ARTICLE IN PRESS

Quaternary International xxx (2015) 1–12

Contents lists available at ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

Changes in the Eurasian distribution of the musk ox (*Ovibos moschatus*) and the extinct bison (*Bison priscus*) during the last 50 ka BP

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ARTICLE INFO

Article history:
Available online xxx

Keywords:
Eurasia
Mammoth steppe
Faunal extinction
Musk ox
Bison

ABSTRACT

A recent update of the PALEOFAUNA database (including new ^{14}C dates) revealed new insights in the changes in the geographical distribution and the (local) extinction of larger mammals in Northern Eurasia during the second part of the Late Pleistocene and the Holocene, a period with dramatic changes in climate. In this paper, we present and discuss the observed changes in the distribution of two herbivore species: the musk ox *Ovibos moschatus* and the extinct bison *Bison priscus*, which are the major components of the "mammoth steppe" mammalian assemblage. The decrease of their ranges and their extinction during the Holocene (as a part of the Megafauna extinction in Eurasia) was primarily connected with changes in climate and partly the result of Anthropogenic pressure.

1. Introduction

To understand the impact of climate change on biota, in particular on large herbivores such as the musk ox and the bison, we have investigated the Late Pleistocene and Holocene Eurasian fossil record of both species. The information about the Eurasian large mammal fossil record is stored in the PALEOFAUNA database. The database has recently been updated and many new data have been added. Earlier reconstructions of the Holocene mammal assemblages from Eastern Europe and Siberia (Markova et al., 2001) should therefore be regarded as outdated.

In this paper, we present the data of two very characteristic species of the "Mammoth Steppe" fauna, which both belong to the family of the Bovidae: the musk ox *Ovibos moschatus* and the extinct bison *Bison priscus*. Only dated fossil remains are taken into account. In many cases, the musk ox or the bison bones have been ^{14}C dated. In other assemblages associated bones from other species or sediment have been dated (e.g. ^{14}C on bones; ESR, OSL or TL on sediments/material). The musk ox remains analyzed in the frame of this study were derived from 133 different localities and the information about the age of the remains is based on 385 ^{14}C dates (including 188 dated musk ox bones), 4 OSL dates, 3 TL dates, 1 ESR date and the age of 11 records is based on the archaeological context.

The main quality parameters for bone dates are the Carbon and Nitrogen content of the collagen, as well as the C/N ratio. These were all in acceptable range, i.e. the bones are not degraded. Such bones yield acceptable ^{14}C dates, no extra purification steps (like filtration) are necessary as shown by intercomparisons (Hüls et al., 2009; van der Plicht and Palstra, in press).

The PALAEOFAUNA database also includes a large number of Late Pleistocene and Holocene *B. priscus* records from 520 localities. The age of the remains is based on 1773 ^{14}C dates (178 dated bison remains), 7 OSL dates, 65 TL dates, 91 ESR dates and 55 dates are based on the archaeological context.

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http://dx.doi.org/10.1016/j.quaint.2015.01.020
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The results of our investigation confirm earlier statements that the observed changes did not take place synchronously in the different parts of Eurasia (Markov, 1960; Markov et al., 1965) due to geographical differences in climatic events that influenced natural components such as the structure of mammalian assemblages and the distribution of species.

Our conclusions about the dynamic changes in the distribution of the Eurasian musk ox and the bison are comparable to earlier conclusions based on modeling of the range and effective size of the musk ox and bison populations for four temporal intervals (Lorenzen et al., 2011). In this paper we present more detailed information about the geographical distribution of the musk ox and the bison during the period from about 46 ka BP until the late Holocene (Fig. 1), subdivided in fourteen different time intervals.

2. The main geochronological intervals of the second part of the Late Pleistocene (MIS 3 and MIS 2) and the Holocene (MIS 1)

The examined time period consists of two major intervals with distinct climatic conditions: a) the second part of the Last Glaciation (referred to as Valdai, Vistulian, Weischelian, Zyrianian/Sartanian Glaciation) correlated with the Marine Isotopic Stages (MIS) 3 and 2, and b) the Holocene Interglacial (MIS 1). The “mega-interstadial” of the Last Glaciation (MIS 3) with an age of 60–24 ka BP is characterized by a relatively warm climate but also by the occurrence of a large number of climatic fluctuations (stadials and interstadials) which differ in intensity (Zagwijn, 1974; van Huissteden, 1990; Vandenberge, 2002; Rasmussen et al., 2006; Svensson et al., 2008; Velichko and Faustova, 2009). The faunas

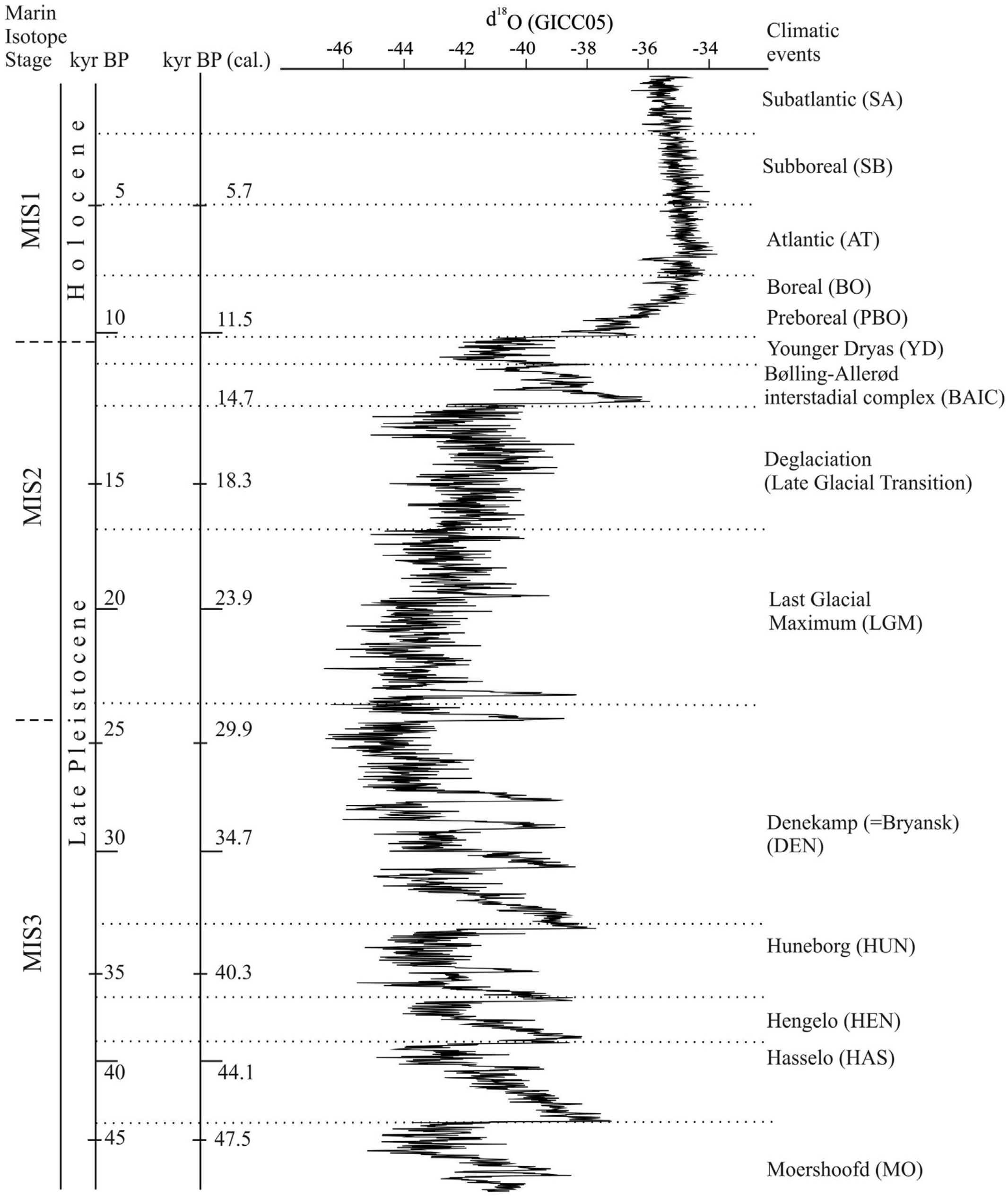

Fig. 1. Chronology of European climatic stages of the Late Pleistocene and Holocene.

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from the earliest part of MIS 3 unfortunately fall outside the ^{14}C dating range and are therefore not included in this study. The later part of MIS 3 includes the Moershoofd Interstadial (MO; ~46–44 ka BP), the Hasselo Stadial (HAS; 44–39 ka BP); the Hengelo Interstadial (HEN; 39–36 ka BP); the Huneborg Stadial (HUN; 36–33 ka BP) and the Denekamp (Bryansk – Dunaevo) Interstadial (DEN; 33–25 ka BP) (Vandenberghe, 2002). The eastern European stratigraphical scheme is less complex. The later part of MIS 3, referred to as the Bryansk long Interstadial (Velichko and Faustova, 2009) is subdivided into three intervals: the Leningrad Interstadial, the Shensk Stadial and the Dunaevo Interstadial. In a later publication the authors presented a revised subdivision: a long Leningrad Interstadial (which correlates with the Moershoofd and the Hengelo Interstadials and with the intermediate Hasselo Stadial), a Shensk Stadial (that might correspond to the Huneborg Stadial) and the Dunaevo (=Bryansk) Interstadial (Novenko et al., 2011). In this paper, we use the traditional, more detailed Western European stratigraphical scheme.

The maximum cooling during the Late Pleistocene corresponds with the second part of the Last Glaciation (MIS 2), a period with a heterogeneous climate. The main climatic events during this period are: the Last Glacial Maximum (LGM; –24–17 ka BP), the Deglaciation or Late Glacial Transition (LGT; 17–12.4 ka BP), the Bølling – Allerød interstadial warming, divided by a short and weakly pronounced Older Dryas Stadial, (BAIC; –12,4–10.8 ka BP) and the Younger Dryas Stadial (YD; 10.8–10.3 ka BP) (Faustova, 1994; Markova and van Kolfschoten, 2008).

The reconstruction of the climatic changes during the Holocene in Northern Eurasia is usually based on palynological data. N.A. Khotinski (1977) and N.A. Khotinski and V.A. Klimanov (2002) subdivided the Holocene Interglacial into five intervals. The first one is the Preboreal warming (PB; 10.3–9.00 ka BP), characterized by the wide distribution of birch and pine forests in Northwestern and Central Europe. The second interval comprises the Boreal (BO; 9.00–8.00 ka BP), a period with significant warming, the beginning of which is characterized by the wide spread occurrence of hazel, whereas during the second part mixed oak forests appear. In this period the modern zonal distribution of landscapes in Northern Eurasia was formed. The climatic optimum (i.e. the maximum warming) of the Holocene is known as the Atlantic period (AT; 8.00–4.75 ka BP). A significant differentiation and increasing complication of the floral communities, as well as the expansion of the forest zone to the south and to the north took place during this period. Later, during the Subboreal period (SB; 4.75–2.10 ka BP) the climate became cooler; however, with some fluctuations. During the Subboreal the lime-tree and the elm decreased in numbers. During the last phase, the Subatlantic period (SA; 2.10 ka BP – recent time) the ocean increasingly influenced the climate of Northern Eurasia (Khotinski, 1977).

The subdivision described above more or less coincides with the subdivision proposed by Walker et al. (2012). The authors consider the prospects for a formal tripartite subdivision of the Holocene Series/Epoch and propose to establish an Early–Middle Holocene Boundary at 8200 a BP and a Middle–Late Holocene Boundary at 4200 a BP, each of which is should be linked to a Global Stratotype Section and Point (GSSP).

3. The Eurasian musk ox and bison record

3.1. Musk ox – *O. moschatus* Zimmermann, 1780

The genus *Ovibos* first appeared in the Middle Pleistocene fossil record. *Ovibos* and *Praeovibos*, which is only known from the Middle Pleistocene, both originated from a hypothetical ancestor most likely during the Early Pleistocene (Villafranchian). The Late Pliocene genus *Boopsis*, which is known from China, is usually considered as one of the most probable distant ancestors of the musk ox (Lent, 1999).

Comparative analyses of the modern *O. moschatus* and the Late Pleistocene musk ox from Eurasia indicate that both differ significantly in several important taxonomical features (Ryziewicz, 1955; Sher, 1971; Tikhonov, 1994). However, a DNA analysis of both the fossil and the modern musk ox from Asia and North America indicate that we are dealing with a single species (MacPhee et al., 2002; Campos et al., 2010). Therefore, we prefer to use the name *O. moschatus* Zimmermann, 1780. The Eurasian Late Pleistocene musk ox bones are usually assigned to *O. moschatus* Zimmermann, 1780. A number of authors (e.g. Gromova, 1935; Baryshnikov, 1981) assign the Late Pleistocene fossil musk ox to a distinct subspecies – *O. m. pallantis* H. Smith, 1827. In 1827, H. Smith described the Late Pleistocene musk ox from Eurasia as *O. pallantis.* However, in literary sources both names (*O. moschatus* and *O. pallantis*) are used to describe the Late Pleistocene musk ox finds.

The musk ox is well adapted to open landscapes with low snow cover and with low summer temperatures (Danilkin, 2005) and is highly sensitive for increasing temperature and humidity. Hence, the musk ox' remains discovered in the Late Pleistocene and Holocene localities undoubtedly indicate severe cold climatic conditions.

The earliest information about the distribution of the musk ox, within the investigated period, dates to the Moershoofd Interstadial (Fig. 2). Eight localities with musk ox remains are known from that interval in Northern Asia; all of them are situated north of 65.5°N.

Eighteen localities (6 in Europe and 12 in N. Asia) are dated to the Hasselo Stadial. The southern boundary of the species range descends to 45°N in Europe and to 67°N in Northern Asia. New data are derived from the northern part of Eastern Europe (Arkhangelsk region, see Table 1).

The geographical distribution of the musk ox during the next interval, the Hengelo Interstadial (Fig. 2), shows a decrease of its range, with a southern boundary at 50°N (Mamutowa cave = Wierzchowska Dolna, Poland) (Ponomarev et al., 2012) in Europe. The majority of localities are located in Northern Asia.

Musk ox remains from ten fossil assemblages date to the Huneborg Stadial (Fig. 2). During that period periglacial landscapes dominated most of Northern Eurasia, the European musk ox localities were found in the area north of 46.4°N and on the modern shelf of the North Sea (Mol et al., 2006). At the most southern locality, which is situated in Slovenia (Pototsk Cave) musk ox remains have been found is association with dated cave bear fossils (Pacher, 1998; Fiebig and Pacher, 2006). Asian records are known from localities on the Taimyr Peninsula and on the Novosibirsk Islands (Bol'shoi Liakhovsky Island) (Sher et al., 2005; Campos et al., 2010).

The early intervals of MIS 3 demonstrate that at least in Europe important climatic fluctuations took place. Due to the small amount of data, however, neither the impact of these fluctuations on the geographical distribution of the musk ox nor the southern limit of its range in Northern Asia can be indicated.

Many musk ox remains are dated to the Denekamp (=Bryansk) Interstadial: a period of about 10 ka with a very inhomogeneous climate with several fluctuations and alternations of cool and warm phases (Fig. 1). Characteristic for this interval is a periglacial landscape with a so-called “Mammoth Steppe” fauna (Markova et al., 2010a). During the Denekamp Interstadial, the musk ox was rather widely distributed and inhabited large territories in Northern Eurasia (Fig. 2). The southern boundary of its range reached 45°N in Western Europe (Abri Pataud, France) (Bouchud, 1975) and 55–56°N in Northern Asia (Chik River, West Siberia; Kamchatka River, Kamchatka Peninsula) (Lobachyov et al., 2011). The northern

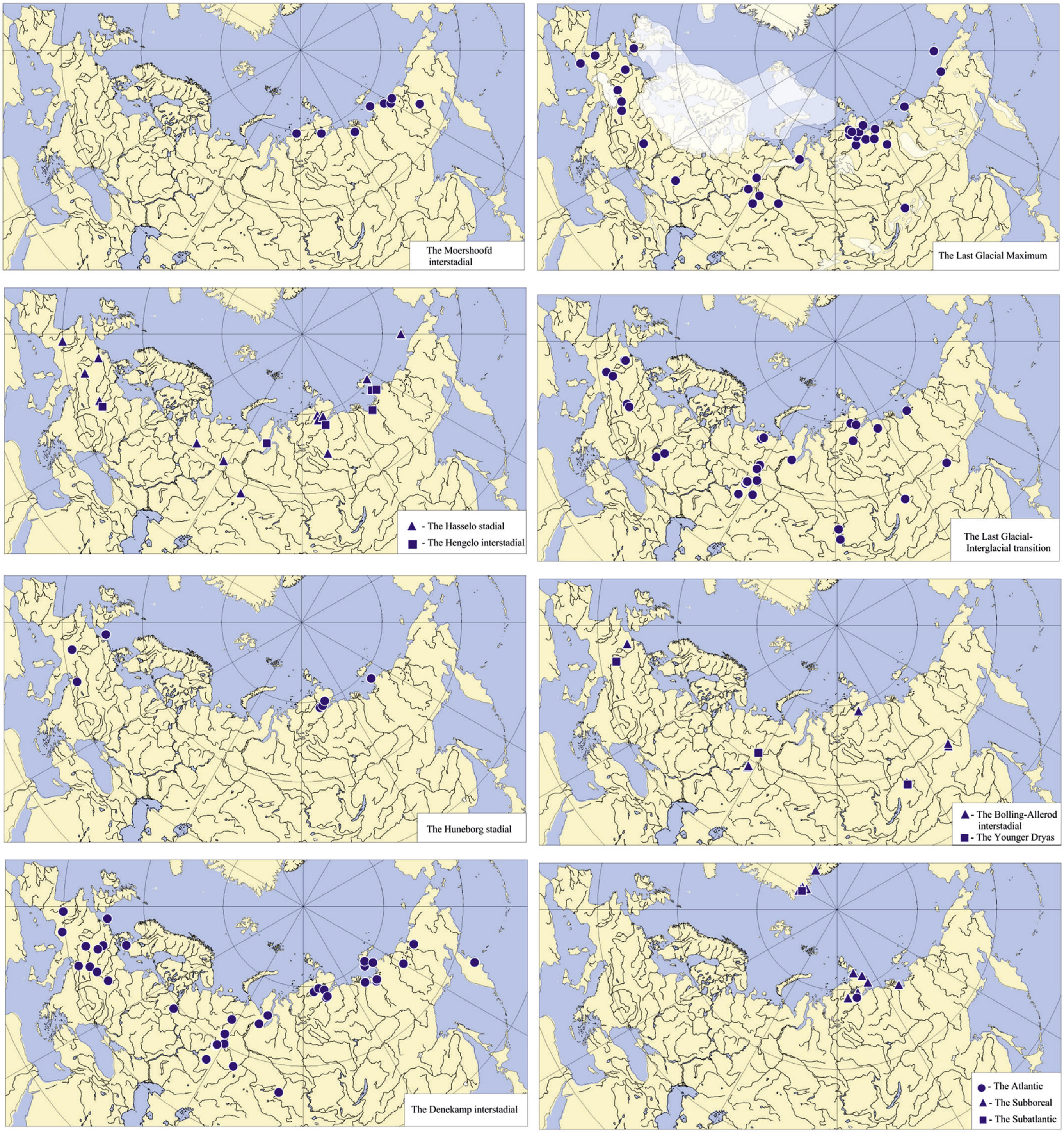

Fig. 2. Geographical distribution of dated musk ox (*O. moschatus*) remains in Europe and Northern Asia during the different time intervals of the Late Pleistocene and Holocene.

boundary of its range reached about 56°N in Western Europe (Denmark) (Lorenzen et al., 2011) and about 57.4°N in Eastern Europe (the Urals, Pechora River, Byzovaya Paleolithic site).

The southern border of the musk ox' range changed slightly during the LGM (Fig. 2). Most of the radiocarbon dates obtained from musk ox bones fall within this interval (Pidoplichko, 1969). The majority of the musk ox sites are located on the Taimyr Peninsula (MacPhee et al., 2002; Sher et al., 2005) and in the Urals (Campos et al., 2010). The southern boundary of its occurrence in Europe was located at 44.9°N (Abri Pataud, France), 42°N – L'Arbreda (Spain), 48.5°N Krems-Wachtberg (Austria). On the East European Plain the boundary was located at 51.4°N (Kostenki Palaeolithic sites, Russia) (Savich, 1975; Damblon et al., 1996; Doppes, 2001; Lorenzen et al., 2011) and in Northern Asia musk ox remains were found near the Aldan River basin, at 57.8°N (Mochanov, 1970). It can be stated that due to the expansion of the Scandinavian ice sheet during the LGM, the northern geographical boundary of the musk ox range shifted to the south and south-east

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Table 1
New radiocarbon dates of bison (*Bison priscus/bonasus*) bones and of musk ox (*Ovibos moschatus)* bones from the territory of Russia.

Location	Dated material	Altitude	Longitude	AMS data, kyr BP	Laboratory
Bison priscus/bonasus					
Neito Lake, Yamal Peninsula, Yamalo-Nenets Autonomous Okrug	bone	70.12	70.461	44000 (+700,−550)	GrA-41250
Krasnoborsk town, Krasnoborsk region, Arkhangelsk province	skull	61.558	45.938	42400 (+550,−450)	GrA-42200
Chauna Bay, Chauna region, Chukotka Autonomous Okrug	bone	69.642	167.933	40200 (+600,−800)	GrA-41643
Krasnoborsk town, Krasnoborsk region, Arkhangelsk province	skull	61.558	45.938	39350 (+370,−330)	GrA-42201
Kelkovo quarry, Kirovsk region, Leningrad province	shoulder blade	59.800	31.005	35520 (+230,−210)	GrA-38820
Kamchatka River, Kamchatka Peninsula, Kamchatka Krai	metapodium	56.0	159.75	33000 (±2000)	GIN-3421
The coast of Finland Bay /near Komarovo village, resort region of S.-Petersburg	skull	60.179	29.765	31080 (+200,−180)	GrA-41239
Isovsk mine, Verkhnesaldinsk town, Sverdlovsk Province	bone	58.017	60.534	30930 (±650)	SOAN-5881
Kelkovo quarry, Kirovsk region, Leningrad province	bone	59.800	31.005	30650 (+190,−180)	GrA-41236
Miass River, Chelyabinsk Province.	bone	55.334	61.9	23500 (±210)	SOAN-5309
Nizhnya Tavda River, Tyumenchk Province	bone	57.41	66.12	19910 (±170)	SOAN-5298
Shaitanskaya Cave, Sverdlovsk Province	bone	60.167	60.35	19140 (±205)	SOAN-5224
Shaitanskaya Cave, Sverdlovsk Province	shoulder bone	60.167	60.35	19050 (±50)	SOAN-5225
Ladeinyi grotto, Aleksandrovsk region, Perm' Krai	bone	59.15	57.517	15310 (±70)	OxA-14556
Khairegas, Yukutia	bone	59.416	116.8	13620 (±140)	AA-79322
Svir' River basin, Podporozhski region, Leningrad Province	skull	60.819	33.875	10390 (±50)	GrA-41241
Oyat' River, Vologda province	skull	60.416	35.317	3045 (±35)	GrA-41240
Ovibos moschatus					
Krasnoborsk town, Krasnoborsk region, Arkhangelsk province	Skull	61.558	45.938	41860 (+500,−420)	GrA-42204
Drovatinskaya cave, Troitsko-Pechora region, Komi Republic	Tooth	62.917	58.333	13680 (±60)	GrA-39244

in Europe (52°N, Clifford Hill site (Great Britain); 48.4°N, the site Krems-Wachtberg (Austria); 62°N – Medvezh'ya Cave, the Ural (Russia)) (Jacobi et al., 2009; Campos et al., 2010).

In Eurasia, during the Last Glacial–Interglacial transition (Deglaciation, LGT) (Fig. 2), the musk ox' range shifted insignificantly. A pronounced decrease and disintegration of the geographical distribution of the musk ox took place in Western Europe, where the latest *Ovibos* records have been found in upland and mountainous areas (e.g. Goyet 3, Trou de Chaleux, Schnurenloch, Kesslerloch). Radiocarbon dates on mammoth bones, found in association with musk ox remains, indicate the occurrence of *Ovibos* on the Russian Plain between 17 and 13 ka BP (Dobranichivka, Mezin, Kostenki sites) (Pidoplichko, 1969) and in N-E Europe and the Middle Ural Range (56.2°N – Bobylek 57.5°N – Pershinskaya cave). In Northern Asia musk ox remains were found in the Upper Yenisei basin at a latitude of 53°N and in the Upper Lena River basin at 57.8°N (Drozdov et al., 1990). The northern boundary of the musk ox' range in Northern Asia was restricted by the Arctic shore. Recently, musk ox remains have been found in the northern part of Eastern Europe (Drovatinskaya cave, Komi Republic, Russia, Table 1).

A catastrophic decrease of the *Ovibos* range took place during the BAIC, from which only 9 dated faunas that include this species are known (Fig. 2). In Western Europe the musk ox was found in the Swabian Alps (Zigeunerfels Cave, Germany) (von Koenigswald and Taute, 1974), and in Belgium (Goyet Cave, Toussaint et al., 1998). In the Urals they were found in Verkhnegubakhinskaya Cave, in Northern Asia on the Taimyr Peninsula (Sher et al., 2005) and in the Lena River basin at the sites Bol'shoy Jakor, Ust' Mil' and Dyuktai Cave (Mochanov, 1977). The low number of localities that are situated far from each other reflects the disintegration of the Eurasian musk ox range and the occurrence of different relic populations.

Relic *Ovibos* populations existed during the short Younger Dryas cooling (Fig. 2), in the Swabian Alps (von Koenigswald and Taute, 1974), in the Middle Urals (Kakva-4 and Medvezhia Caves) (Campos et al., 2010), in Northern Asia (Bol'shoy Jakor) and possibly on Kotel'nyi Island (Makeev et al., 1989) and Taimyr Peninsula and in the estuary of the Lena River.

The Musk ox might have survived on Taimyr Peninsula (Campos et al., 2010) during the Preboreal and the Boreal. The youngest *Ovibos* populations inhabited Taimyr Peninsula and the estuary of the Lena River where they existed until the Late Holocene (Subboreal) (Fig. 2). Their latest occurrence (based on ^{14}C dates) is recorded on the Taimyr Peninsula – 2700 ± 70 (GIN-3803) to 2754 ± 27 (OxA-17062) ka BP (Sher et al., 2005; Stuart and Lister, 2012) and in the Lena River estuary – 3180 ± 100 (GIN-10259) ka BP (Kuznetsova et al., 2001).

Fig. 3 presents the quantity of fossil assemblages with *O. moschatus* remains that were dated to the different intervals of MIS 3, MIS 2 and MIS1. Most abundant are those from the Denekamp and the LGT and it seems that during these intervals the musk ox had its largest geographical distribution in Eurasia. There is a negative correlation between the number of assemblages with musk ox and the mean temperature during a certain time interval (Fig. 3). However, during the extra cold LGM, the range of the musk ox range decreased slightly. A real decline in the musk ox range started during the LGT, due to the increasing temperature and humidity and due to the impact of these climatic changes on the palaeoenvironment. The most dramatic and sudden decrease in the range of *O. moschatus* took place at the very end of the Pleistocene, during the BAIC and the Younger Dryas.

Summarizing it can be stated that the *O. moschatus* populations during the Late Pleistocene and Holocene were relatively small compared to other herbivores in the “Mammoth Steppe” community. The mammoth and reindeer populations, for example, were much larger. This difference can be explained by the fact that these species are ecologically more tolerant than the musk ox (Markova et al., 2013). The latest palaeogenetic and paleogeographical data indicate that the extinction of *O. moschatus* in Eurasia is the result of climate change and is not related to human predation (Currant and Jacobi, 2001; Lorenzen et al., 2011).

3.2. *Primitive bison–Bison priscus Bojanus, 1827*

The taxonomy and evolution of the genus *Bison* is nowadays a matter of debate and need to be revised while taking into account traits of both cranial and post-cranial bones (Croitor, 2010). Ancestors of the genus *Bison* are found among representatives of the genus *Leptobos* (Late Pliocene – Early Pleistocene), which is known from Europe and Asia. The subgenus (genus) *Eobison* that first appeared in the Late Villafranchian is considered either as an intermediate taxon between *Bison* and *Leptobos* (Flerov, 1979; De

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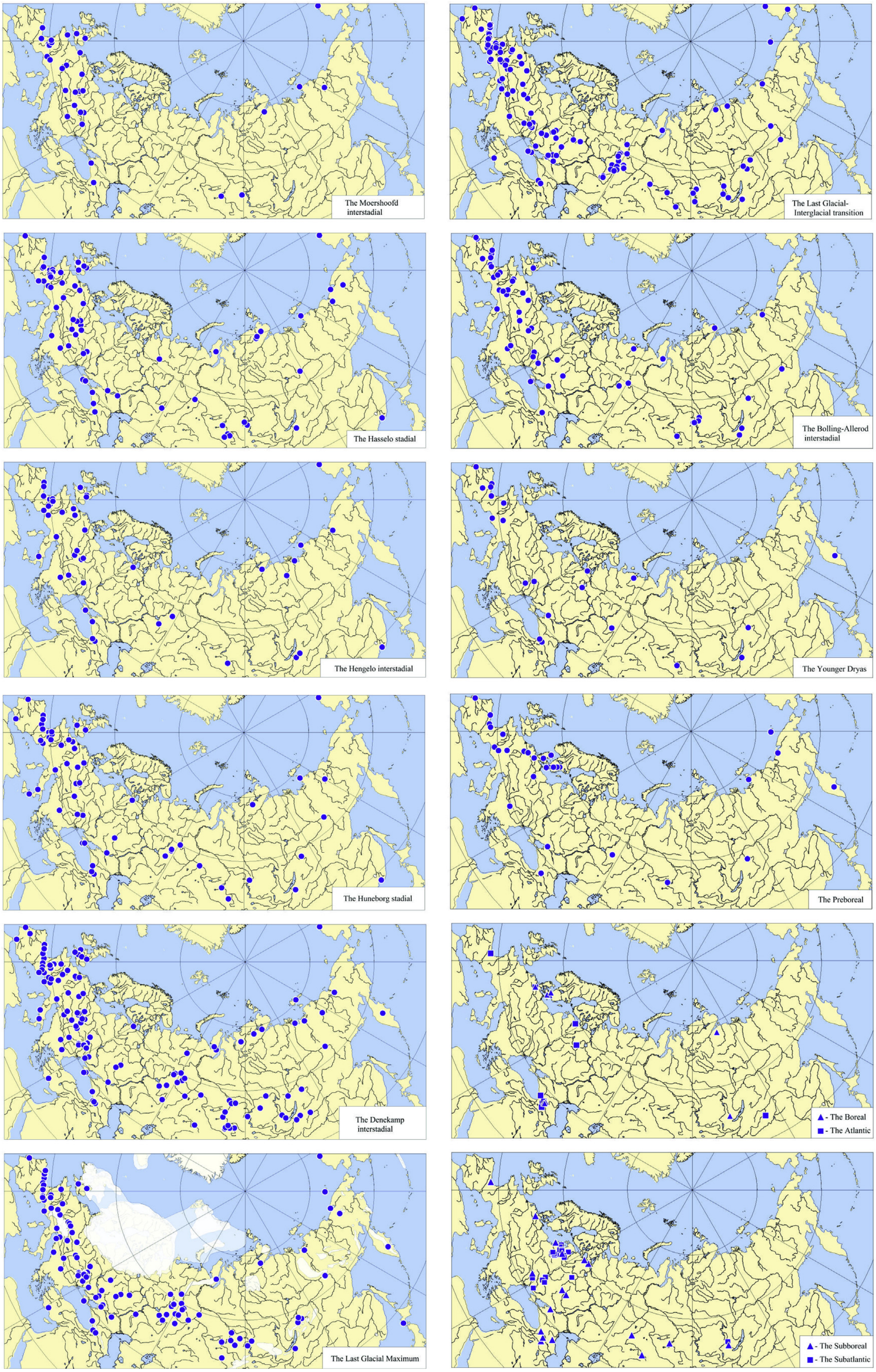

Fig. 3. Geographical distribution of dated primitive bison/wisent (*B. priscus/bonasus*) remains in Europe and Northern Asia during the different time intervals of the Late Pleistocene and Holocene.

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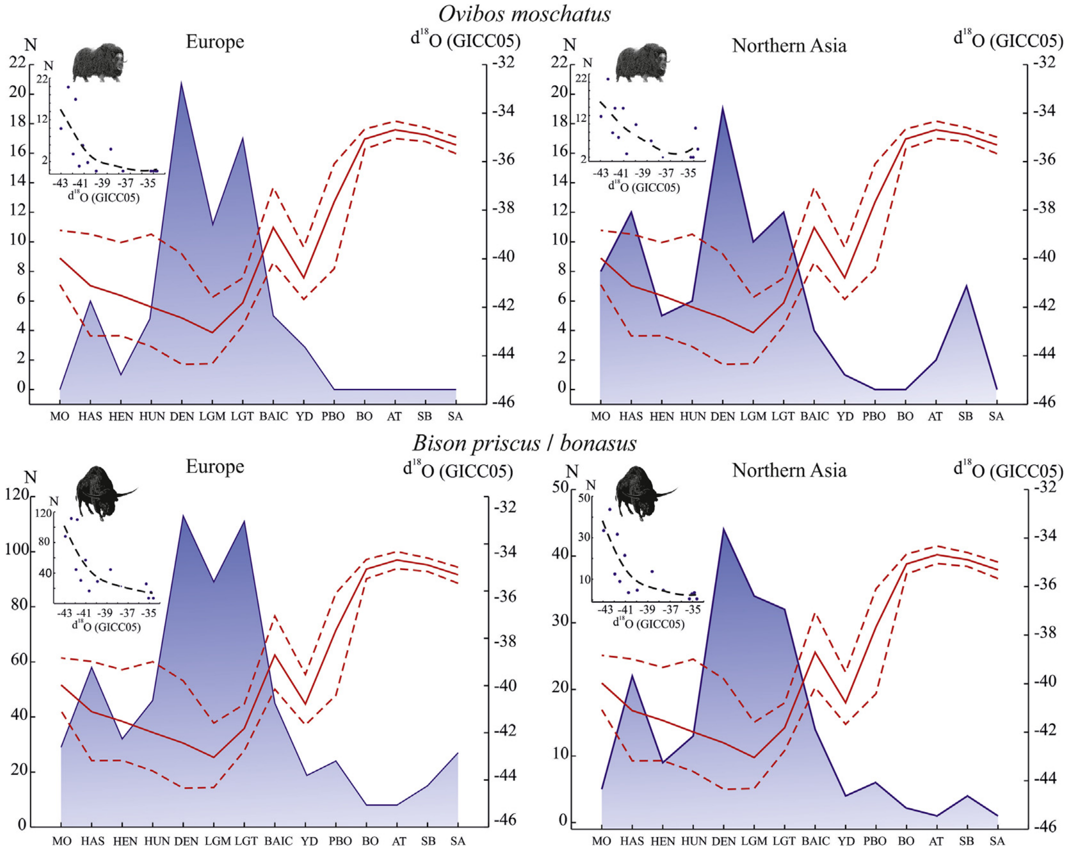

Fig. 4. The number of dated localities (N) with the musk ox (*O. moschatus*) and the primitive bison/wisent (*B. priscus/bonasus*) per time interval. The red line shows the mean ^{d18}O values (Greenland Ice Core Chronology 2005 (GICC05)); the dashed lines show the 90th and 10th % percentiles for the ^{d18}O values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

Giuli et al., 1987) or as a sister taxon of *Bison* (Brugal and Croitor, 2007). *B. menneri*, recorded at the late Early Pleistocene locality Untermassfeld (Germany), is probably the earliest species of the subgenus (genus) *Bison* (Sher, 1997; Brugal and Croitor, 2007; Croitor, 2010).

There are two points of view on the evolution of bisons in Eurasia. According to the most acknowledged one, bisons developed within one phylogenetic line: *B. schoetensacki* – *B. priscus* – *B. bonasus* (*B. bison*) (Gromova, 1935; Flerov, 1979; Croitor, 2010). The second hypothesis (Hilzheimer, 1918) suggests two parallel lines of bisons: the first one is the line of forest bisons from *B. schoetensacki* to the recent *B. bonasus* and the second one is the line of steppe bisons *B. priscus*. There are some indications that the steppe bison *B. priscus* existed in the steppes of the southern Russian Plain until the beginning of the Holocene and that the divergence between *B. priscus* and *B. bonasus* probably started during the Early Pleistocene (Vereshchagin and Baryshnikov, 1985; Nemtsov et al., 2003). If the second hypothesis is correct, the bone remains from the Pleistocene localities have to be assigned to *B. priscus* or to *B. bonasus*. However, *B. priscus* and *B. bonasus* are morphologically almost identical and there is an overlap in the proportions of the extremity bones. Hence, it is very difficult to differentiate the two species and to assign fossil bison material to either one of them. So far, it is not clear which of the two hypotheses is correct and we probably have to wait for aDNA data that can answer this question. In this paper, we follow (as in the vast majority of the publications on Quaternary faunas) the traditional assignments, i.e. the Late Pleistocene bison remains are referred to as *B. priscus* and the Holocene *Bison* of Europe is referred to as *B. bonasus*.

B. bonasus is a typical representative of plain and montane broad-leaved and mixed forests and the species' dentition demonstrates several specific adaptations related to the consumption of branches and rinds of trees (Nemtsov et al., 2003). Recent investigations have indicated that during the LGM the Eastern European bison followed a diet that included typical steppe and grassland (C_3) vegetation and that the animal probably consumed lichens during the cold season (Julien et al., 2012). Stable isotope analyses showed that *B. priscus* lived a sedentary way of life on the East European Plain, with limited inter-seasonal migrations (Julien et al., 2012).

The Asian *B. priscus* population is genetically very similar to the recent American forest bison *B. b. athabasca* Rhoads, 1897. Researchers therefore conclude that the Eurasian Late Pleistocene bison and the American bison had a single ancestor *B. priscus* and that their divergence took place about 160 ka BP (Shapiro et al., 2004; Gates et al. eds., 2009). The taxonomy of the Holocene *Bison* from Southern and North-Eastern Siberia is therefore still unclear.

The Late Pleistocene and the Holocene *Bison* record of Northern Eurasia are extensive and the PALAEOFAUNA database includes a large number of dated records. The database contains 36 localities with bison remains dated to the Moershoofd Interstadial (Great Britain, Western and Central Europe, Western and Eastern Siberia) (Fig. 4). The ^{14}C-dated records indicate that the species also occurred on the Pyrenean Peninsula (43.3°N, Castillo locality, Spain (Dari and Renault-Miskovsky, 2001)), in France (43.2°N. Gatzarria cave (Ready, 2013), Draye Blanche (44.9°N)), in Romania (45.6°N, Bordul Mare d'Ohaba Ponor site) and in Georgia (42.3°N, Ortvale Klde (Bar-Oz and Adler, 2005)). These data indicate that the southern border of the bison range during the Moershoofd Interstadial in Europe was located around 42°–45°N. Only five localities in Northern Asia with bison have been dated to the Moershoofd Interstadial. The bison range probably extended to approximately 45°N in Southern Siberia and in N-E China (Hedges et al., 1987; Valladas et al., 1987; Raynal and Pautrat, 1990; Shapiro et al., 2004).

A more reliable picture has been obtained for the Hasselo Stadial (Fig. 4). The former set of dated bison remains has been expanded by new ^{14}C dates from the N-E of Eastern Europe (Archangelsk province) (Table 1) (Ponomarev et al., 2012). The geographical position of the fossil localities with *B. priscus* indicates a very wide distribution of the species ranging from the British Isles in the west to N-E of Siberia in the east and from the Polar regions in the north to the far south of Western, Central and Eastern Europe (Crimea, Western Caucasus) and the southern part of Western and Eastern Siberia. In Europe, the southern boundary of the species' range extended to 38.4°N in the Pyrenean Peninsula (Figueira Brava Cave, Portugal), 42.7° N-43.7°N in the Balkan Peninsula (Crvena Stijena (Montenegro), Kozarnika cave (Serbia)) and 44.8°N –45.1°N in Crimean Peninsula. Remains from the Geographical Society Cave (43.3°N, Russia) have marked the southeastern boundary of the bison range in Northern Asia.

Based on the record of dated bison remains it is obvious that the species inhabited huge territories during the Hengelo Interstadial and the Huneborg Stadial, ranging from the Polar regions in the north (59.8°N in Europe (Kelkolovo Quarry, Russia, Table 1)) to the Pyrenean, Apennine and Balkan Peninsulas and the Crimea, Caucasus and southern Siberia in the south (Fig. 4).

The Denekamp (=Bryansk) Interstadial fossil record shows a high density of localities with fossil bison remains. A high concentration of bison sites has been discovered in the central and southern regions of Western Europe. The southernmost distribution of the species is indicated by localities in the S-W of the Pyrenean Peninsula (36.8°N, Higueral de Valleja, Spain), on the Apennine Peninsula (40.5°N, Castelcivita, Italy), on the Balkan Peninsula (42.9°N, Bacho Kiro, Bulgaria), in the Crimea (Emine-Bair-Khosar Cave, Zaskal'naya Cave) and Caucasus (42.3°N, Sakadgia Cave, Geogia), in Western Asia (37.1°N, Karain B, Turkey; http://ees.kuleuven.be/geography/projects/14c-palaeolithic/index.html), in the Altai Mountains, in Transbaikalia (51.4°–51.7°N) and in the N-E part of the Far East (45.6°N, Yan Jia Gang, China; 43.3°N, Geographical Society Cave, Russia) (Fig. 4). The northern limit in Western Europe is located at about 53°N (British Isles). Two new ^{14}C dated finds (Table 1) mark the northern border of this species in the N-W of Eastern Europe (about 60°N). On the Yamal Peninsula the northern expansion reached 69°N. In Asia, on the Taimyr Peninsula, bison populations occurred even more north and reached 75.5°N. The bison range also covered the Kamchatka (Table 1) and possibly Chukchi Peninsulas, but so far, there are no ^{14}C dates available for bison records from these territories. The fossil record shows that *B. priscus* had its largest geographical distribution during the Denekamp Interstadial.

During the LGM the northern boundary of the bison range shifted significantly to the south (Fig. 4). The most northern locality in Western Europe is located at 51.3°N – 53.3°N (Soldier's Hole and Ash Tree Cave, Great Britain) (Currant and Jacobi, 2001). In the eastern part of Western Europe the northern boundary was located at ~46°N–47°N (La Balme d'Epy, Grotte du Renne at Arcy-sur-Cure, France) (Evin et al., 1973; David et al., 2005). In Central Europe the southern boundary was located at ~48°–48.8°N, north of the Alps (Willendorf, Austria; Balla Cave, Hungary; Aschenstein, Czech Republic) (Allswarth-Jones, 1986; Musil, 1994). In Eastern Europe the *Bison* range gradually shifted to the north in a N-E direction (the Desna River basin, 52.7°N, Yudinovo, Russia) and reached 60°–62°N in the Cis-Urals region and in the Urals (Medvezhia Cave and Shaitanskaya cave, The Urals, Russia) (Abramova, 1993; Kosintsev and Bobkovskaya, 2003) (Table 1). In Siberia, the northern and southern boundaries of the bison distribution were approximately the same as during the Denekamp Interstadial (Drozdov, 1992; Sulerzhitsky and Romanenko, 1997; Kosintsev and Bobkovskaya, 2003; Orlova et al., 2004; Ineshin et al., 2005; Shpansky, 2006; Vartanyan et al., 2008) (Table 1). At the same time, there was a significant decrease in the number of sites located north of 60°N. Remarkable is a single dated locality on the Hokkaido Island, and possibly on the Honshu Island (Japan), which was connected to the continent during the LGM (Iwase et al., 2012). Summarizing it can be stated that the geographical distribution of the bison in Europe and Northern Asia during the LGM is smaller than its distribution during the Denekamp Interstadial. The highest density of bison localities is found in central and southern parts of Western and Eastern Europe, in the Middle and Southern Urals and in the south of Siberia.

During the LGT the distribution of the bison is almost identical to its distribution during the LGM (Fig. 4); however, the number of localities in Europe with fossil remains of bison is higher during the LGT than during the LGM and the northern boundary of its range shifted to the North, up to 51°N (Abri Stendel, Germany). In Northern Asia, the northern boundary of its range was located on the coast of the Arctic Ocean as indicated by the discoveries of bison bones in the lower streams of the Olenek and the Indigirka Rivers. Undated bison remains from Late Paleolithic sites confirm the occurrence of the species in the South-West of Eastern Europe (Bug-Prut rivers basins) (Anisutkin et al., 1986; Savich, 1975 and others).

The number of localities with a fossil record that includes the Eurasian *Bison* decreased significantly during the BAIC (Fig. 4). This could indicate a decrease in the size of the entire population and the beginning of the disintegration of its geographical range. Bison remains that are dated to the Younger Dryas are known from only 21 localities in Eastern Europe and Siberia (Fig. 3). This shows a continuation of the decrease in quantity of the bison populations and a further disintegration of its range during the very end of the Pleistocene. During the Younger Dryas *Bison* herds might have occurred north as well as south of the extensive former geographical range. Younger Dryas *Bison* remains were found in the Svir' River basin (Leningrad province), in the Pechora River basin (Nenets Autonomous Area, Russia), on the Taimyr Peninsula, and in the southern regions of the Lower Don basin, along the Azov Sea coast, in Transbaikalia and on the Kamchatka Peninsula.

The majority of dated Eurasian mammalian assemblages that include *B. priscus* are dated to the Denekamp Interstadial (Figs. 3 and 4). The fossil record shows a sharp decrease in the number of sites with bison remains and the disintegration of its geographical distribution at the end of the Pleistocene.

During the Early Holocene (Preboreal and Boreal) bison populations occurred at a significant quantity of localities in the north of Western Europe and at a few localities in the north of Eastern Europe and in Western and Eastern Siberia, in the Cis-Baikalia (Angara basin) and in the south of the Taimyr Peninsula (Katanga River basin) (Fig. 3). The Boreal record indicates a very significant reduction of the bison range.

The Middle and Late Holocene fossil record of Eurasia (Fig. 4) includes only a few dated bison (wisent) remains found along the southern coast of the Baltic Sea, on the Middle Russian Upland (Volga basin). In Asia, they are only found in the Angara River basin. Bison remains found at Neolithic sites indicate that the bison inhabited the Caucasus and the Cis-Carpathians (Ketraru, 1973; Bendukidze, 1979; David, 1982).

The number of Late Pleistocene localities with *Bison* remains from a specific time interval shows a negative correlation with the temperature during that period (Fig. 3). This negative correlation indicates that the bison, as well as the musk ox, belongs to the psychrophilic “Mammoth Steppe” fauna.

During the Holocene *B. priscus*/*B. bonasus* gradually became extinct. In the Asian part of its range bison survived until the Subboreal (indicated by finds in the Northern part of the Angara River basin, with an age of about 4500–4400 yrs BP), and possibly even later (Vasilevski et al., 1988). The decrease of the European bison *B. b. bonasus* populations during the Holocene was the result of hunting and the gradual destruction of the forest vegetation in Western and Central Europe. This subspecies was fully extirpated in its natural domain during the 1920-s. In the Caucasus the bison subspecies (*B. b. caucasicus* Satunin, 1904) adapted to montane conditions; this subspecies was finally extirpated in 1927 (Nemtsov et al., 2003).

4. Conclusion

The studies of the geographical distribution of the Eurasian musk ox and the primitive bison during the Late Pleistocene and the Holocene elucidated significant fluctuations of their ranges due to changes in climate and environmental conditions. These cold-adapted representatives of the mammoth steppe faunal community had their maximum range during the Denekamp (=Bryansk) Interstadial and the LGT (early) intervals. During the LGM the geographical range of both species decreased significantly, in particular in Northern Europe. This decrease is primarily related to the increase of the volume of the Scandinavian ice sheet at that time. The European Late Pleistocene bison is predominantly found at Paleolithic sites and is regarded as one of the major game species. A decrease in the range of Paleolithic humans might also have resulted in a decrease in the range of fossil bison records.

The reduction of the range of the bison in the beginning of the Holocene is related to the degradation of widely distributed open, periglacial landscapes and the increase of snow cover (Flerov and Zabolotski, 1961). It is remarkable, however, that in North America similar changes in the ecosystems did not lead to the extinction of the American bison, which is genetically very close to the Eurasian bison (Shapiro et al., 2004). This might be explained by the possibility that the extinction of the Eurasian bison was not only the result of climate changes, but also the result of anthropogenic pressure. It is obvious that humans played a role in the extinction of the European bison (wisent) and possibly also in the extinction of the remnants of Asian bison populations during Middle and Late Holocene.

The extinction of the musk ox was the result of rising temperatures and the reorganization of the ecosystems at the very end of Pleistocene and in the Holocene, and by the disintegration of its range into small isolated populations. The decrease of the genetic diversity of the musk ox also contributed to its extinction. The extinction of the relict musk ox on Taimyr Peninsula is a natural phenomenon.

The high positive correlation between the numbers of localities with bison and musk ox remains (Fig. 5) shows a general synchrony in the range of the species at a Eurasian scale. However, there are some species-specific peculiarities. In Europe and N. Asia, the musk ox is compared to the bison more abundant during the Denekamp Interstadial and less abundant during the LGM relative to the bison range. The relative number of localities with musk ox remains in N. Asia was higher than that of localities with bison remains during the Moershoofd Interstadial, the Hasselo Stadial, the Denekamp Interstadial and it was lower during the LGM. We should draw attention to the quick and complete disappearance of the musk from Europe close to the Pleistocene-Holocene boundary and its persistent survival in the north of Asia (the Taimyr Peninsula – “terminal refugia” (Lister and Stuart, 2008)) during the Holocene, up to the Subboreal period.

The results of our investigation have confirmed earlier statements that the observed changes in the bison and musk ox ranges as well as in the ranges of the other large herbivores of the “Mammoth steppe” fauna (*Mammuthus primigenius*, *Coelodonta antiquitatis*, *B. priscus*, *O. moschatus*, *Equus ferus*) did take place roughly synchronously in Eurasia during Late Pleistocene. One of the specific characteristics of the end-Pleistocene-early-Holocene mass extinctions was the decline of the large herbivorous species populations and of their ranges before the LGM, between 36 and 26 ^{14}C ka BP (Shapiro et al., 2004; Markova et al., 2010b; Lorenzen et al., 2011). However, as indicated in the literature (Stuart et al., 2004; Lister and Stuart, 2008; Stuart and Lister, 2011, 2012; Markova et al., 2013) and shown in Fig. 6, the changes in the geographical distribution are species specific and asynchronous.

Primitive bison populations in the European part of the bison range probably had a more intensive increase of their numbers between the Moershoofd Interstadial and the Hasselo Stadial, between the Huneborg Stadial and the Denekamp Interstadial, and after the LGM depression in the early LGT period than in the Asian part of its range. Overall, in N. Asia the number of localities with this species is in average 2 to 5 times less per time unit than in Europe

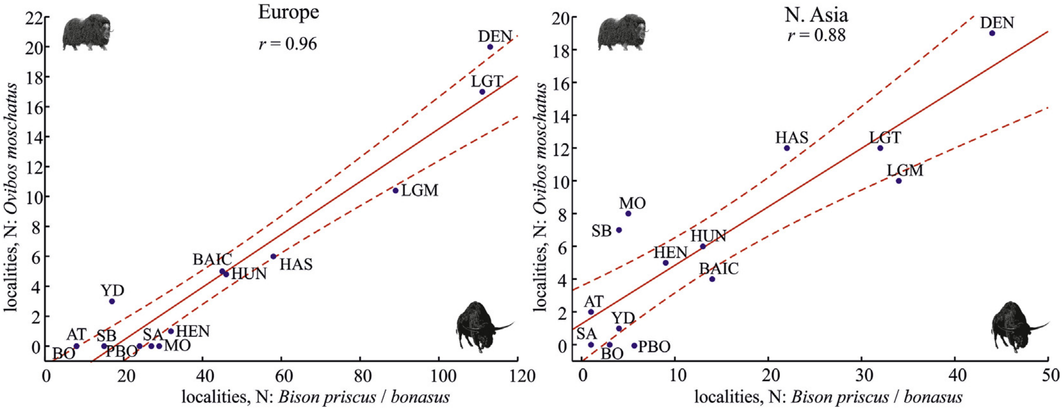

Fig. 5. Correlation between the numbers of localities with the primitive bison/wisent (*Bison priscus/bonasus*) and with the musk ox (*O. moschatus*) in the European and Asian parts of the species ranges.

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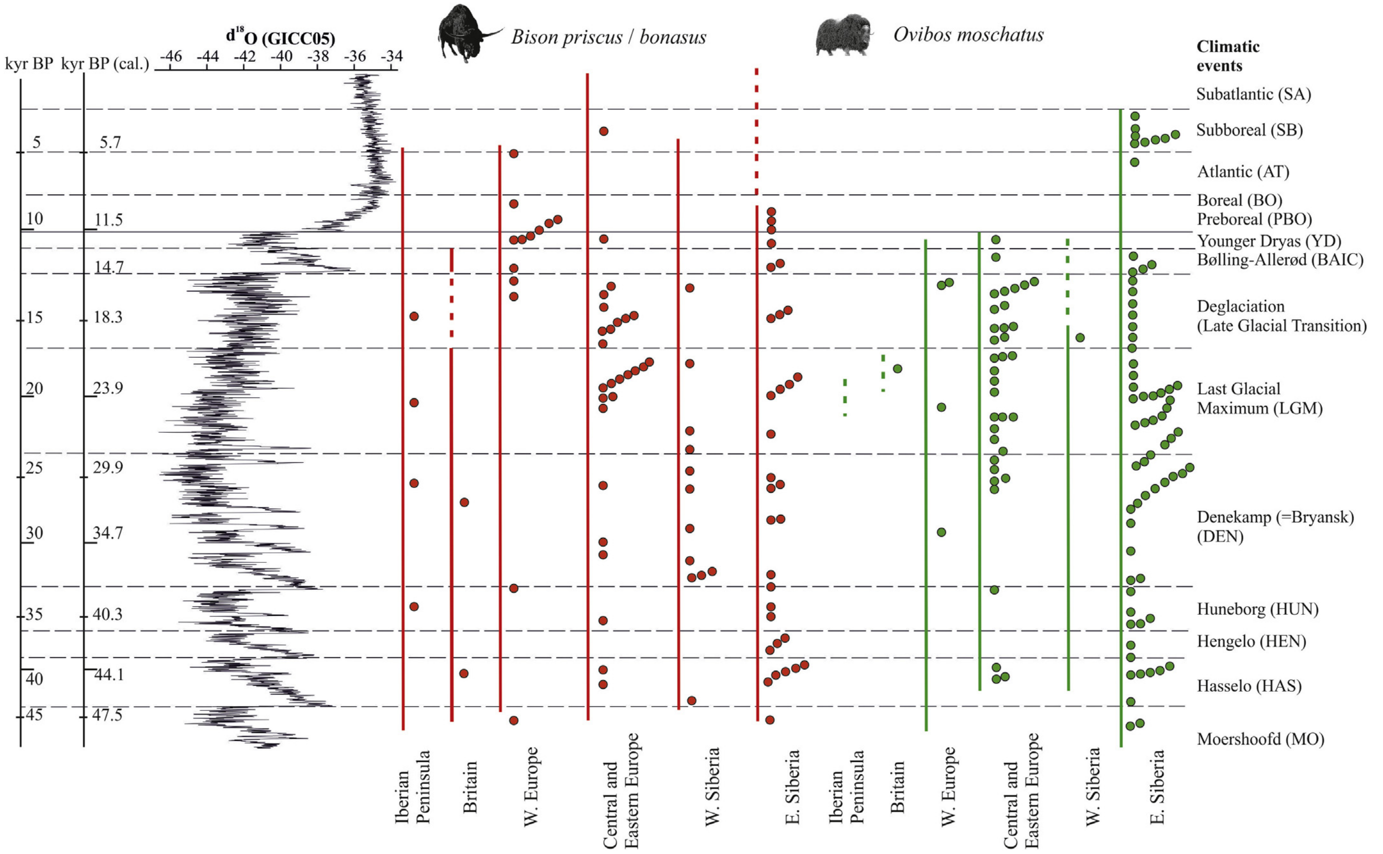

Fig. 6. Plot showing the direct radiocarbon dates of the primitive bison/wisent (*B. priscus/bonasus*) and the musk ox (*O. moschatus*) for the different geographical areas. The bars show the estimates of survival for the species in different parts of N. Eurasia based data obtained using all possible dating methods. The ^{d18}O curve is based on the Greenland Ice Core Chronology 2005 (GICC05).

(Fig. 3). This difference between Europe and N. Asia may depend on: a) the different levels in investigation of these parts of the range, b) the difference in the density of Paleolithic human populations, or c) differences in the size of the bison populations in western and eastern parts of its range. There are no data that could explain a lower density of the bison population density in the Asian part of its range in comparison to the density in the European part. So, the number of the sites with bison remains should be at least approximately equal in Europe and Asia (as in *O. moschatus*). However, it should be taken into account that Paleolithic sites yielded most of the bison data and second, there was selective hunting of bison (along with reindeer, reddeer, horse or aurochs, but no musk-ox). The observed significant difference in the numbers of bison localities in the European and Asian parts of its range might be explained by a higher density of the Paleolithic human populations in Europe (in particular in South-Western and South-Eastern Europe) during the Middle and Late Paleolithic time.

Lorenzen et al. (2011) indicated that the potential geographical ranges in Eurasia of the musk ox should be larger than that of the bison based on modelling. However, this assumption significantly contradicts the numerous paleontological data (Figs. 2 and 3 in this contribution). Our results have shown that *B. priscus* had a significantly wider range and penetrated further southwards (Iberia Peninsula, Apennines, Western Asia) during the cold climatic events of the Late Pleistocene compared to the musk ox, in particular in Europe. In all time intervals considered in our study, bison populations probably were significantly bigger than the populations of the musk ox. The musk ox had a narrower ecological niche in comparison with the primitive bison. However, the ancient musk ox populations distributed over Eurasia and North America might have had a wider ecological niche (less restricted to specific temperature and humidity conditions) than during the Late Pleistocene (Lister, 2004; Lister and Stuart, 2008).

Although a great quantity of data has been analyzed, more direct ^{14}C dates of remains from Western and Central Europe are needed for the 50–10 ka BP time interval in order to obtain a more detailed picture of the changes in the distribution of *Ovibos moschatus* and *B. priscus*, in particular along the boundaries of their ranges.

Acknowledgements

This study was financially supported by grants of the NWO foundation № 47.009.004, 047.017.2006.014, by grant of the NWO-RFBS № 07-05-92312 HBO, and by grants of the RFBS № 10-05-00111, № 12-04-00165 and N 13-05-00056.

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