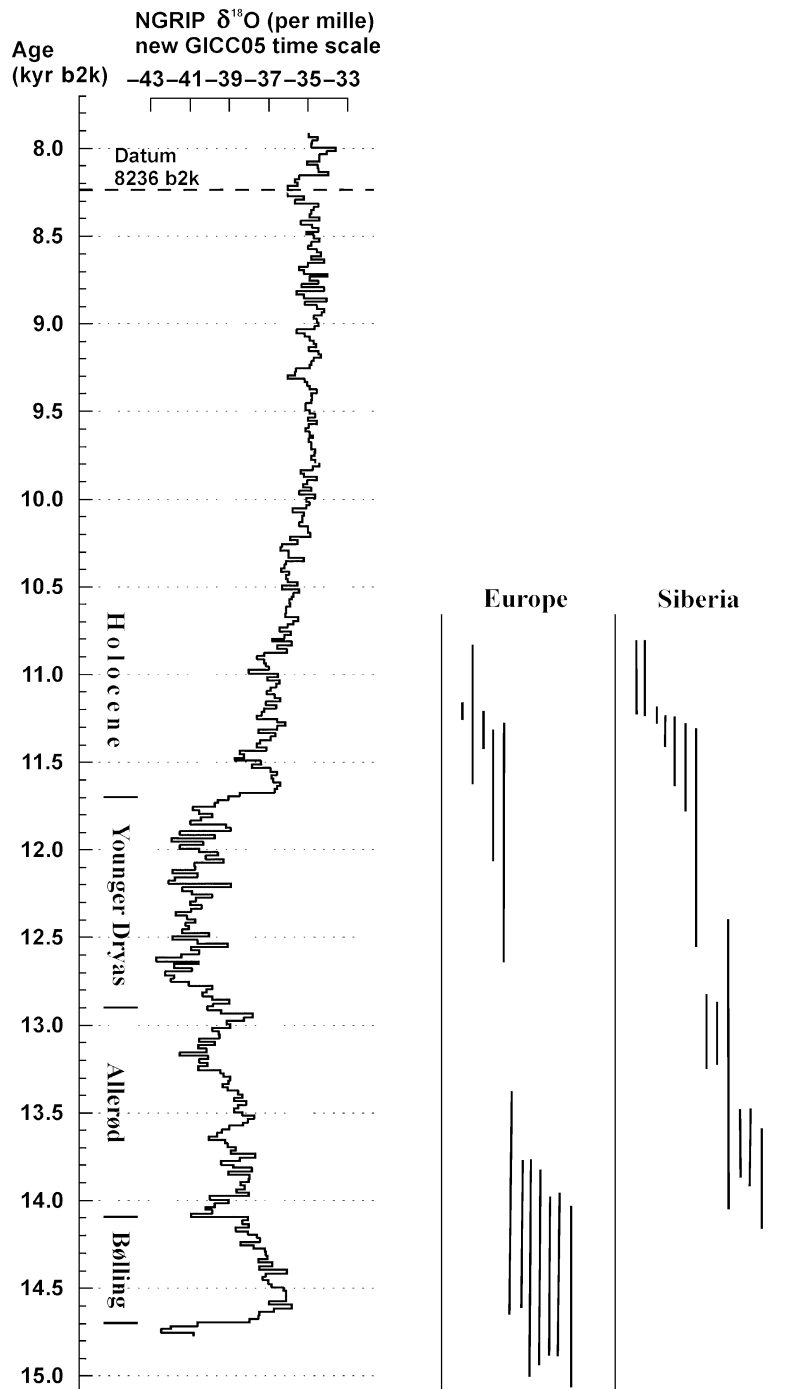


Fig. 3. Distribution of the Lateglacial calibrated age ranges for the woolly mammoths in Eurasia (see Table 1) on the background of GICC05 chronology (after Rasmussen *et al.* 2006, modified).

c. 10 000 yr BP (Andreev *et al.* 2003). At the onset of the Holocene (*c.* 10 000 yr BP), trees and shrubs increased in the vegetation cover while herbs and dwarf shrubs decreased (e.g. Tarasov *et al.* 2007: p. 294). At *c.* 9600 yr BP, larch forests expanded greatly into the High Arctic, and were dominant at *c.* 9600–9200 yr BP (Andreev *et al.* 2004a). By *c.* 10 000 yr BP, tundra-steppe vegetation in southern Taymyr was replaced by a shrub tundra with shrub birch and alder (Andreev *et al.* 2002). On the neighbouring Severnaya Zemlya archipelago,

vegetation at *c.* 11 500–9500 cal. yr BP (about 10 000–8500 yr BP; see Reimer *et al.* 2004) was represented by tundra-like sedge-grass associations (Andreev *et al.* 2008).

In the Novosibirskiye Islands region, the early Holocene vegetation may be reconstructed as tundra, although long pollen records from this archipelago are few in number. Pollen data from the southern coast of the Laptev Sea (Lena River delta) show that at least at *c.* 10 000 cal. yr BP (or *c.* 8900 yr BP, see Reimer *et al.*

2004) shrub tundra dominated the landscape (Andreev *et al.* 2004b, 2009). At the Pleistocene–Holocene boundary (*c.* 10 000 yr BP; or 11 500 cal. yr BP), shrub birch and alder had begun to replace the herb-dominated tundra, and finally at *c.* 8500 yr BP larch forests appeared (Pisaric *et al.* 2001; Schirrmeister *et al.* 2002).

In the northeasternmost part of Siberia (Chukotka region), the mammoths could survive even longer, up to about 9000–8700 yr BP (Kyttyk Peninsula) (Table 1). At that time, trees like birch and shrub alder expanded from mountainous regions to the coast of the East Siberian Sea (e.g. Lozhkin *et al.* 1993: p. 321; Kaufman *et al.* 2004). A clear warming trend and related expansion of trees is observed in coastal northeastern Siberia at *c.* 12 000–11 000 cal. yr BP (about 10 200–9500 yr BP; see Reimer *et al.* 2004) and ended at *c.* 10 000–9000 cal. yr BP (or *c.* 8900–8000 yr BP) (Kaufman *et al.* 2004). In the early Holocene, the vegetation of Chukotka was represented by a combination of shrub-grass tundra and birch forest tundra, although shrub formations became common at *c.* 9900 yr BP while trees might have existed in the river valleys (Lozhkin *et al.* 2007).

The survival of small (but not dwarf – see Lister 1993 and Vartanyan *et al.* 1993 vs. Tikhonov *et al.* 2003 and Vartanyan *et al.* 2008) mammoth sub-species, *Mammuthus promigenius vrangeliensis* (Garutt *et al.* 1993), on Wrangel Island in the Siberian Arctic deserves special attention. The phenomenon of a very late survival of mammoths was discovered in the early 1990s (e.g. Vartanyan *et al.* 1995), and several issues arose about the relationship of these animals with environmental conditions and human occupation (e.g. Martin & Stuart 1995). The latest results based on pollen composition from lacustrine deposits (Lozhkin *et al.* 2001; Vartanyan 2007) show that the mid-to-late Holocene environment of Wrangel Island was relatively stable and represented grassland with dwarf willow (Lozhkin *et al.* 2001). Vartanyan (2007: p. 120) noted that peat accumulation began in the early Holocene and ended at *c.* 8000–7500 yr BP, thus reflecting cooling conditions. Palynological data for the period *c.* 4300–3800 yr BP (Vartanyan 2007: p. 122) testify to the presence of dwarf birch and perhaps willow. After *c.* 3000 yr BP, the area covered by shrubs reduced significantly, and dwarf birch and willow disappeared (Vartanyan 2007: p. 123). Vartanyan (2007: p. 128) connects this event with the final extinction of the Wrangel population of mammoths, because shrubs were an important part of their winter diet. Over 100 ¹⁴C dates on the Wrangel Island mammoths suggest that at the end of Late Pleistocene they settled the region at *c.* 22 400–12 000 yr BP until *c.* 9000–3700 yr BP, with a gap at *c.* 12 000–9000 yr BP (Vartanyan *et al.* 2008). It seems unlikely that humans had anything to do with the final demise of the Wrangel Island mammoths (Vartanyan *et al.* 2008) (also see below).

The compilation of a pollen database for northern Asia (Tarasov *et al.* 2007: p. 294) has demonstrated that trees expanded into Arctic regions of mainland Siberia after *c.* 12 000 cal. yr BP (corresponding to *c.* 10 300 yr BP; see Reimer *et al.* 2004). This is in accord with data on the treeline history in northern Siberia (MacDonald *et al.* 2000).

The content of mammoth stomachs is one of the most reliable sources concerning the food and vegetation available to the animal just before its death. In this respect, the results of the analysis of Yuribei mammoth remains (Ukrainitseva 1993; Ukrainitseva *et al.* 1996) are very important. The most reliable ¹⁴C date for this individual is *c.* 10 000 yr BP (Stuart *et al.* 2002: p. 1566) (Table 1). In the gut, the identified macrofossils were represented mainly by grasses (95%), with some arboreal species (1%) and mosses (0.5%); about 3.5% of plants were unidentifiable (Ukrainitseva 1993). Taking into account the results of the analysis of gut content for other mammoths in Siberia (Ukrainitseva 1993), it is concluded that the main type of food was herbaceous plants, with the addition of some shrubs (dwarf alder and birch) and trees (larch). The last meal of the Yukagir mammoth, which died at *c.* 18 500 yr BP in the Siberian Arctic, consisted mainly of grasses and sedges, with significant amounts of dwarf willow twigs and different herbs and mosses (van Geel *et al.* 2008). The clear tendency of mammoths in eastern Europe to occupy periglacial grasslands can be seen repeatedly (e.g. Velichko & Zelikson 2005). Thus, the presence of a grass-dominated landscape was vital for mammoths, and the loss of open habitats coincides in northern Eurasia with their final extinction (see the generalized vegetation dynamics from the LGM to the middle Holocene in Edwards *et al.* 2000 and Zheng *et al.* 2004).

Human role in the extinction of mammoth in Eurasia: current results

The contribution of humans to the final extinction of the mammoth is one of the hotly debated subjects in archaeology and palaeoecology (e.g. Gaudzinski *et al.* 2005). Scholars working in Europe tend to accept mammoth hunting on a significant scale (e.g. Germonpré *et al.* 2008), while those from Siberia do not accept widespread human hunting of mammoths and a strong human impact on the population (e.g. Derevianko *et al.* 2000; Zenin *et al.* 2000; Kuzmin & Orlova 2004: 155–160). By any means, it should be kept in mind that the final mammoth extinction took place over a vast area of northern Eurasia in a relatively short period of time, *c.* 12 000–8700 yr BP (Table 1), and it is almost impossible to imagine that humans exterminated mammoths everywhere, including Arctic regions that were sparsely populated

in the Upper Palaeolithic. In a recent review, Koch & Barnosky (2006: p. 240) rejected the 'blitzkrieg' model of megafauna extinction for northern Eurasia. Numerical analysis of ^{14}C data for mammoths and humans in the Late Pleistocene worldwide (Ugan & Byers 2007, 2008) shows that environmental changes were chiefly responsible for the disappearance of mammoths in Europe and Siberia, and that the human contribution to this phenomenon was minor.

Another aspect of megafauna extinction is that in most of Eurasia (including northern parts of eastern Europe and Siberia) people and mammoths co-existed in the same regions for millennia (e.g. Orlova *et al.* 2004c). In recent attempts to model the human–mammoth interaction (Nogués-Bravo *et al.* 2008), some authors have made assumptions and factual mistakes which greatly affect their conclusions. First, the suggestion that there was an increase in hunting pressure at the time of their collapse is not justified by archaeological data; in northern Siberia, there are no final Upper Palaeolithic sites with mammoth bones. Second, the human habitats at 30 000 yr BP and 21 000 yr BP covered northern parts of Eurasia (e.g. Vasil'ev *et al.* 2002; Pitulko *et al.* 2004; Pavlov 2008) which were void of people according to Nogués-Bravo *et al.* (2008: p. 0867). Third, the authors projected sizes of human populations, estimated for Europe only, have been applied to all northern Eurasia (Nogués-Bravo *et al.* 2008: p. 0690). Finally, their statement 'the first recorded human presence above 60°N dated from 11 ky BP' (Nogués-Bravo *et al.* 2008: p. 0690) citing Dolukhanov *et al.* (2002) as a source (see Nogués-Bravo *et al.* 2008: p. 0692) is based on incorrect information. Conclusions by Dolukhanov *et al.* (2002) suffer from numerous factual mistakes and misinterpretations (e.g. Kuzmin & Keates 2004, 2006), and as a result the conclusions by Nogués-Bravo *et al.* (2008), in the opinion of the present author, have little value.

Leshchinskiy (2009: p. 73) put forward the idea of unprecedented geochemical changes on the Pleistocene–Holocene boundary in landscapes of northern Eurasia, which resulted in mineral deficiency for mammoths and caused stress and enzootia. This, according to Leshchinskiy (2009), was one of the major causes of mammoth extinction, and the role of ancient hunters was negligible compared to the natural extinction process.

It is possible that Upper Palaeolithic humans in northern Eurasia hunted mammoths (probably only occasionally or opportunistically), but even in relatively well-studied regions like western/central Europe direct data on this subject are still very scanty, and it is impossible to derive any reliable conclusion about the contribution of human hunting to the final demise of mammoth. Therefore, this issue needs more research.

Major patterns in the extinction of woolly rhinoceros in Eurasia

The chronology of the rhinoceros in northern Eurasia at the end of the Pleistocene is not known as well as that of the mammoth, and only general patterns of its existence and extinction can be established (Orlova *et al.* 2004a; Stuart & Lister 2007). In Europe, the 'youngest' rhinoceros (*c.* 13 600 yr BP) is known from the Gönnersdorf site in the Rhine River valley (Fig. 2; Table 2); another find, from Vaumarcus (Switzerland), has a similar age of *c.* 14 000 yr BP (Stuart & Lister 2007). In Asia, the latest rhinoceroses have ^{14}C ages of *c.* 14 400–12 280 yr BP in the Urals and Trans-Urals regions and *c.* 13 170–10 770 yr BP in western Siberia (Table 2). In other regions of Asia, the rhinoceros ^{14}C dates are older than *c.* 14 000 yr BP (Orlova *et al.* 2004a).

The extinction of the rhinoceros in Europe corresponds with the Older Dryas cold event. At that time, the landscapes of most of western, central and eastern Europe were steppe-like periglacial tundra and forest-tundra (Simakova & Puzachenko 2008c: 366–367). Stuart & Lister (2007: p. 291) relate the disappearance of rhinoceros from Europe to the Allerød when forest formations expanded. However, they do not accept the post-12 000 yr BP age of rhinoceros in Siberia (Stuart & Lister 2007: p. 291).

In the Urals and western Siberia, rhinoceroses became extinct during the Bølling–Allerød warming phase (Table 2), when landscapes of forests with some open spaces prevailed in the central West Siberian Plain (Krivonogov 1988: p. 89). In the Urals and adjacent regions, open landscapes with some birch forests dominated (e.g. Kremenetski *et al.* 1999).

The latest ^{14}C date for the rhinoceros in Eurasia, *c.* 10 770 yr BP, is known from the Lugovskoe locality in the central West Siberian Plain (Table 2). This time corresponds to the Younger Dryas cold event when the central West Siberian Plain was covered by steppe-like formations with chenopods, grasses and sedges (e.g. Krivonogov 1988: pp. 89–90; Velichko *et al.* 2002: p. 78). In terms of the reliability of this ^{14}C date, it should be pointed out that there are also several mammoth ^{14}C dates of *c.* 13 700–10 200 yr BP from this site (Orlova *et al.* 2004b). This testifies in favour of a secure determination of the ^{14}C age for this specimen. Because the megafaunal bones in this locality experienced some re-deposition (Leshchinskiy 2006: p. 34), more work is needed to confirm the age of the latest rhinoceros and mammoth there.

However, the pattern of a late survival of rhinoceros in the Urals and western Siberia seems evident (Table 2), and is similar to that of giant deer (Stuart *et al.* 2004). Continuity of the existence of rhinoceros in the Urals and western Siberia – testified by a series of ^{14}C dates from *c.* 14 700 yr BP to *c.* 12 300 yr BP and further to *c.* 10 780 yr BP (Table 2) – is a strong argument in

Table 2. The latest ^{14}C dates for woolly rhinoceroses in Eurasia.

Region, site	Latitude, N	Longitude, E	^{14}C date (yr BP)	Lab. no.	Calibrated date (cal. yr BP) ¹	Climatic event	Reference
Europe							
Gönnersdorf	50°31'	07°18'	13 610±80	OxA-10201	16 640–15 800	Older Dryas	Stuart & Lister (2007)
Vaumarus	46°53'	06°45'	13 980±140	ETH-8777	16 150–15 150	Older Dryas	Stuart & Lister (2007)
Urals and the Trans-Urals							
Lobvinskaya Cave	59°28'	60°04'	12 275±55	KIA-5670	14 500–13 970	Bolling	Stuart & Lister (2007)
Zlatoustovka	52°58'	55°19'	12 330±120	BashGI-107 (L.U-1668)	14 880–13 960	Bolling	Latypova & Yakheemovich (1993)
Kotel Grotto	57°45'	58°45'	13 245±65	OxA-10921	16 090–15 340	Older Dryas	Stuart & Lister (2007)
Perehinsky I Grotto	57°27'	61°27'	13 575±65	OxA-10928	16 570–15 770	Older Dryas	Stuart & Lister (2007)
Bobylek Grotto	56°23'	57°37'	14 200±400	IERZH-164	18 480–15 910	Older Dryas	Orlova <i>et al.</i> (2008)
Bobylek Grotto			14 630±80	OxA-11296	18 010–17 180	GS 2b stadial	Razhev <i>et al.</i> (2005)
Serpievskaya I	54°50'	57°53'	14 300±110	SOAN-5307	17 640–16 590	Older Dryas	Orlova <i>et al.</i> (2008)
Kurgan City	55°26'	65°21'	14 390±150	SOAN-5880	17 890–16 700	Older Dryas	Orlova <i>et al.</i> (2008)
Western Siberia							
Lugovskoe	60°58'	68°32'	10 770±250	SOAN-4757	13 200–11 990	Younger Dryas	Orlova <i>et al.</i> (2004a)
Orda River	54°24'	81°40'	13 165±180	SOAN-6385	16 180–15 070	Older Dryas	Orlova <i>et al.</i> (2008)
Orda River			14 700±210	SOAN-6386	18 570–17 030	GS 2b stadial	Orlova <i>et al.</i> (2008)

¹Calib 5.1.0 software is used (with ± 2 sigma, all intervals combined).

favour of rhinoceros survival in these regions until the end of the Lateglacial, i.e. later than anywhere else in Eurasia.

Some ^{14}C dates for rhinoceros from northern Asia within a range of *c.* 11 000–9500 yr BP cannot be accepted at face value. For example, the ^{14}C date of 9510±260 yr BP (IERZH-93) from Lobvinskaya Cave in the Urals (Stuart & Lister 2007: p. 291; Kosintsev 2008: p. 265) is less reliable because a second rhinoceros date from this locality has turned out to be older, *c.* 12 280 yr BP (Stuart & Lister 2007; Orlova *et al.* 2008). Fu (2002: p. 12) and Jin & Kawamura (1996: p. 319) assumed that rhinoceros existed in northeastern China until *c.* 10 600 yr BP (*c.* 10 940 yr BP according to 5730 yr half-life value for ^{14}C isotope used in China), based on the ^{14}C date of 10 940±170 yr BP (no laboratory code given). However, there is no evidence that rhinoceros remains were directly ^{14}C -dated, and the association of the rhinoceros bones and dated material at the Qingshantou locality is vague; this date is therefore rejected. Another quite 'late' ^{14}C date on rhinoceros bone was published for the Hutouliang locality in northern China (40°10'N, 114°09'E): 11 000±210 yr BP (PV-0156) (Radiocarbon Dates 1991: p. 22) and corresponds to *c.* 10 690 yr BP using Libby's half-life value for ^{14}C isotope (5568 yr). This date is also suspiciously young, taking into account general patterns of rhinoceros extinction in Eurasia (Table 2). At least additional dating of this site is necessary before it will be accepted as a reliable age determination.

Concluding remarks: where to now?

After summarizing the available evidence for Eurasia, the spatiotemporal patterns of extinction of the woolly mammoth and rhinoceros take shape. It is clear that the final disappearance of the rhinoceros was in general the gradual shrinking of its habitat, and that the last refugium was located in the Trans-Urals and western Siberia (Fig. 2). It is important that the final extinction of the rhinoceros took place not in the Arctic but in the temperate zone of the European/Asian border area, unlike woolly mammoth, which finally became extinct in the Arctic regions (Stuart & Lister 2007; Vartanyan *et al.* 2008). The problem with the rhinoceros is the still inadequate degree of direct ^{14}C dating of its remains; for example, fewer than 100 ^{14}C values are known for eastern Europe, the Urals and Siberia (Garutt & Boeskorov 2001; Orlova *et al.* 2008). Therefore, increasing the ^{14}C database for the rhinoceros in Eurasia is an urgent task in the years to come.

As for the mammoth, it is important to note that the 'patchy' landscapes of northeast Europe, western Siberia and the Urals in the Lateglacial allowed mammoths to survive in the shrinking open biomes outside the Arctic for some time at *c.* 12 000–9800 yr BP (Fig. 1). Several extra-Arctic refugia existed in northern

Eurasia after *c.* 12 000 yr BP, and this model now replaces Sher's (1997) 'retreat to the north' scenario. The 'decay' of the mammoth habitat at *c.* 12 000–9600 yr BP in northern Eurasia was complex, with several 'pockets' of late mammoths (Figs 1, 3). This may be tentatively called patchy survival of mammoths in the Lateglacial beyond the High Arctic. The absence of direct correlation between mammoth extinction and climatic events highlights that mammoth–environment interactions were complex, with a significant delay of its final disappearance ('extinction lag' *sensu* Lister & Stuart 2008).

However, there are still several problems that need further research – among them the role of humans in the mammalian extinction of the Pleistocene–Holocene boundary in different parts of Eurasia. It seems that hunting pressure on mammoth populations might have been quite different in relatively densely settled western and central Europe, and to some extent eastern Europe, compared to the vastness of Siberia with its sparse human communities.

The discovery of a new Holocene mammoth refugium on Chukotka (Vartanyan *et al.* 2005) raises the issue of other possible places where mammoths could have survived until the early–middle Holocene. It is clear that more work needs to be done in northern and northeastern parts of Siberia, as well as in northeastern Europe, in terms of the direct ¹⁴C dating of mammoths.

Therefore, among the most important tasks for the next decade with respect to study of the final Pleistocene extinction of woolly mammoth and rhinoceros in Eurasia are the following: (1) the accumulation of ¹⁴C data for rhinoceros from the Urals and western Siberia, and (2) study of the extreme northeastern Siberia for potentially very late mammoths.

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[Corrections added after online publication November 2009: firstly, 'In 1987,' was removed from the third line of the left column of p. 3. Secondly, 'Fig. 1.' was inserted in the twelfth line of the left column of p. 3. Thirdly, on p. 5, in table 1, '0' was changed to '90' in the ^{14}C date' column, 'Volchya Griva' row. Finally, the page range of the Nogués-Bravo et al. (2008) reference on p. 13 was incorrect in the originally published version.]