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New data on changes in the European distribution of the mammoth and the woolly rhinoceros during the second half of the Late Pleistocene and the early Holocene

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ABSTRACT

The PALEOFAUNA database developed by the authors contains information on more than 5500 Eurasian localities that yielded Late Pleistocene and Holocene mammalian fossils. The database is used to analyze the changes in the geographical distribution during the second half of the Late Pleistocene and the Holocene of two significant species – the mammoth *Mammuthus primigenius* and the woolly rhinoceros *Coelodonta antiquitatis*. Based on the geographical information, combined with (new) radiocarbon data, a correlation has been established between the observed shifts in the ranges of the two species and the climatic changes that occurred during the past 50 000 years. The results indicate that both species changed their distribution repeatedly; the expansion of the ranges increased during stadial intervals and decreased during most interstadials. Both species reached their maximum expansion during the Denekamp (=Bryansk) Interstadial, a relatively long interval that includes a number of cold phases. Later, the ranges in Europe of both mammoth and rhinoceros were reduced, a process that started before the end of the LGM. Progressive warming from the end of the Pleistocene onwards resulted in dramatic changes in the environment that appeared to be critical for the distribution of those animals. Mammoth and woolly rhinoceros ranges disintegrated into isolated spots, and later they disappeared completely from Eurasia. Relict populations of small mammoths persisted longer on isolated islands such as Wrangel Island. However, not only climate change had an impact on the distribution of the two species. Late Paleolithic and Mesolithic hunters might also have affected the size of the mammoth and woolly rhinoceros populations. Their impact was probably particularly high when the species were close to extinction.

1. Introduction

During the Late Pleistocene, the environment of the Northern Hemisphere was dominated by the so-called Mammoth Steppe ecosystem, characterized by a community of large and small mammals with a non-analogue composition. The Mammoth Steppe ecosystem covered a huge area that stretched from Western Europe, via Siberia to North America. The fossil record shows that the spatial distribution of the mammalian taxa differed geographically. The woolly rhinoceros *Coelodonta antiquitatis*, for example, never crossed Beringia to inhabit North America. In order to investigate the dynamic changes in the faunal composition of the Mammoth Steppe, fossil assemblages have been analyzed and a large number of Late Pleistocene mammal bones have been ^{14}C-dated. A series of new radiocarbon dates could be obtained for a number of localities in Eastern Europe and Asia in the frame of projects supported by the Netherlands Organization on Scientific Research (NWO) and the Russian Foundation for Basic Research (RFBR). These dates have given new insights into the geographical distribution of specific mammals during different climatic periods (interstadials and stadials) of the Late Pleistocene. This paper presents and discusses the changes in the geographical distribution of the mammoth and the woolly rhinoceros during the time span from about 50 000 years ago to the late Holocene.

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2. Geochronology of the second half of the Late Pleistocene

In recent decades, detailed studies of the Late Pleistocene and early Holocene have revealed the occurrence of a large number of climatic fluctuations. By definition, the Late Pleistocene starts at the beginning of the Eemian or Mikulino Interglacial as well as at the beginning of MI Sub-stage 5e (at the mid-point of Termination II or the MIS 6/5 transition) following the acceptance that MIS 5, Sub-stage 5e is the ocean equivalent of the terrestrial NW European Eemian Stage interglacial (Shackleton, 1977; Gibbard and van Kolfschoten, 2004). The interglacial is followed by the Weichselian/Valdai Glaciation, a period in which extensive glaciers developed. The Weichselian/Valdai has been divided into Early, Middle and Late Weichselian or Early, Middle and Late Valdai. The study of the terrestrial Late Pleistocene geological and botanical record indicated that the Weichselian/Valdaian stage encompasses a number of interstadials and stadials. The study of high-resolution logs, such as deep-sea cores, lake cores and especially the Greenland GRIP, GISP2, and NGRIP ice cores indicate the occurrence of major climatic oscillations. After the thermal maximum of MIS 5e (the Eemian/Mikulino Interglacial), a significant cooling has been indicated at the Marine Isotope Sub-stage 5e/5d boundary that marks the transition from the Eemian/Mikulino Interglacial to the Weichselian/Valdai Glaciation. A second significant cooling marks the transition from MIS 5 to MIS 4, which is dated to ca. 70 000 years ago. The isotopic signal suggests a major increase in continental ice volumes during MIS 4 and especially during MIS 2. The global ice volumes were somewhat reduced during MIS 3 (Middle Weichselian/Middle Valdai) (Lowe and Walker, 1997). The MIS 3 interval is characterised by a number of climatic fluctuations (interstadials) that have also been recognized in the continental record of Western and Central Europe: the Glinde and Oerel interstadials during the first half of MIS 3 and the Moershoofd, the Hengelo and the Denekamp interstadials (the equivalent of the Bryansk interstadial) during the second half of MIS 3. The Bryansk/Denekamp Interstadial is followed by a severe drop in temperature and a major increase in continental ice volumes: MIS 2. This cold period is often referred to as the Last Glacial Maximum (LGM) or Pleniglacial, representing the coldest phases of MIS 2. The end of the last cold stage is generally indicated as Deglaciation or as the Late Glacial. The end of the period of deglaciation is marked by two interstadial

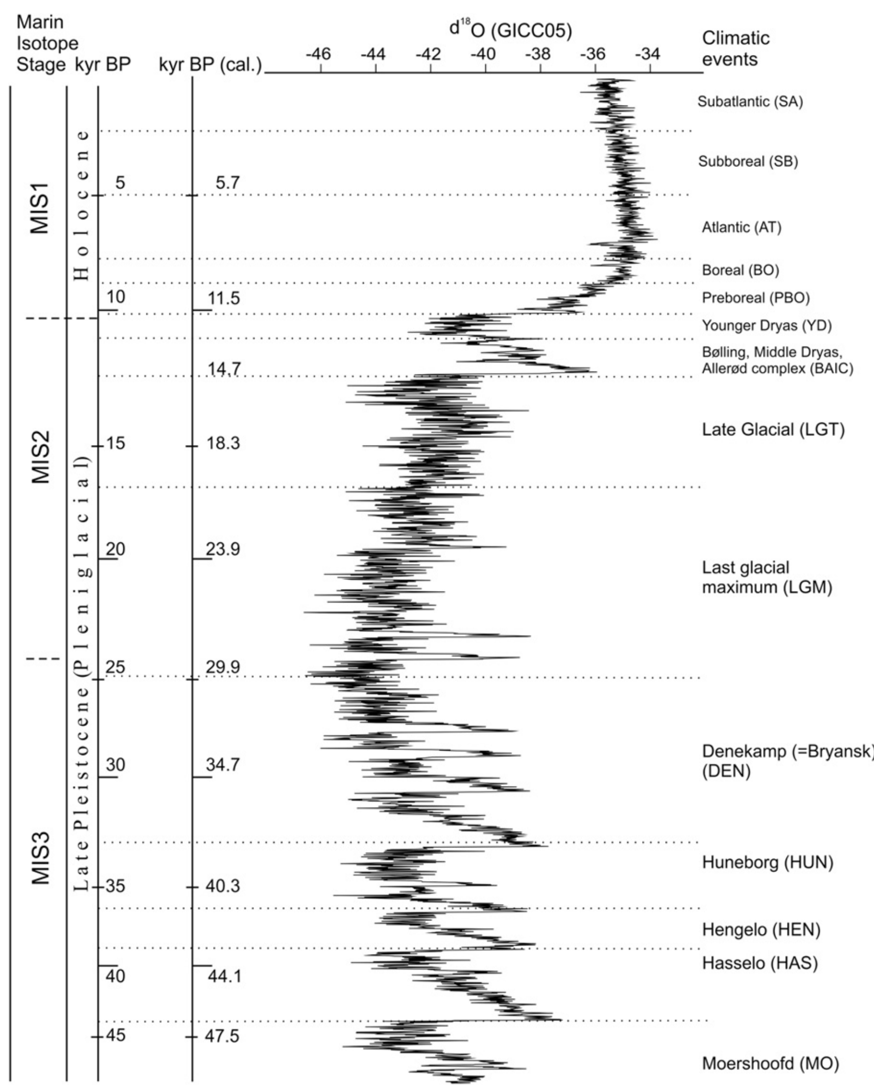

Fig. 1. Late Pleistocene – Holocene geochronological scheme (based on data published by Litt et al., 2001, 2007; Andersen et al., 2006; Svensson et al., 2006, 2008; Vinther et al., 2006; Gerasimenko, 2006, 2011; Mol, 2008).

episodes, namely Bølling and Allerød, separated by a brief stadial (Older Dryas) and followed by the longer Younger Dryas Stadial. The increase in temperature at the end of the Younger Dryas Stadial marks the Pleistocene/Holocene transition.

Discussion in this contribution is restricted to the second half of the Late Pleistocene and the beginning of the Holocene, a period that falls within the limits of ^{14}C dating. The following climate-stratigraphic units are covered (Fig. 1): the Moershoofd

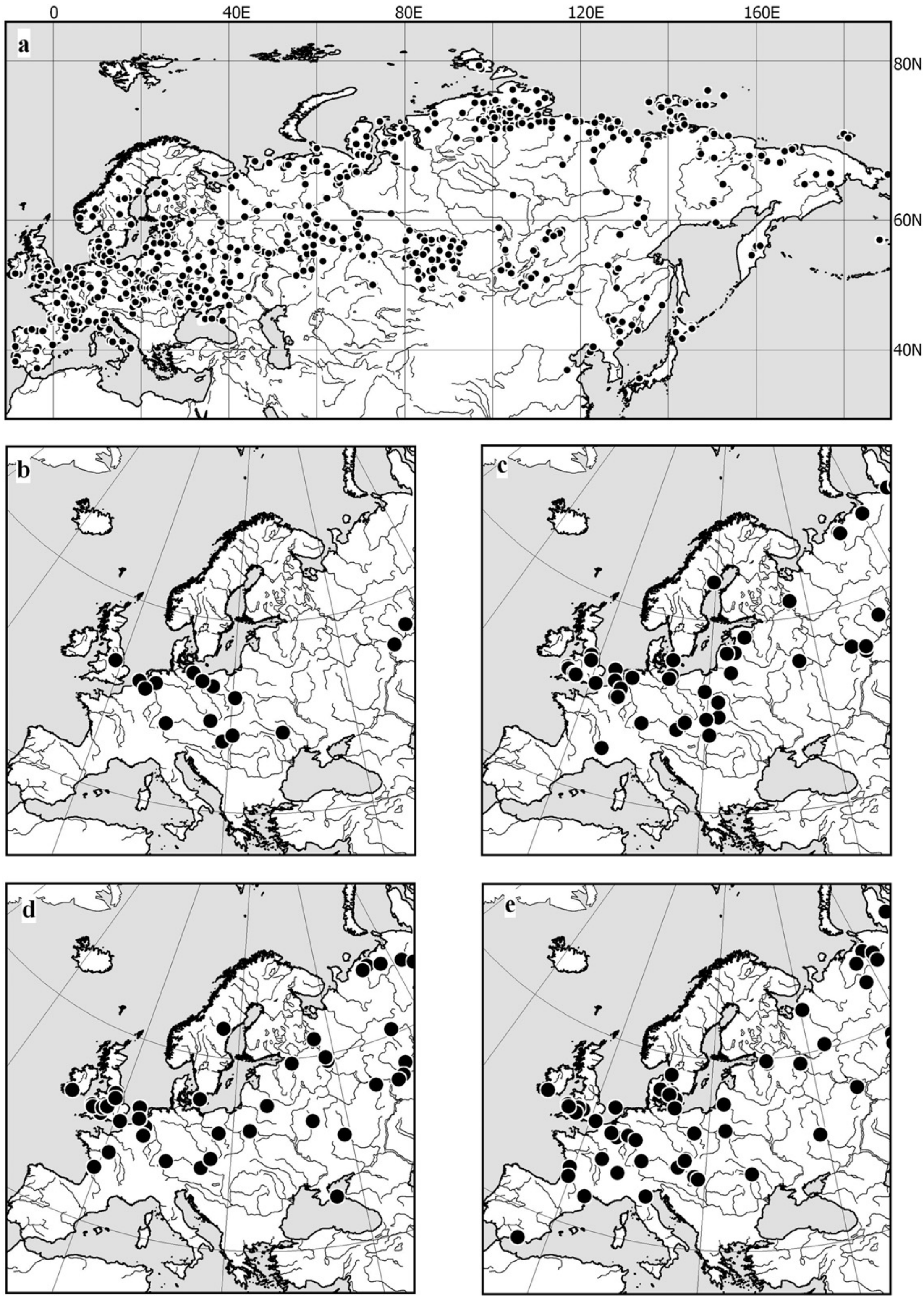

Fig. 2. Mammoth (*Mammuthus primigenius*) localities dated to: a – the Late Pleistocene localities in Northern Eurasia (PALEOFAUNA (Markova et al., 1995)); b – Moershoofd interstadial (MO), c – Hasselo stadial (HAS), d – Hengelo interstadial (HEN), e – Huneborg stadial (HUN).

Interstadial (^{14}C ages ~46 to 44 ka BP, MO), the Hasselo Stadial (44–39 ka BP, HAS); the Hengelo Interstadial (39–36 ka BP, HEN); the Huneborg Stadial (36–33 ka BP, HUN), the Denekamp (=Bryansk) Interstadial (33–24 ka BP, DEN), the Valdai (Weichselian) glacial epoch (24–17 ka BP, LGM), the Late Glacial (or Deglaciation) (17–12.4 ka BP, LGT), the Bølling and Allerød interstadials separated by the Middle Dryas cooling (12.4–10.9 ka BP, BAIC), the Younger Dryas Stadial (10.9–10.2 ka BP, YD) and the Preboreal warming (10.2–8.0 ka BP, PB) (Velichko et al., 2002; Chabai and Uthmeier, 2006; Gerasimenko, 2006;

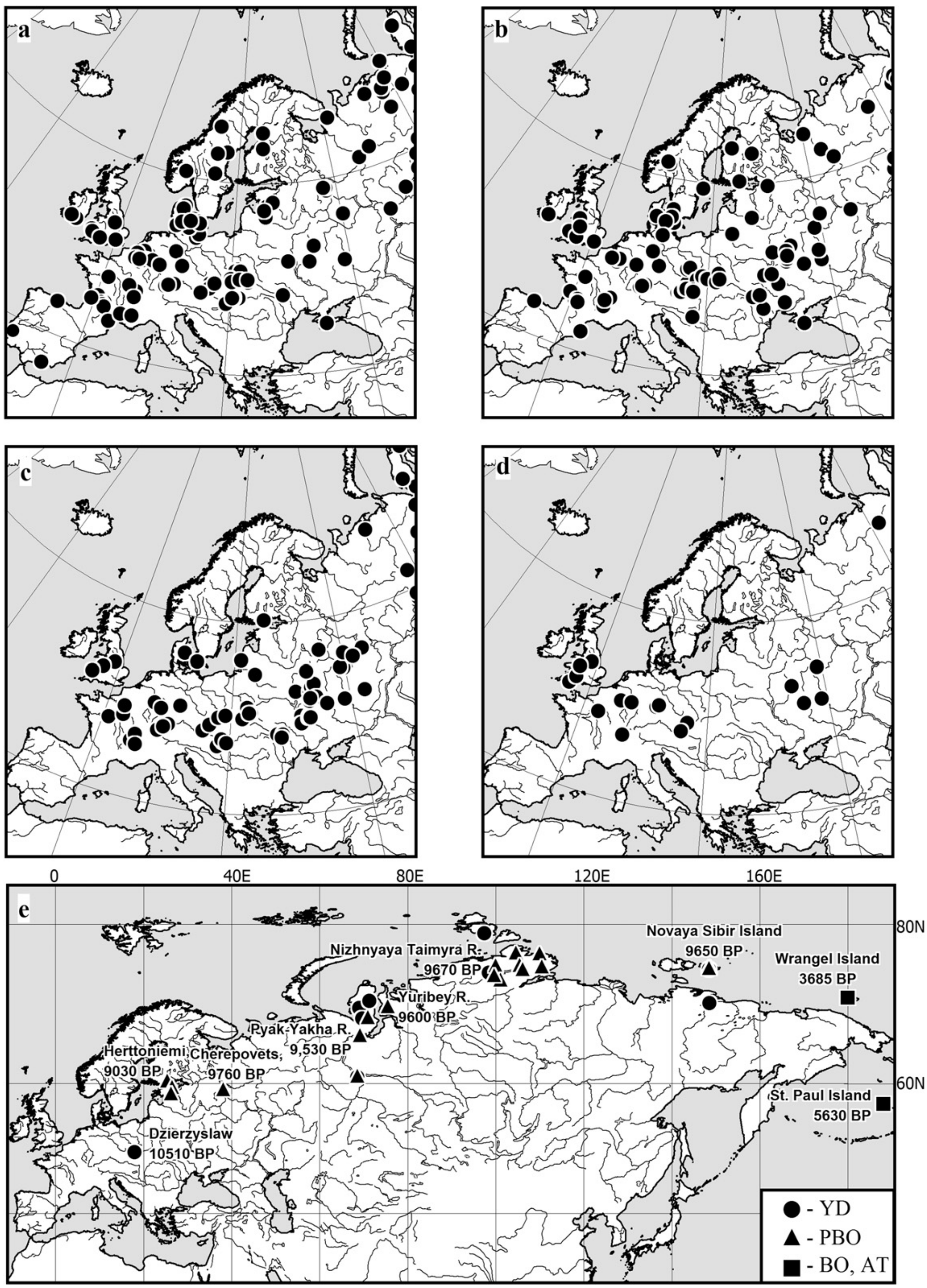

Fig. 3. Mammoth (*Mammuthus primigenius*) localities dated to: a – Denekamp (= Bryansk) interstadial (DEN); b – the maximum LGM cooling; c – Late Glacial time (LGT); d – interstadial warmings of Bøllng-Allerød (BAIC); e – Younger Dryas Stadial (YD); Preboreal (PB), Boreal and Atlantic (BO, AT) and Subboreal (SB).

Mol, 2008; Velichko and Faustova, 2009). The age scale in Fig. 1 is GICC05 as obtained from NGRIP (Vinther et al., 2006). It is connected with the ^{14}C timescale (BP) via the radiocarbon calibration curve Intcal09 (Reimer et al., 2009).

3. Methods and materials

Maps showing the geographical distribution of European localities where mammoth and woolly rhinoceros are recorded, have been compiled for the chosen time intervals using the PALEOFAUNA electronic paleontological database (Markova et al., 1995). The analyzed theriological material has been ^{14}C-dated. Recently, new radiocarbon dates have been obtained from Groningen University in the frame of RFBR-NWO (Project № 047.017.2006.014). These new dates are included in the analysis.

Localities in Northern Eurasia with dated bones of mammoth and woolly rhinoceros are shown in Figs. 2a and 5a. For information about the localities and the mammalian faunas the reader is referred to Vereshchagin (1979), Baryshnikov and Markova (2002, 2009), Orlova et al. (2008), Sher et al. (2005), Markova and Puzachenko (2007), Lister and Sher (2001), Stuart et al. (2002, 2004), Stuart (2005), Musil (1985), Kalhke (1994), Ukkonen et al. (1999, 2007), Lougas et al. (2002), Alvares-Lao and Garcia (2011) and many others included in the PALEOFAUNA database. There are also a number of summarizing publications including Markova and Kolfschoten (2008), Velichko (2009), Kuzmin (2010), Lorenzen et al. (2011), Stuart and Lister (2012).

The ^{14}C dates are reported by convention in BP, i.e. not calibrated.

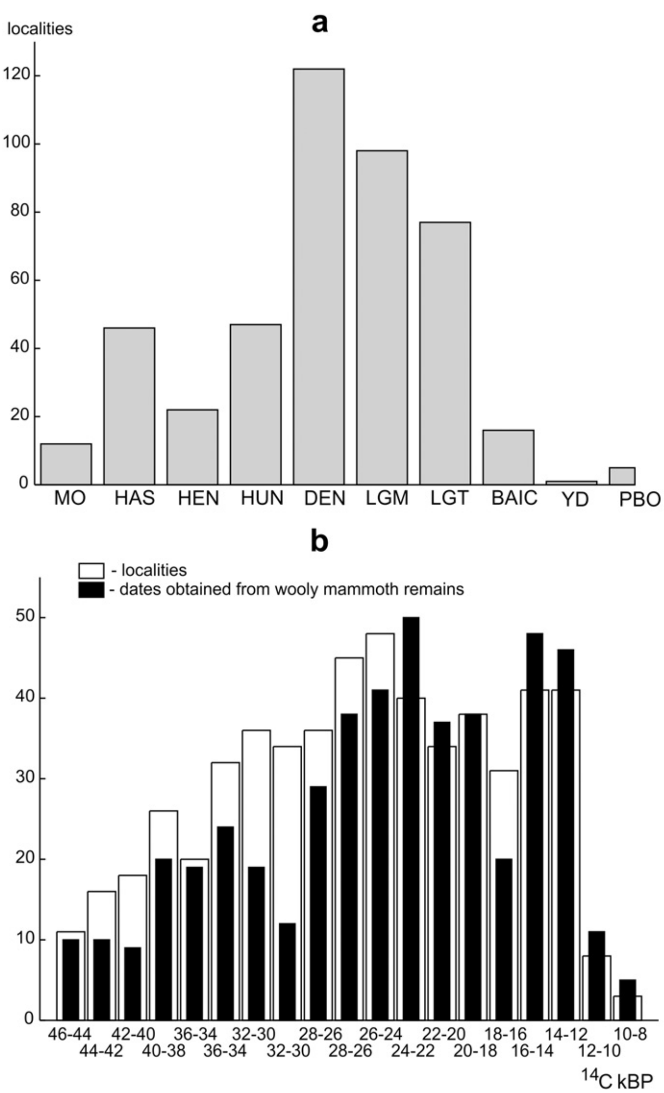

Fig. 4. Distribution of the localities in Europe with *Mammuthus primigenius* during the 'mega-interstadial' (MIS 3), at the last stage of the Valdai (Weichselian) glaciation (MIS 2), and in the Holocene (MIS 1): a – data clustered according to the time slices (for abbreviations see the text), b – data clustered according to fixed time intervals of 2000 years.

3.1. Mammoth *Mammuthus primigenius*

The geographical distribution of *M. primigenius* in Northern Eurasia shown in Fig. 2a is based on the mammoth records from 778 localities. A total of 1817 radiocarbon dates obtained from mammoth remains (1316 dates) or associated materials (plant remains, humus, charcoal) are available to put the data in a time frame. For the European territory the number of considered data is more restricted: 341 localities and 894 ^{14}C dates.

3.2. Woolly rhinoceros *C. antiquitatis*

The Northern Eurasian range of the woolly rhinoceros *C. antiquitatis* (Fig. 5a) was reconstructed based on 377 localities where the species has been recorded. The analyzed European record counts 141 localities with *C. antiquitatis*. To put the woolly rhinoceros record in a stratigraphical order, 546 radiocarbon dates from Northern Eurasia (328 dates from Europe) obtained from woolly rhinoceros remains (242 dates) or associated materials (bone and plant remains, humus, and charcoal) were available.

4. Dynamic changes in the spatial and temporal distribution of *M. primigenius* Blumenbach, 1799

Fig. 2a shows the geographical position of all the localities with records of *M. primigenius* in Northern Eurasia that were dated and included in the PALEOFAUNA database or described in numerous publications (e.g. Vereshchagin, 1979; Vereshchagin and Baryshnikov, 1985; Kahlke, 1994; Markova et al., 1995; Foronova, 2001; Garrut and Tikhonov, 2001; Lister and Sher, 2001; Lougas et al., 2002; Stuart et al., 2002; Kosintsev, 2003; Markova and Puzachenko, 2007; Markova and van Kolfschoten, 2008; Lorenzen et al., 2011; Nikolskiy et al., 2011). During the Late Pleistocene *M. primigenius* inhabited a vast area in Eurasia. However, the geographical distribution changed through time during the Middle and Late Valdai (Weichselian). The changes in the mammoth distribution from earlier intervals during MIS 3 up to the Holocene are discussed here (Figs. 2 and 3).

4.1. Moershoofd Interstadial – Denekamp (=Bryansk) interstadial (MIS 3)

Mammoth remains dated to the Moershoofd Interstadial (^{14}C ages ~46 to 44 ka BP, MO) are mostly confined to the central part of Europe (Fig. 2b). *M. primigenius* seems to have expanded its range during the Hasselo Stadial cooling (44–39 ka BP, HAS), when it penetrated into Northern Europe as far as the Arctic Ocean coasts (Fig. 2 c). It seems plausible that its expansion into the north was facilitated by the decay of the forest zone due to cooling. There are numerous mammoth localities on the British Isles where mammoths could have appeared at earlier stages of glaciation when the shelf became partly exposed. Later, during the Hengelo Interstadial (39–36 ka BP, HEN), the species occurred widely over Europe, as indicated by radiocarbon dated finds of mammoth bones. Mammoth remains have been found in Scandinavia (Ukkonen et al., 2007), which suggests that during this time, specific regions were free of inland glaciers (Fig. 2d).

During the next cold stage, the Huneborg Stadial (36–33 ka BP, HUN), the northern boundary of the mammoth range in Western Europe shifted southwards. The species disappeared from Fennoscandia except the southernmost part, but persisted in the north of Eastern Europe (Fig. 2e). This may be considered as

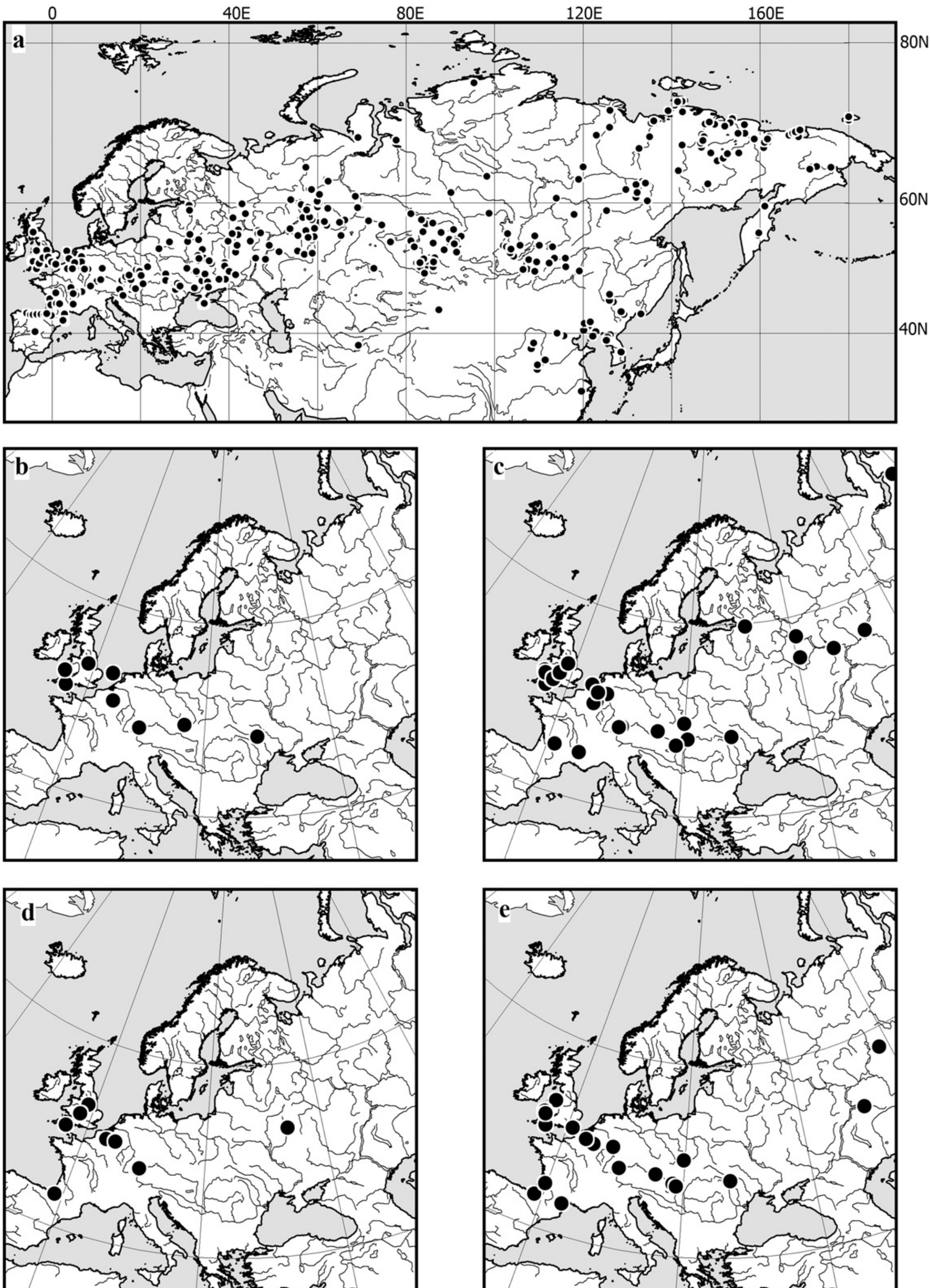

Fig. 5. Woolly rhinoceros (*Coelodonta antiquitatis*) localities dated to: a – the Late Pleistocene localities in Northern Eurasia (PALEOFAUNA (Markova et al., 1995); Tong and Moigne (2000), Pokee (1991)): b – Moershoofd interstadial (MO), c – Hasselo stadial (HAS), d – Hengelo interstadial (HEN), e – Huneborg stadial (HUN).

circumstantial evidence that the Scandinavian ice sheet expanded at that time. There are unique records of the species in southern Spain that indicate cooling and hence, the expansion of periglacial landscapes (Alvares-Lao et al., 2009).

At the end of the Middle Valdai (Weichselian), during the Denekamp (=Bryansk) Interstadial (33–~24 ka BP, DEN), mammoth was widely distributed all over Europe. Its bones are known from a geographically vast area including the Iberian Peninsula, northern Germany (Sommer and Benecke, 2009), the British Isles and the northern and northeastern parts of Eastern Europe. A number of finds from localities on Vaigach Island and in northeast Russia have been dated in the frame of the NWO–RFBR Project to that interval (Table 1). The numerous *Mammuthus* finds in Scandinavia indicate a noticeable shrinking of the ice sheet and the presence of ice-free areas (Ukkonen et al., 2007). More localities with mammoth remains were discovered on the British Isles (Fig. 3a). The majority of the radiocarbon dated mammoth sites date from the Moershoofd–Denekamp time interval and the geographical distribution of the mammoth reached its peak before the last glacial maximum, 28–24 ka BP (Fig. 4).

Table 1
New ^{14}C dates (uncalibrated) obtained on remains of *Mammuthus primigenius* from Eastern Europe.

Locality	Lat	Long	^{14}C age (BP)	Sigma	Lab. number
Vaygach Isl.	69.684	60.028	32 150	+210/−160	GrA-42211
Vaygach Isl.	69.684	60.028	24 550	120	GrA-42209
Megra	66.149	41.621	31 690	200	GrA-42205
Arkhangelsk	64.537	40.566	34 590	+240/−220	GrA-42207
Arkhangelsk	64.537	40.566	18 300	70	GrA-42227
Topsa	62.618	43.633	24 430	110	GrA-42197
Bogoslovo	62.174	49.102	29 530	150	GrA-42206
Krasnoborsk	61.560	45.936	21 690	120	GrA-42199
Stepanitsa	61.382	46.389	28 080	+140/−130	GrA-42210
Kelkolovo	59.774	31.038	33 160	+220/−210	GrA-39117
Shapki quarry	59.597	31.203	35 140	+280/−260	GrA-41235
Berdyzh	52.833	30.917	27 790	±120	GrA-38018
Yurovichi	51.920	29.550	25 660	+160/−150	GrA-38919

4.2. *LGM –deglaciation interval (MIS 2)*

During the maximum cooling of the last glaciation (LGM, 24–17 ka BP) (Fig. 3b), mammoth was still widespread over most of Europe except for the Apennine and Balkan peninsulas. The species seem to have retreated from the south, which might be attributed not only to climatic changes but also to a growing impact of human hunting. Remarkable is the conspicuous absence of mammoths in the Scandinavian North (Ukkonen et al., 1999) and a reduced number of mammoth finds in northeast Europe, most probably due to ice sheet gradual expansion and an extremely severe climate. For NE Europe there are some dates obtained recently for that time interval (see Table 1).

During the Late Glacial (LGT, 17–12.4 ka BP), the mammoth range was noticeably shrinking (Figs. 3c and 4). The species disappeared completely from the Scandinavian Peninsula, though still occurring at the periphery of Fennoscandia. The southern limit of the range shifted northward. The geographical density of *M. primigenius* localities was considerably reduced at that time, in particular during 18–16 ka BP (Fig. 4b). These changes might be attributed to the impact of the ongoing warming accompanied by further deterioration of the existing environments. The growing human population in Europe might also have had a negative effect on the mammoth habitats. The steady decrease of the range was interrupted during a short period, from about 13 to 10 ka BP, when an expansion of the range can be observed.

During the next interval (Bølling and Allerød warm phases) (BAIC, 12.4–10.9 ka BP) the European mammoth range shrank dramatically. Mammoth remains attributable to this warm interval have been recovered from 16 localities, mostly in the north of Western and Central Europe (Stuart et al., 2002) (Figs. 3d and 4). Mammoth might have occurred further north, but the evidence is missing. The mammoth distribution between 12.4 and 10.9 ka BP seems to point to disintegration of the mammoth range in Europe. The latest Holocene mammoth locality in Europe is dated to 9760 ± 40 BP (Cherepovets, Russia) or 9030 ± 165 BP (Herttoniemi–Helsinki, Finland) (Pearson, 1965; Stuart et al., 2002) (Fig. 3e).

Fig. 3e shows the latest finds of mammoth remains in Eurasia dated to the Younger Dryas (YD, 10.9–10.2 ka BP); the Early Holocene/Preboreal (PB) and Boreal (BO), 10.2–8 ka BP; the Middle Holocene (Atlantic (AT), 8–5 ka BP); and the Late Holocene (Subboreal (SB), 5–2.5 ka BP). Undoubtedly, the mammoth range broke into isolated populations during the short Younger Dryas stadial. The decline of the range continued throughout the Holocene. In the Early Holocene, mammoth herds inhabited the Baltic region (Stuart et al., 2002), the Yamal peninsula (Arslanov et al., 1982), the Taymyr peninsula (MacPhee et al., 2002), the Gydan peninsula, the Severnaya Zemlya archipelago (Oktyabrskaya Revolutsiya Island), the Ob' drainage basin, the New Siberian Islands (Novaya Siberian Island) (Stuart et al., 2004; Sher et al., 2005) and Wrangel Island (Vartanyan et al., 1995). In the Middle and Late Holocene the last known populations of mammoth persisted on Wrangel Island and on St. Paul Island in the Bering Sea (the Pribyloff Islands) where ^{14}C dates converge on 5630 BP (Fig. 3e). The latest date obtained on mammoth bones from Wrangel Island is 3685 ± 60 BP (Kuzmin and Orlova, 2004).

It can be concluded that the mammoth was adapted to a) a dry and cold climate controlled primarily by an anticyclonic circulation pattern, to b) a highly productive steppe environment, and to c) a thin snow cover during winter. However, during the LGM the environment was not favorable for *M. primigenius*. A gradual decline of the mammoth range from 22 to 12 ka BP resulted in the rapid extinction of the species at the Pleistocene/Holocene boundary. Since the beginning of the Holocene, marked by an increase in humidity, an increase of cloudiness and a related decrease of incoming solar radiation, the "mammoth steppe" began to degrade, along with the loss of productivity in open landscapes and reforestation. The newly formed climatic and environmental conditions resulted in the extinction of *M. primigenius.*

5. Dynamic changes in the spatial and temporal distribution of *C. antiquitatis* Blumenbach, 1799

The woolly rhinoceros fossil record of Eurasia has been analyzed is a more or less identical way. The data presented in Figs. 5 and 6 are retrieved from the PALEOFAUNA database as well as from the literature (e.g. Kahlke, 1994; Foronova, 2001; Garrut and Boeskorov, 2001; Kahlke and Lacombat, 2008; Kuzmin, 2010; Stuart and Lister, 2012). A number of bones from localities in the north of Eastern Europe (Russia) have been dated in the frame of the NWO–RFBR Project (Table 2).

Table 2
New ^{14}C dates (uncalibrated) obtained of *Coelodonta antiquitatis* remains from localities in the north of Eastern Europe. The data are collected in the frame the NWO–RFBR Project.

Locality	Lat	Long	^{14}C age (BP)	Sigma	Lab. number
Kelkolovo	59.774	31.038	>45 000		GrA-38903
Kelkolovo	59.774	31.038	38 360	+300/−270	GrA-38819
Smorgon'	54.500	26.533	30 990	+220/−200	GrA-38943

The localities in Eurasia where woolly rhinoceros bones have been found that radiocarbon dated within the interval of ~50 000 to ~10 000 BP, are shown in Fig. 5a. There is a remarkable difference between the general outline of the mammoth range and that of the woolly rhinoceros during the Late Pleistocene. The geographical distribution of the latter is less extensive and confined mostly to the central part of Northern Eurasia and to the northeastern part of Eurasia, where a specific Beringian population of *C. antiquitatis* could exist. In addition, the woolly rhinoceros moved further south into the Far East (Tong and Moigne, 2000; Takahashi et al., 2007).

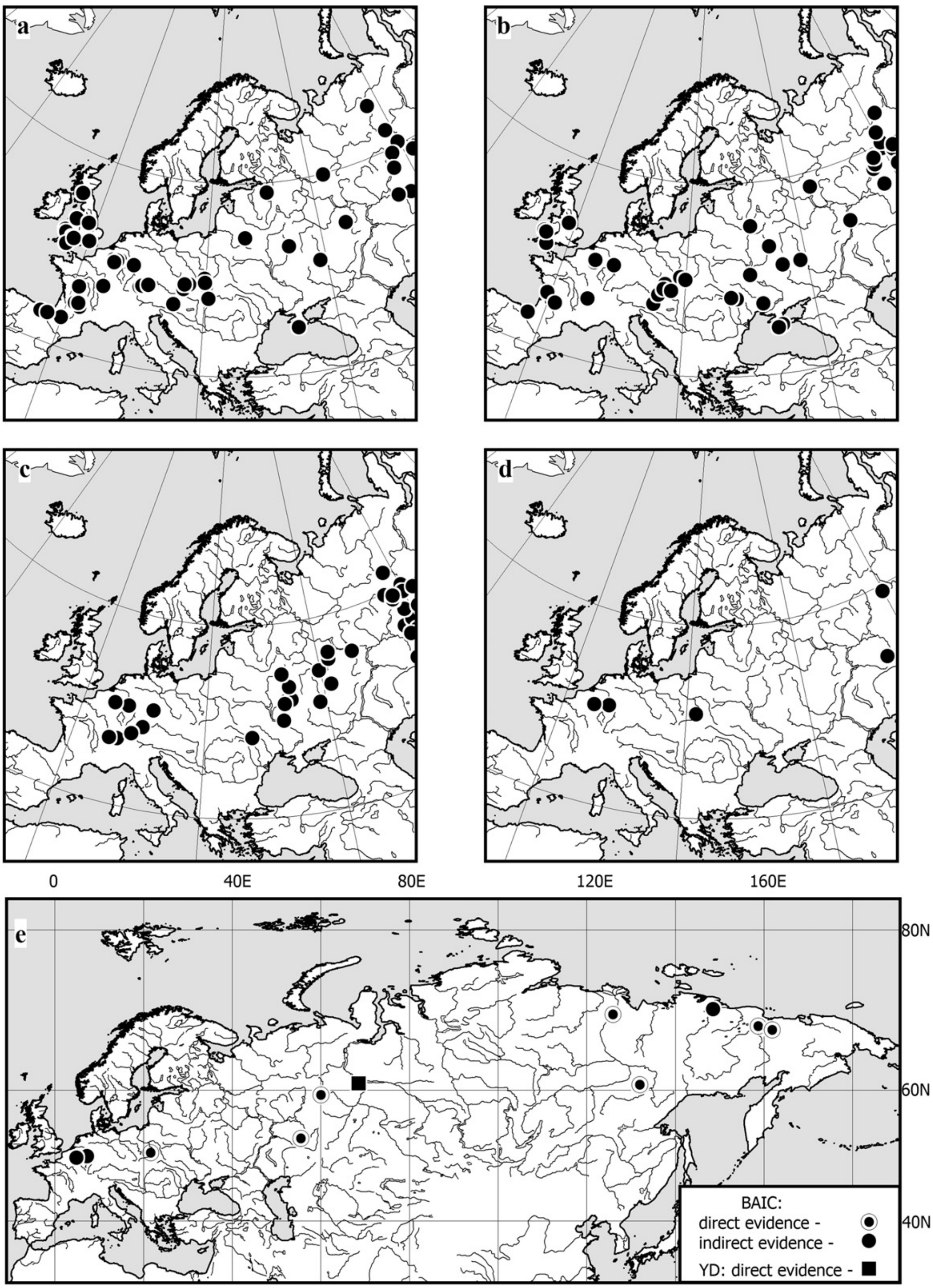

Fig. 6. Woolly rhinoceros (*Coelodonta antiquitatis*) localities dated to: a – Denekamp (= Bryansk) interstadial (DEN); b – the maximum LGM cooling; c – Late Glacial time (LGT); d – Bøllng-Allerød (BAIC); e – the latest records of woolly rhinoceros bones in Northern Eurasia during Bølling-Allerød (BAIC) and Younger Dryas (YD).

Maps presented in Figs. 5 and 6 show the fluctuations in the geographical distribution of the woolly rhinoceros; fluctuations that are related to changes in climatic conditions. The last optimum for that species in the European part of its range dates back to the Denekamp (=Bryansk) Interstadial (Figs. 6a and 7); that is about 7 or 8 thousand years before the optimal conditions for the mammoth. The available data indicate a shrinking of the distribution to a belt between ~43°N (or southward to ~40°N, Iberian Peninsula (Alvares-Lao and Garcia, 2011)) and ~55°N during the cooler, stadial phases in Southern, Western and Central Europe (Fig. 6b). This shrinking and shifting southward during the LGM is especially noticeable in Eastern Europe and on the British Isles. To the east, along the Ural Mountains the northern distribution extended to ~60°N (Fig. 6b).

The reduction of the geographical range of the woolly rhinoceros is likely to have begun during the Late Glacial (Figs. 6c and 7b), before the decay of the mammoth's range. During the Last Glacial maximum (LGM), about 20–18 ka BP, the environmental conditions were particularly unsuitable for the species. Later, during Late Glacial time, the rhinoceros range began to restore itself. During the Bølling and Allerød interstadials the woolly rhinoceros inhabited North-Eastern Asia (Yakutia and Chukchi Peninsula) (Fig. 6e) (Lorenzen et al., 2011).

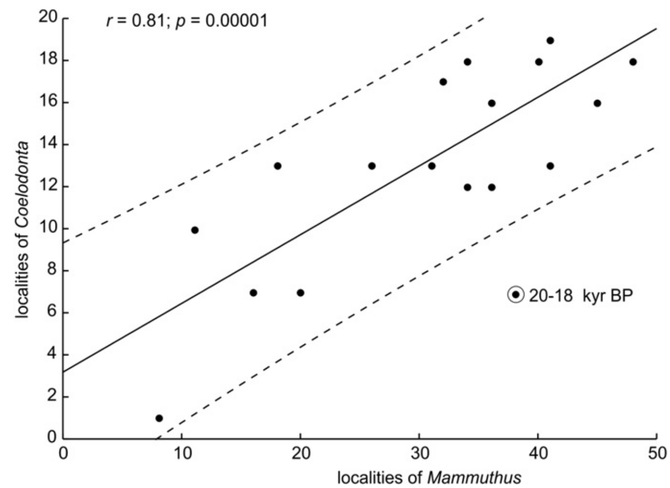

Fig. 8. The correlation between the number of localities with of mammoth and woolly rhinoceros in Europe for the different time intervals (based on data presented in Fig. 4b and 7b).

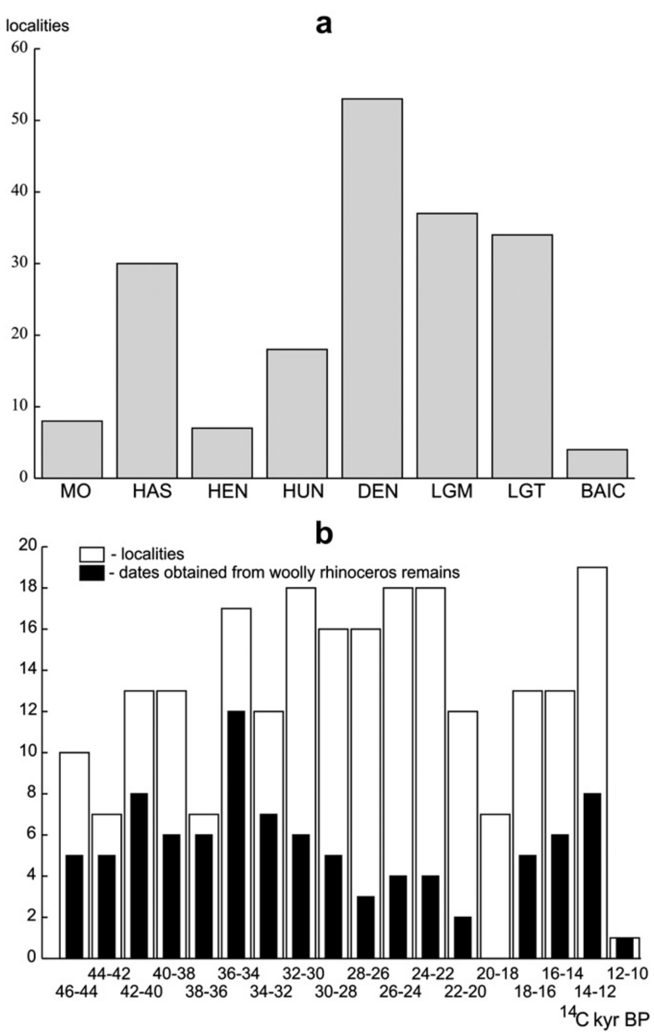

Fig. 7. Distribution of the localities in Europe with *Coelodonta antiquitatis* during the 'mega-interstadial' (MIS 3), at the last stage of the Valdai (Weichselian) glaciation (MIS 2), and in the Holocene (MIS 1): a – data clustered according to the time slices (for abbreviations see the text), b – data clustered according to fixed time intervals of 2000 years.

The catastrophic extinction of the species took place in a rather short period time (~1000 years), between 13 and 12 ka BP. The woolly rhinoceros practically disappeared from Europe as early as the Bølling and Allerød interstadials. There are only three localities in Western and Central Europe (Germany and Poland) of that age that yielded woolly rhinoceros remains: Gönnersdorf (50.328 N, 6.597 E) – 12 380 BP, Oelknitz (50.51 N, 11.37 E) – 10 855–12,900 BP (based on a series of ^{14}C dates on charcoal, bones of reindeer and horse) and Wilczyce (50.75 N, 21.66 E) – direct data obtained from rhino tooth 11 400 ± 135 BP; Ua-15720 (Fig. 6d, e) (Musil, 1985; Hedges et al., 1998; Stuart et al., 2002; Street et al., 2006; Vermeersch, 2006; Fiedorczuk et al., 2007).

The latest remains of the European woolly rhinoceros have been discovered in the Ural region. Fossils from Zlatoustovka (12330 ± 120 BP, BashGI-107 (LU-1668)) (53.16 N, 55.51 E) Lobvinskaya (12275 ± 55 BP, KIA-5670) (59.47 N, 60.06 E) and Lugovskoye (10770 ± 250 BP, SOAN-47757) (61.05 N, 68.57 E) (Orlova et al., 2008; Kuzmin, 2010) indicate the occurrence of *C. antiquitatis* in the Middle Ural region until the end of Younger Dryas or even as late as the Early Holocene. There is a date of 10220 ± 500 BP (IPAE-136) of a bone recovered from the Bobylek rock shelter, from a bed that yielded rhinoceros remains. The same bed appeared to contain remains of one of the latest *Megaloceros giganteus* (9960 ± 50 BP; OxA-11063) (Stuart et al., 2004). However, until more dates have been obtained on remains of the woolly rhinoceros which support the late occurrence, it is assumed that the extinction of this species in Eurasia is dated to the BAIC–YD interval (see also Kuzmin, 2012).

6. Conclusion

The European distribution patterns of the mammoth and the woolly rhinoceros during the Late Pleistocene, not only differ from each other in some aspects, but also show many commonalities (see Figs. 4, 7 and 8). Both species appear to change their distribution range repeatedly. Both species reached their maximum expansion at different times during the Denekamp (=Bryansk) Interstadial between 34 and 24 ka BP, a rather long interval which includes several cooler phases. It might be possible that both species occurred together during earlier periods as suggested by finds from Mousterian sites (Baryshnikov and Markova, 2002). Later, the ranges of both the mammoth and the rhinoceros in Europe were dramatically reduced, a process that started before the end of LGM. The most significant difference between the two species is the number of localities in the period between 20 and 18 ka BP, when the number of rhinoceros localities became disproportionately lower than that of mammoth sites (Fig. 8). The recorded dissimilarities between the geographical distribution of the mammoth and the rhinoceros may be attributed to differences in the ecological niche of the two species. The woolly rhinoceros occupies a niche that was narrower than that of the mammoth.

The results presented in this paper show successive stages in the shrinkage of the geographical distribution of the mammoth and the woolly rhinoceros during the Late Pleistocene/Holocene transition, as well as where and when the two species became extinct. Progressive warming since the end of the Pleistocene resulted in dramatic changes in the environment, such as the formation of an uninterrupted forest zone and the disappearance of open periglacial landscapes with a rich herb and grass vegetation, “the mammoth steppe”. Other changes such as the increase in snow cover thickness appeared to be critical for the distribution of those animals. Mammoth and woolly rhinoceros ranges disintegrated into isolated spots, and later they disappeared completely from Eurasia. Relict populations of small-sized mammoths persisted longer, as late as the Late Holocene, on some isolated islands (for example Wrangel Island). However, not only climate change had an impact on the distribution of the two species. Late Paleolithic and Mesolithic hunters might also affect the size of the last mammoth and woolly rhinoceros populations in Europe. Their impact is particularly high when the species are close to extinction.

Although a great quantity of data have been analyzed, further investigations are needed in order to obtain a more complete picture of the changes in the distribution of the mammoth and the woolly rhinoceros, in particular during the final stage of their existence.

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