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Invited review

Extinction chronology of the woolly rhinoceros *Coelodonta antiquitatis* in the context of late Quaternary megafaunal extinctions in northern Eurasia

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ABSTRACT

Megafaunal extinctions in northern Eurasia (excluding Mediterranean islands) since the Last Interglacial claimed about 37% of species with body weights >44 kg. Here we review the dating evidence for the timings of these extinctions, which were staggered over tens of millennia. Moreover, individual species disappeared at different times in different geographical areas. For example, cave bear probably disappeared ca. 30.5–28.5 ka, at approximately the onset of GS-3 (beginning of 'LGM'), whereas cave lion survived until the Lateglacial ca 14 ka. Others survived into the Holocene: woolly mammoth until ca 10.7 ka in the New Siberian Islands and ca 4 ka on Wrangel Island, giant deer to at least 7.7 ka in western Siberia and European Russia. It is evident that climatic and vegetational changes had major impacts on species' ranges, and moreover the contrasting chronologies and geographical range contractions are consistent with environmental drivers relating to their differing ecologies. However, the possible role of humans in this process has still to be satisfactorily explored.

We present a detailed review of the radiocarbon record and extinction chronology of an exclusively northern Eurasian species, the woolly rhinoceros *Coelodonta antiquitatis*, an animal adapted to feeding on low-growing herbaceous vegetation and a dry climate with minimal snowfall. During the Last Glacial the overall (time-averaged) range of *C. antiquitatis* extended across most of northern Eurasia, but the species failed to reach North America. On the basis of 233 ultrafiltered AMS radiocarbon dates, together with 50 others which pass our auditing criteria, we reconstruct a detailed chronology for this species. *C. antiquitatis* was widespread over most of the time span covered by radiocarbon dating, but from ca 35 ka (calibrated) it apparently contracted towards the east, culminating in its probable extinction ca 14 ka, with the latest dates from north-eastern Siberia. It disappeared from Britain, at the western, more oceanic end of its range, at ca 35 ka BP apparently corresponding with the onset of Interstadial GI-7. In north-eastern Siberia *C. antiquitatis* survived through much of GI-1d,e and probably went extinct at or close to the onset of GI-1c (Allerød) ca 13.9 ka BP. Its final extinction probably relates to Lateglacial interstadial warming and increased precipitation (especially snowfall) accompanied by the replacement of low-growing herbaceous vegetation by shrubs and trees. The survival of woolly rhinoceros in north-eastern Siberia when it had disappeared further west may relate to the later persistence of open vegetation in that region. The timing of its final extinction could relate to the fact that the Lateglacial interstadial was significantly warmer than any other event in the previous 50 millennia.

There are indications of gaps in the pattern of dates in certain areas that may have significance in terms of temporary absences of *C. antiquitatis*, some of which may correspond to interstadial phases. The radiocarbon record of *C. antiquitatis* is still poor in some potentially important areas, and further work will corroborate or reject the hypotheses of regional 'gaps' in occurrence, and might perhaps reveal currently unsuspected later survival.

1. Introduction

Megafaunal extinctions in northern Eurasia since the Last Interglacial were substantial, claiming about 37% of species with body weights >44 kg (18 out of 49, including *Homo neanderthalensis*), as well as many island forms not discussed here. Losses in this region

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(here defined as Europe, Russian Federation, Kazakhstan, Mongolia, northern China and Japan) were therefore significant, despite often being downplayed in comparison with other regions such as North or South America. As elsewhere, in northern Eurasia the largest animals were most affected, so that three species of elephant (each weighing 5–8 tonnes), two rhinos (each exceeding 2 tonnes) and most other large mammals over 500 kg disappeared (Table 1). Moreover, northern Eurasia is an especially fruitful region for the study of late Quaternary extinctions, not only because of the wealth of available archaeological, palaeontological and environmental data, but also because it has by far the largest number of radiocarbon dates made directly on megafaunal remains. These have made it possible to construct detailed chronologies for several of the extinct species, including mammoth (Stuart et al., 2002), giant deer (Stuart et al., 2004), cave bear (Pacher and Stuart, 2009) and cave lion (Stuart and Lister, 2011); see also syntheses and other taxa in Lister and Stuart (2008), Stuart (2005), Stuart and Lister (2007), Kuzmin (2010), Lorenzen et al. (2011) and others. Here we present a detailed review of the radiocarbon record and extinction chronology of a species restricted to northern Eurasia, the woolly rhinoceros, *Coelodonta antiquitatis*. The woolly rhinoceros has been widely regarded as having been a 'fellow traveller' of the woolly mammoth *Mammuthus primigenius*, as their remains commonly occur together in Last Glacial deposits. However, there are major differences between the two species in geographical distribution, palaeobiology and extinction chronology.

DNA sequence data indicate the Sumatran rhinoceros *Dicerorhinus sumatrensis* as the closest (but distant) living relative of *Coelodonta* (Orlando et al., 2003), while morphological analysis by Deng et al. (2011) suggests that the extinct Pleistocene genus *Stephanorhinus*, specifically *Stephanorhinus hemitoechus*, may be its true sister-group. The recently-described earliest known member of the woolly rhinoceros group, *Coelodonta thibetana*, dates to the middle Pliocene (ca 3.7 Ma) of the Tibetan plateau, leading to the suggestion that the genus originated in this area and gained its adaptations to cold, open habitats as a result of living at high altitudes (Deng et al., 2011). From there it spread to lowland areas during glacial phases of the Pleistocene. *Coelodonta nihowanensis*, ca 2.5 myr ago, inhabited central Asia, from the border of the Tibetan Plateau to eastern China (Kahlke and Lacombat, 2008). By the early Middle Pleistocene a form of *Coelodonta* comparable with *Coelodonta tologoijensis* is recorded by several finds from eastern and central Europe, including a skull recovered from Elsterian cold stage sediments (MIS 12, about 460 ka) at Bad Frankenhausen, Germany (Kahlke and Lacombat, 2008). Evolutionary trends in the *Coelodonta* lineage include elongation and narrowing of the skull, which became more inclined and low-slung, a posterior shift of the orbits, changes in the position of the cheek tooth rows and the thickening of enamel and secondary cementum. All of these changes can be seen as adaptations for efficient grazing (Kahlke and Lacombat, 2008; Deng et al., 2011).

During the Last Glacial the overall (time-averaged) range of *C. antiquitatis* extended in a broad swathe from northern Spain and Britain in the west, across central and eastern Europe to north-east Siberia, northern China and Mongolia. However, it was absent from Ireland, much of southern Europe, central and northern Scandinavia, north-central Siberia and the Japanese Islands (Fig. 1). Moreover, woolly rhinoceros did not cross into Alaska, although it is recorded from Wrangel Island and the Chukotka Peninsula in north-eastern Siberia within a few hundred kilometres of the former Bering Land Bridge (Boeskorov, 2001). This failure to colonize North America appears surprising, especially as many other animals, such as woolly mammoth *M. primigenius* and cave lion *Panthera spelaea*, did make the crossing. This question will be discussed further below.

2. Palaeobiology

For the woolly rhinoceros (as also for the woolly mammoth), there is a wealth of evidence for reconstructing its appearance and mode of life, not only from skeletal anatomy (Borsuk-Białynicka, 1973), but also from many representations in Palaeolithic art, occasional mummified remains, rare stomach contents, and stable isotope analyses.

C. antiquitatis possessed an impressive battery of high-crowned cheek teeth with thick enamel and packed with cementum, which would have been well adapted to feeding on grasses and other low-growing vegetation with a high silica content, together with accidentally ingested soil and grit. The sloping occiput and posterior position of the foramen magnum indicate a low slung carriage of the head, much as in the living African white rhinoceros *Ceratotherium simum* (Burchell), which is a grass eater (Haltenorth and Diller, 1980; Kingdon, 2008). The large bulk and short legs, lacking spreading hooves or pads, indicate an animal unable to traverse deep snow (Kahlke, 1999).

Soft-tissue adaptations of *C. antiquitatis* are seen in mummified material from the Siberian permafrost (Boeskorov et al., 2011) and the two carcasses preserved in salt and hydrocarbons from an

Table 1
Megafaunal species extinct in northern Eurasia within the last ca 120 ka. Current estimates of extinction dates are taken from Table 2 and other evidence discussed in the text.

Species		Latest known occurrence
Camelus knoblochi	A large camel	No information
Hippopotamus amphibius	Hippopotamus	ca 117 ka[a]
Palaeoloxodon antiquus	Straight-tusked elephant	ca 70–50 ka[a]
Stephanorhinus hemitoechus	Narrow-nosed rhinoceros	ca 45 ka[a]
Sinomegaceros yabei	A giant deer	ca 45 ka[b]
Spiroceros kiakhtensis	Spiral-horned antelope	after 37 ka
Crocuta crocuta	Spotted hyaena	30.8 ka
Ursus spelaeus	Cave bear	28.5–30.5 ka
Palaeoloxodon naumanni	Naumann's elephant	28.3 ka
Homo neanderthalensis	Neanderthal	ca 28 ka[a]
Panthera spelaea	Cave lion	14.1–14.4 ka
Coelodonta antiquitatis	Woolly rhinoceros	14.0 ka
Mammuthus primigenius	Woolly mammoth	10.7 ka (4 ka Wrangel Island)
Bison priscus	Steppe bison	9.8 ka
Megaloceros giganteus	Giant deer	7.7 ka
Equus hydruntinus	European ass	ca 3.5 ka
Ovibos moschatus	Muskox	2.8 ka
Bos primigenius	Aurochs	0.38 ka

[a] Approximate estimate.
[b] very uncertain

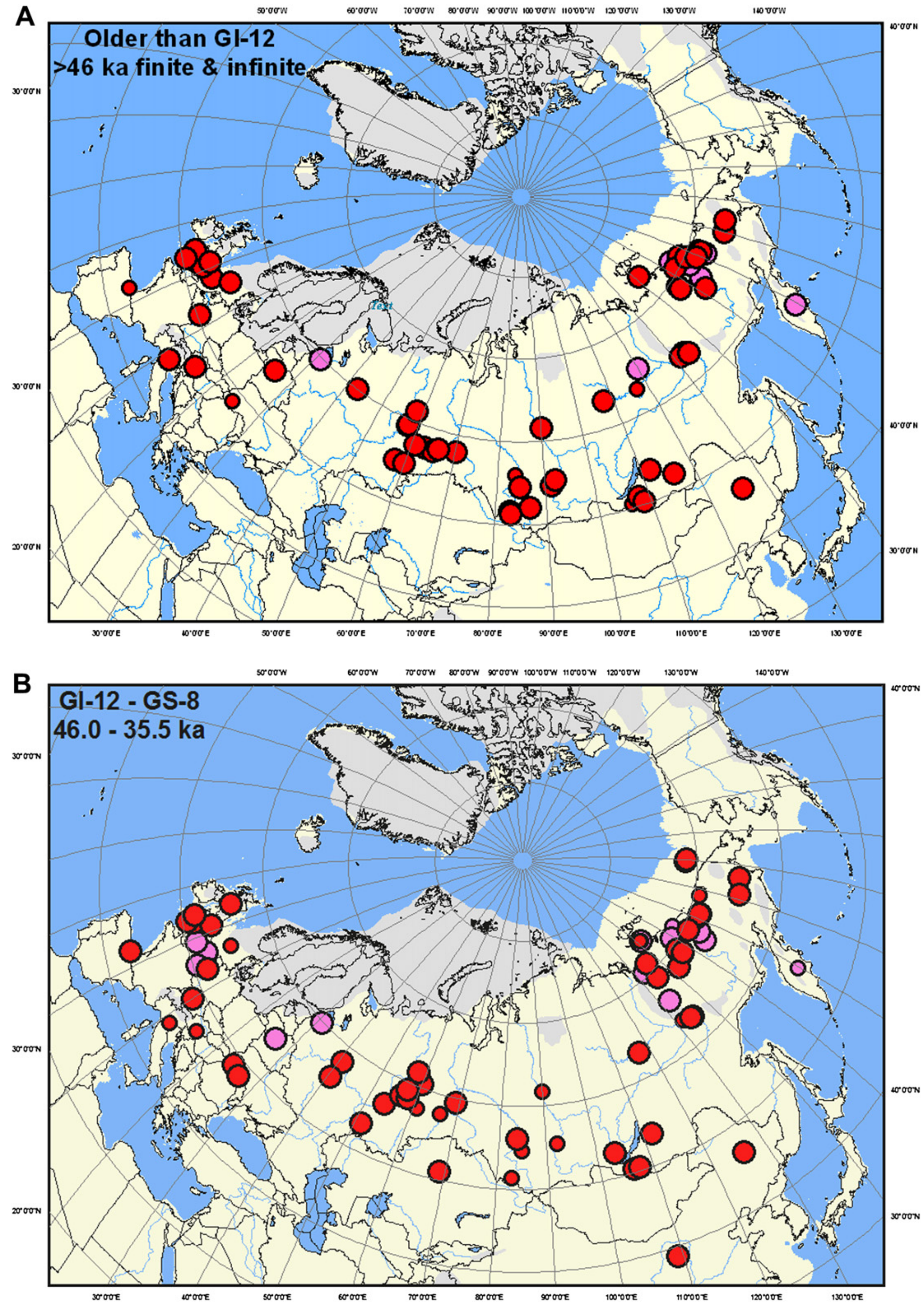

Fig. 1. Time-sliced maps of radiocarbon dates for *C. antiquitatis*. Red: ultrafiltered date; pink: non-ultrafiltered date. Large icon: median calibrated date falls within time-slice; small icon: some part of 95% confidence interval of calibrated date (but not the median) falls within time-slice. Grey: ice sheets.

ozocerite (natural paraffin wax) mine from Starunia in south-western Ukraine (Nowak et al., 1930; Kubiak, 1969; Kotarba et al., 2008).

Until recently only partial woolly rhino carcasses had been recovered from the Siberian permafrost, but in 2007 a largely complete frozen mummy of an adult female was discovered by gold miners on the Kolyma River, north-eastern Siberia (Boeskorov et al., 2011). The mummy comprises the left part of the body including fore and hind legs and the head with both horns and the mandible. The intestines and stomach and their contents were also recovered.

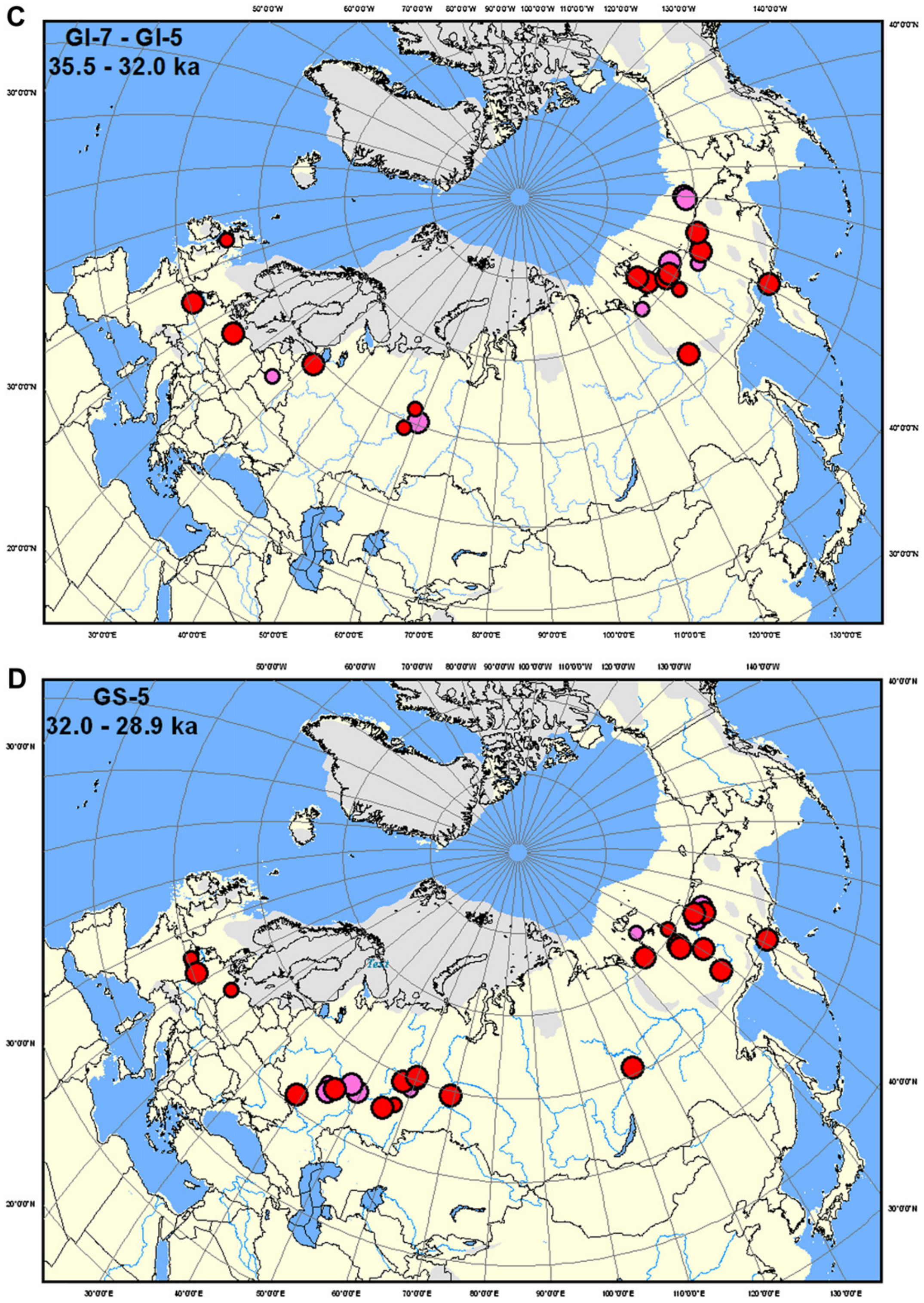

Fig. 1. (*continued*).

A rib fragment gave a median calibrated date (OxA-18755) of 43,359 BP (42,706–44,120) (39,140 ± 390 ^{14}C years BP). Skin thickness varies from 5 to 15 mm on different areas of the body. Partial mummies of other individuals were also recovered. Pollen and spores recovered from the stomach contents of the principal carcass comprised mainly grass and *Artemisia* together with a diversity of other herbs, giving an indication of the last food consumed by this individual prior to its death. Boeskorov et al. (2011) note that grasses and *Artemisia* similarly predominated in plant remains recorded previously from woolly rhino teeth from the Khalbui River, and in the gut contents of a partial mummy from Churapcha, central Yakutia.

Several of the Siberian finds indicate that *C. antiquitatis* had long, bristly guard hairs, especially on the neck and shoulders, and

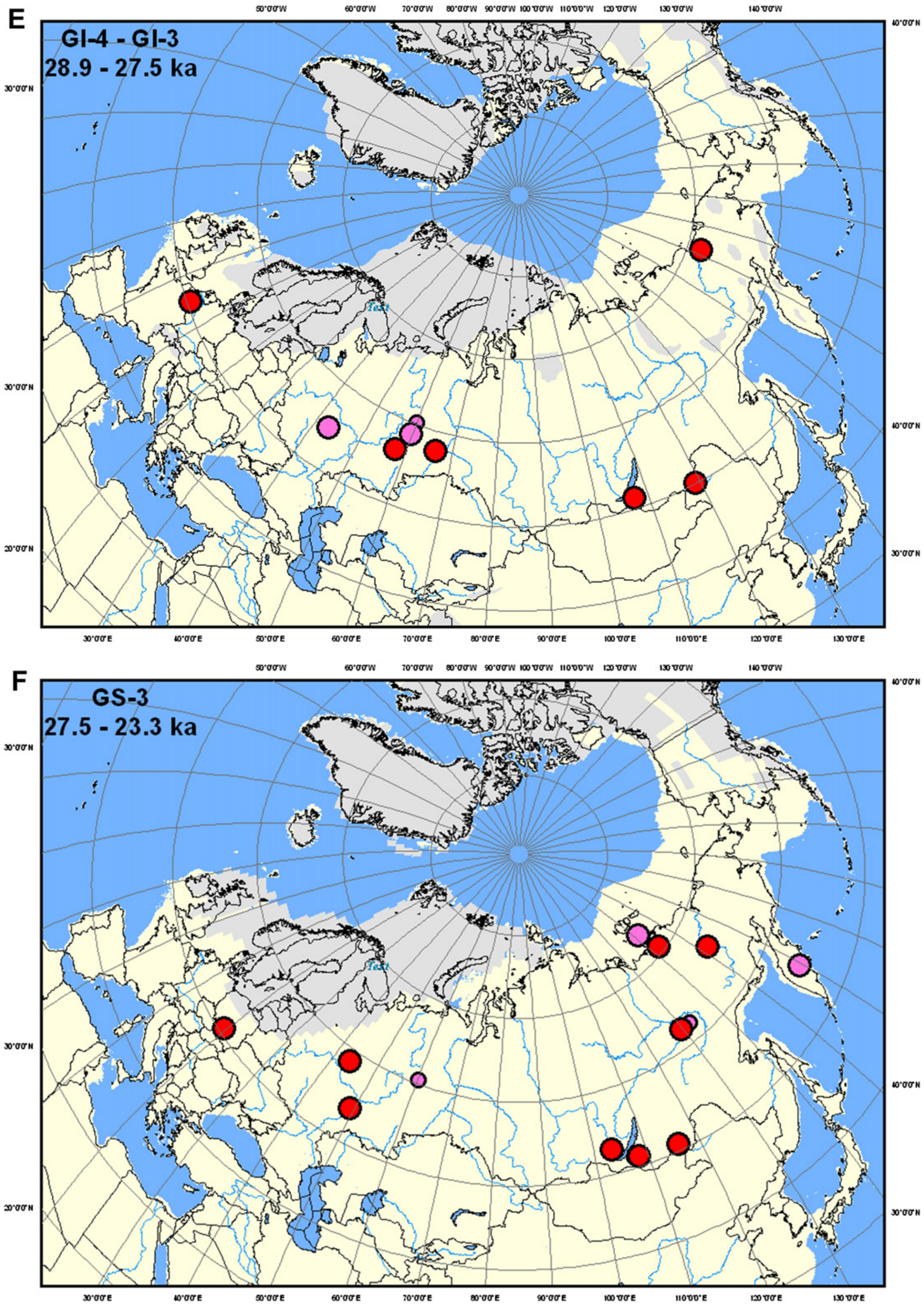

Fig. 1. (*continued*).

a dense, insulating under wool (Kahlke, 1999; Kahlke and Lacombat, 2008). The short hair of the limbs, especially well preserved on the hind legs of the Churapcha mummy, would have prevented large amounts of snow or ice adhering to the legs and feet and hampering movement. Muzzles preserved in partial frozen carcasses discovered in 1771 at the Vilyui River, north-eastern Siberia, and in the two mummies from Starunia, western Ukraine, clearly indicate that *Coelodonta* possessed very wide lips, consistent with adaptations for grazing, as in the extant *Ceratotherium simum*.

Many well-preserved *C. antiquitatis* horns, composed of keratin as in modern rhinos, have been recovered from the permafrost of northern Siberia. These show that the large, long and heavy skull bore two horns: a relatively small frontal horn and a much larger nasal horn as much as 1.35 m long (Fortelius, 1983), as also seen in

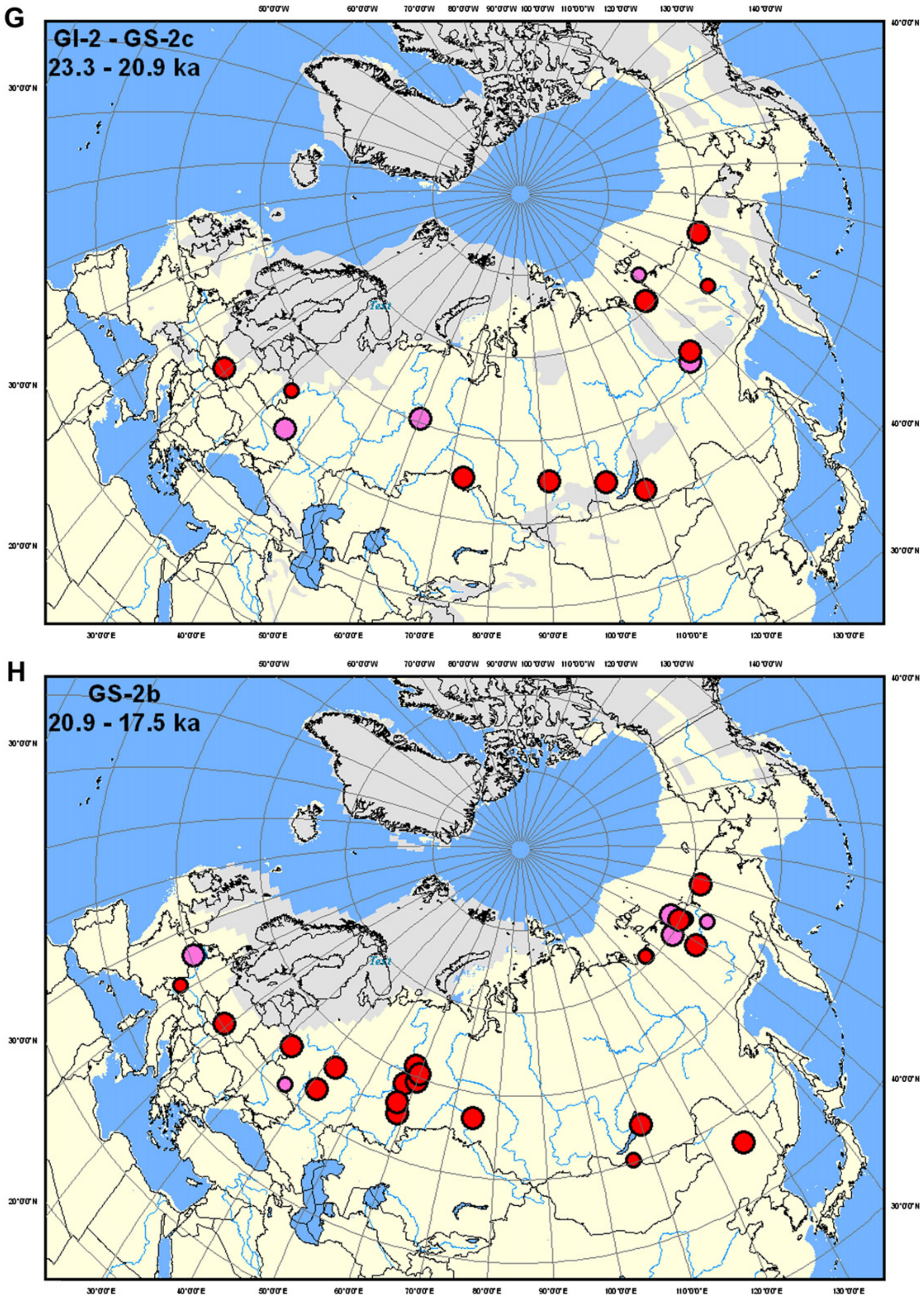

Fig. 1. (*continued*).

many Palaeolithic paintings and engravings. The nasal horn, which because of the low-slung position of the head would have been carried nearly horizontally, was laterally flattened, unlike the frontal horn or the horns of any of the five living species of rhinoceros which are rounded in cross section. Elongated paired left and right wear facets strongly suggest that the horns were used in a side to side motion, probably to clear thin snow cover to expose vegetation or to free plants frozen to the ground, and by analogy with living rhinos it is also very probable that the horn was used as a weapon and intraspecific status symbol (Fortelius, 1983; Deng et al., 2011). One of the paintings from Chauvet Cave shows two individuals facing each other and locking horns.

The horns show prominent transverse bands which are very probably annual (Fortelius, 1983). A recent study of the stable

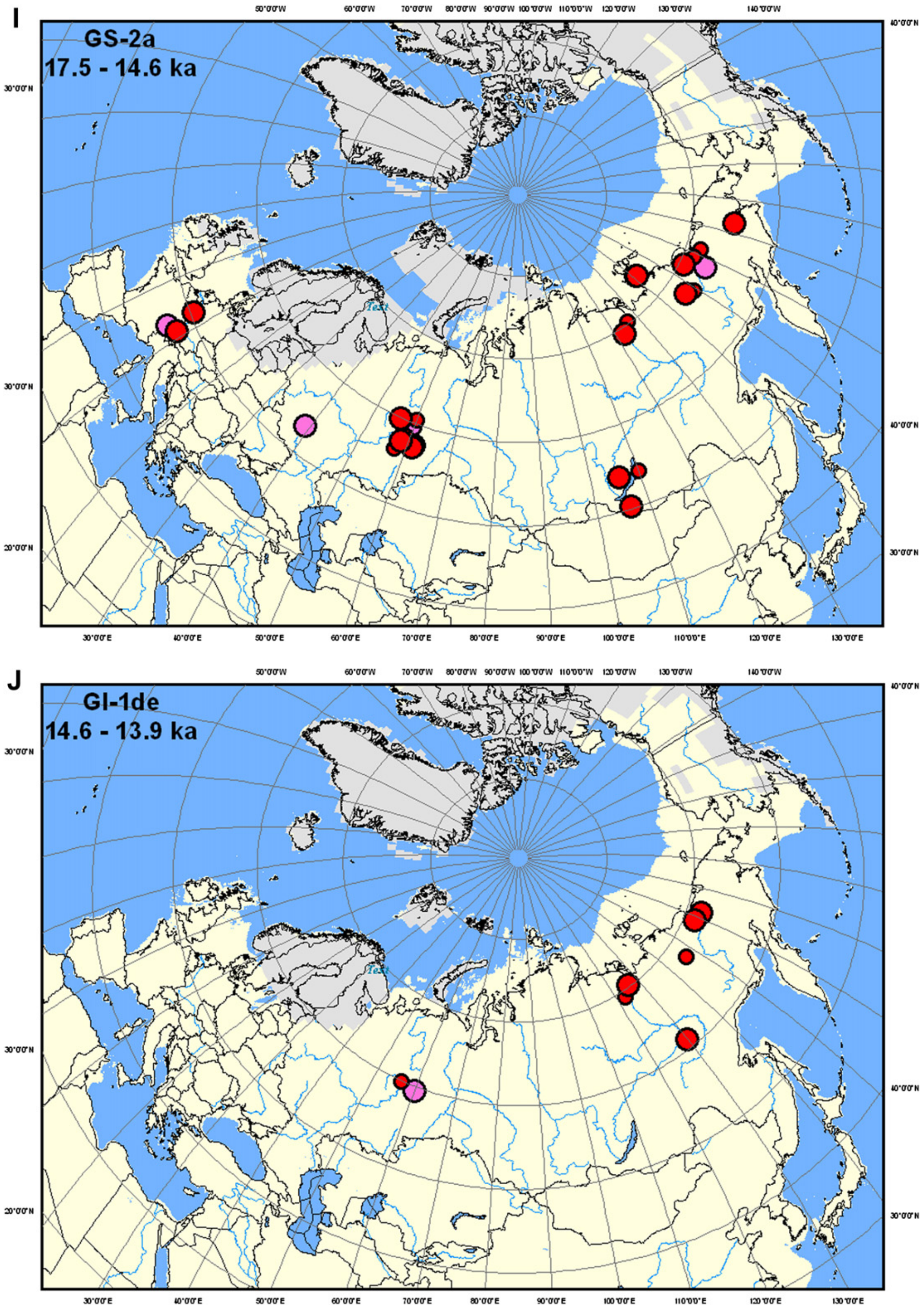

Fig. 1. (*continued*).

isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) by Tiunov and Kirillova (2010) suggests that variations in isotopic composition between bands reflect seasonal changes in the diet and that the denser and lighter-coloured bands, with lower $\delta^{13}C$ and $\delta^{15}N$, possibly indicate that more woody and shrub vegetation was eaten in the winter. The considerable weight of the head and horns was evidently balanced by massive muscles and ligaments attached to the long neural spines on the anterior thoracic vertebrae. Kahlke (1999) suggests that this probably formed a region where abundant fat accumulated – an important adaptation to marked seasonal variations in food availability.

Although *Coelodonta* is relatively rare in Palaeolithic art, there are clear depictions from a number of sites, e.g. portable engravings on slate from the open site of Gönnersdorf, Germany

Fig. 1. (*continued*).

(Bosinski, 2008), mural art from the caves of Font de Gaume, Rouffignac, and Lascaux in Southern France, and especially the 65 superb paintings and engravings at Chauvet Cave, Ardèche. The latter, originally attributed to the Aurignacian and Gravettian, (Chauvet et al., 1995; Clottes, 2003), are regarded by others as Solutreo-Magdalenian on stylistic grounds (Pettitt et al., 2009). The depiction of cave bear *Ursus spelaeus* at Chauvet Cave argues for the earlier age as there is good evidence that this animal became extinct by ca 28 cal ka BP (Pacher and Stuart, 2009). Some of the images of *C. antiquitatis* depict a woolly coat. The Chauvet representations also show a broad vertical band across the animal's flank, which may represent the deep skin folds seen in living rhinos or alternatively colour patterning of the coat.

3. Materials and methods

We assembled a database of radiocarbon dates made directly on *C. antiquitatis* remains, comprising Oxford AMS dates from our megafaunal extinctions project, together with Aarhus and Oxford AMS dates kindly supplied in advance of publication by Jonas Binladen, Eline Lorenzen and Eske Willerslev as part of their ancient DNA (aDNA) study (Lorenzen et al., 2011). The samples for dating were chosen to span as wide a geographical and potential chronological range as possible. Our study relies primarily on 233 ultrafiltered Oxford (ORAU) and Aarhus AMS dates, together with 50 other dates which pass our auditing criteria (Supplementary Information Table 1). There is evidence that ultrafiltration of gelatin from archaeological bone can, in many instances, remove low molecular weight contaminants, leading to improved reliability (Jacobi et al., 2006).

All of the dates used are from material identified morphologically and/or by aDNA analysis as *C. antiquitatis*. Dates were excluded from the study if identification could not be corroborated – this includes cases where the sampled skeletal element is unknown from published data or our requests for information from laboratories. We also exclude dates obtained before 1980, as exclusive use of collagen and adequate pretreatment (especially cleaning) were not in regular use until the early 1980s (Stafford et al., 1987). Where a date has been superseded by a date on the same specimen more recently and/or using more advanced methods, the earlier date has been excluded. In other cases of multiple dates on a specimen, a combined date has been calculated in OxCal 4.1 – these cases are indicated in SI Table 1. Excluding dates because they are outliers is problematic because it risks losing novel information, but our policy is that significant outliers (e.g. dates much more recent than any others) should be corroborated by another laboratory (Stuart et al., 2004). In this study, the only date excluded solely on grounds of being an outlier is IPAE-93 (9510 ± 260 ^{14}C years BP) (see below). Other auditing criteria that would have led to exclusion are: samples mixed taxonomically or comprising more than one skeletal element; analyses on apatite or burnt bone; locality or laboratory number uncertain or unknown; however, none of these applied to *C. antiquitatis* dates known to us. Excluded dates are listed in SI Table 2 and discussed where appropriate in the text.

All dates have been calibrated using the IntCal09 curve implemented in OxCal version 4.1 (https://c14.arch.ox.ac.uk/). They are presented here both as time-sliced maps (Fig. 1) and chronological charts (Fig. 2). Maps were plotted in ArcGIS 9.3. Time-slices for maps follow Greeland stadial (GS) and interstadial (GI) boundaries designated by the INTIMATE group (Walker et al., 1999; Lowe et al., 2008), with recent updates from the NGRIP project (ftp://ftp.ncdc.noaa.gov/pub/data/paleo/icecore/greenland/summit/ngrip/gicc05-20yr.txt). Older GI and GS stages, some of which are very short and for which we have few radiocarbon dates, have been combined (SI Table 3). Modelled ice-sheets were taken from the Palaeoclimate Modelling Intercomparison Project 2 (http://pmip2.lsce.ipsl.fr/design/ice5g/), except for 'Last Glacial Maximum' (23.3–20.9 ka), 'Younger Dryas' (12.8–11.7 ka), and mid-Weichselian ice-sheets, from Ehlers and Gibbard (2004a–c). Sea levels evidently fluctuated markedly during the Last Glacial, (Bard et al., 1990; Rohling et al., 2008; Hu et al., 2010). Global eustatic sea levels used in Fig. 1 are taken from Lambeck & Chappell (2001, Fig. 3b) for intervals 21–12 ka and Hu et al. (2010, Fig. 1a) for preceding intervals. For the ice-sheets and bathymetries chosen for each time-sliced map, see SI Table 3.

The 95% confidence interval of the probability density function of each calibrated date is shown, in the charts by a vertical line and in the maps by plotting a specimen in each map whose time-interval is overlapped by the specimen's 95% range. Medians are indicated as a convenient visual guide, although the median may not fall in a region of high probability. Finite dates >46 ka (ca 42,000 ^{14}C years BP) are treated as 'infinite'.

4. Results

On the evidence of radiocarbon dated finds (finite dated records and infinite dates), until ca 40 ka *C. antiquitatis* was widespread across northern Eurasia from Spain and Britain in the west, eastwards to northern China and north-eastern Siberia. Subsequently there appears to have been a progressive contraction in its range (Fig. 1). In general there is good agreement between the ultrafiltered and audited non-ultrafiltered dates, but there are a few important instances where a non-ultrafiltered date is younger than the available range of ultrafiltered dates for the region (Fig. 2C, D).

C. antiquitatis is known from a number of sites in central and northern Spain (Álvarez-Lao and García, 2011) but there is only one available direct date, with a median >45 ka (95% range 42,919–49,559 BP) (SI Table 1). There is a single known specimen of woolly rhino from northern Italy (Gallini and Sala, 2001), with a median >49 ka (95% range 45,199–56,986). An extensive series of ultrafiltered *C. antiquitatis* dates from Britain terminates at ca 35 ka and since there are also no undated finds from contexts post-dating the Last Glacial Maximum (LGM) in Britain (Currant and Jacobi, 2011), it was almost certainly absent by this time. In marked contrast, the youngest available date (ultrafiltered) from western or central Europe, from Gönnersdorf in the mid-Rhine region of Germany, combining OxA-10200/10201, has a median of 16,835 BP (95% range 16,658–17,016 BP). The Upper Palaeolithic (Magdalenian) engravings on slate from this site, which clearly depict woolly rhino, mammoth and other animals (Bosinski, 2008), are constrained chronologically by a large series of associated calibrated dates between about 16.3 and 15.1 ka (Stevens et al., 2009), suggesting that *C. antiquitatis* survived a few hundred years or so later somewhere in the territory known to the Magdalenian engravers, i.e. western and central Europe. At Gönnersdorf the discrepancy between the direct dates on *C. antiquitatis* remains and the younger Magdalenian occupation of the site probably can be attributed to collecting of sub-fossil material by humans.

Moving further east, the youngest ultrafiltered date from European Russia (OxA-15859) is 19,487 BP (19,381–19,836 BP), and there is one later conventional date (GIN-9503) of 15,127 BP (14,745–15,582 BP). A substantial series of woolly rhino dates from the Urals terminates with an ultrafiltered date (combining AAR-11042 and OxA-18604) of 14,933 BP (14,589–15,192 BP) (SI Table 1; Fig. 2). There is also one younger non-ultrafiltered date (KIA-5670) of 14,165 BP (13,925–14,850 BP), which although overlapping with the former date at 2σ, may indicate somewhat later survival in the region. However, our extensive sampling of putatively late *C. antiquitatis* material in the Ekaterinburg collections (see above) failed to produce a date corroborating this possibility. We do not accept the non-ultrafiltered early Holocene date on a scapula from the Urals site of Lobvinskaya Cave (IPAE-93; Kosintsev 2007) as it is an extreme outlier which could not be tested by further dating (SI Table 2).

C. antiquitatis evidently survived until at least 16.1 ka in the Baikal area, to ca 16.5 ka in Chukotka (the easternmost region of Siberia), and to ca 16.1 ka in the New Siberian Islands (northern Yakutia, in the Arctic Ocean). There are only a few dates on woolly rhino from Wrangel Island (northern Chukotka, in the Arctic Ocean), with the latest ca 35 ka contrasting strongly with the survival of woolly mammoth on Wrangel Island well into the Holocene (see below). The youngest known woolly rhino dates are from north-eastern Siberia. The very youngest, from the Lena-

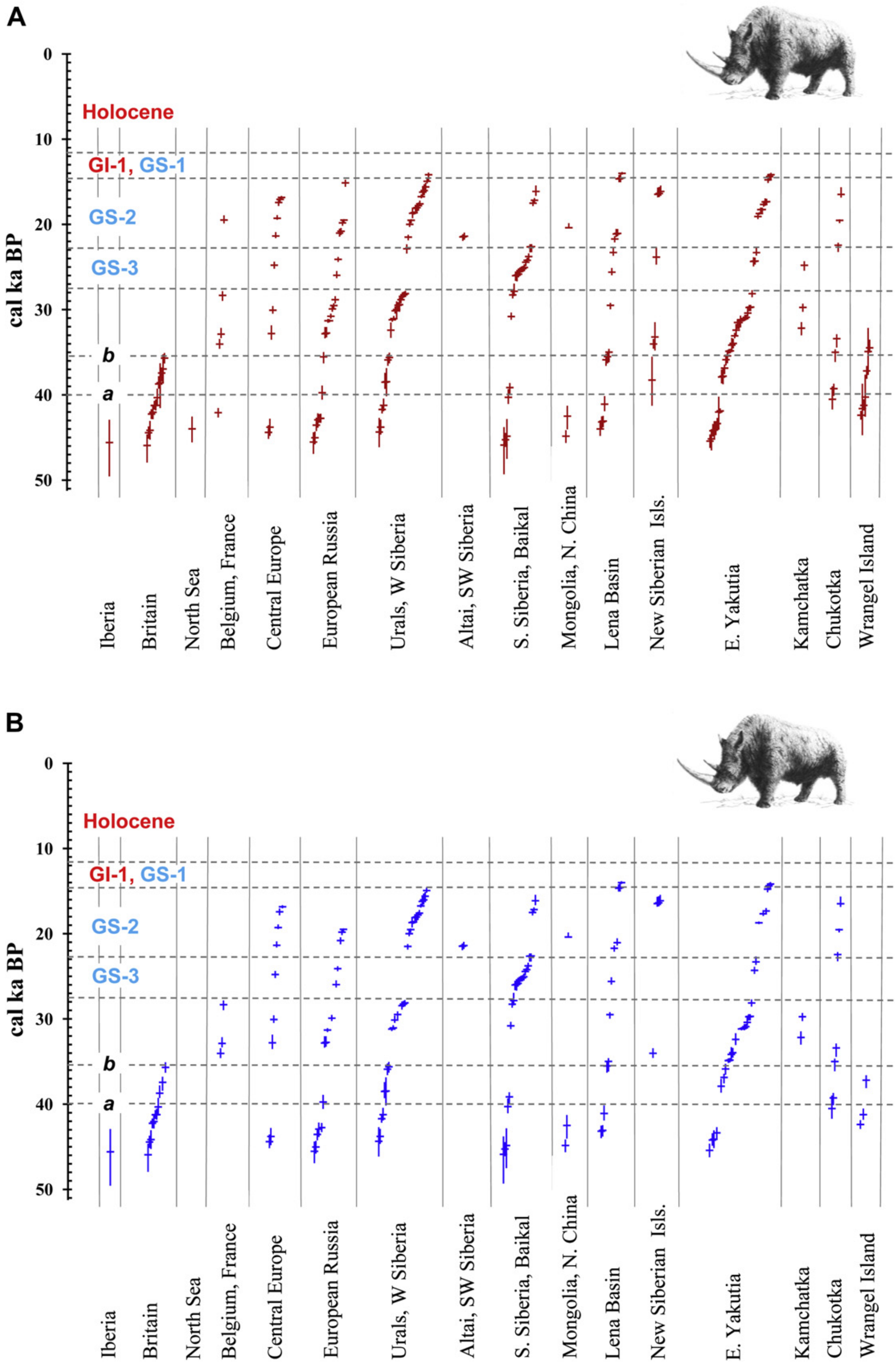

Fig. 2. Plot of radiocarbon dates for *C. antiquitatis* grouped geographically. Median dates shown with 95.4% confidence limits. A. Plot of ultrafiltered and other audited calibrated dates < 46 ka BP. Greenland stadials GS-3, GS-2, GS-1 and interstadial GI-1 are indicated; cold phases lettered in blue, warm phases red. *a*, onset of GS-9, *b*, onset of GI-7. B. As A, ultrafiltered dates only. C. Plot of ultrafiltered and other audited calibrated dates <18 ka BP. Greenland stadials GS-2, GS-1 and interstadials GI-1a–e are indicated; cold phases lettered in blue, warm phases red. D. As C, ultrafiltered dates only.

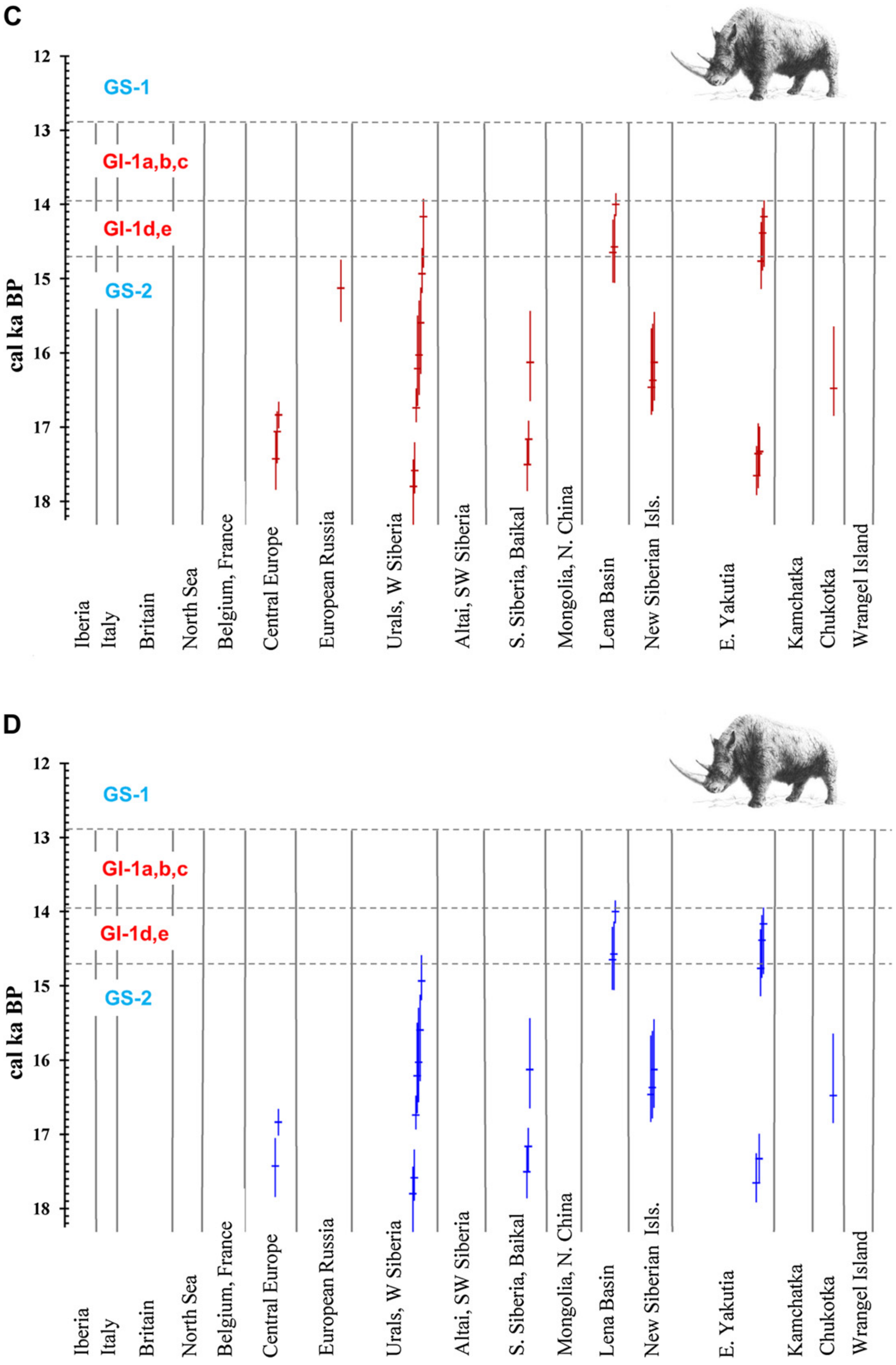

Fig. 2. (*continued*).

Amga interfluve, are OxA-18602, median 13,978 BP (14,144–13,826 BP), and AAR-11027, 14,040 BP (14,475–13,812 BP) on the same specimen. Combining the two gives a median of 13,999 BP (13,851–14,156 BP), largely within the GI-1de interval but overlapping the GI-1abc interval by 50 years (Figs. 1K and 2D). A date from Ust'-Omolon in north-east Yakutia, (OxA-20097) overlaps the latter combined date substantially at 95% with its median only a little earlier at 14,164 BP (13,947–14,839 BP). This situation contrasts with dates indicating significantly later survival of woolly mammoth *M. primigenius* into the early Holocene in Taimyr and the New Siberian Islands (see below).

There are indications of gaps in the pattern of dates in certain areas (Fig. 2A, B) that may have significance in terms of temporary absences of *C. antiquitatis*. The most prominent apparent gaps are ca 40–34 ka BP in central and eastern Europe and southern Siberia, and ca 27–21 ka BP in the Urals. In addition there is an apparent thinning of dates corresponding with the latter interval from Europe (Fig. 1F, G).

5. Extinction of *C. antiquitatis*

Although *C. antiquitatis* was widespread over most of the time span covered by radiocarbon dating, we find a progressive reduction in its range, essentially a contraction towards the east, from about 35 ka until its probable extinction ca 14 ka (Fig. 1C–L). This conclusion contrasts with Lorenzen et al. (2011), who believed that extinction had occurred more or less synchronously across its entire range. The extirpation of *C. antiquitatis* from Britain, at the western, more oceanic end of its range, at ca 35 ka BP corresponds with the onset of Interstadial GI-7. The apparent gap in dates in parts of Europe and southern Siberia ca 40–34 ka covers a series of stadials and interstadials (GS-9, GI-8, GS-8, and GI-7), including a prominent interstadial (GI-8) from 38.2 to 35.6 ka BP. Lorenzen et al. (2011) suggested, on the basis of DNA sequence data, a five-fold increase in population size of woolly rhino at some time in the interval ca 34–19 ka, but the timing of the increase was poorly-constrained. It is possible that this event corresponds to a resurgence of numbers after GI-7 or one of the other 'gaps' indicated by the radiocarbon data. However, in the Urals *C. antiquitatis* persisted through these episodes but was evidently absent during stadial GS-3, corresponding with Greenland ice core cold episode GS-3, which in regions further east seems to have been favourable for this animal. In common with woolly mammoth but in contrast to some other megafaunal species such as giant deer *Megaloceros giganteus* (Stuart et al., 2004), there is no major gap in the pattern of *C. antiquitatis* dates corresponding to much of the interval GS-3 plus GS-2, (the 'last glacial maximum' *sensu lato*) across most of its range. Interestingly, there is a possible inverse relationship in date density between Britain and more eastern parts of Europe, with the changeover at the GS-8/GI-7 boundary; and between southern Siberia and the Urals with the changeover at the GS-3/GS-2 boundary. Inferring climate-controlled shifts of range between adjacent regions at these times must remain provisional until they can be confirmed by further dating. Overall, the pattern of dates suggests that interstadial conditions in some areas were unfavourable to this animal, which very probably preferred a dry climate, firm ground, only light snow cover and extensive low-growing vegetation. The available data suggest that the full picture could be very complex, with presence or absence of woolly rhino in different areas responding to variations in temperature, precipitation – especially snowfall – and vegetation cover.

On the basis of the ultrafiltered dates only, the final disappearance of woolly rhinoceros in the Urals might correspond with the onset of the major warming of Interstadial GI-1e (Bølling) at ca 14.7 ka BP. However, if it could be corroborated, the non-ultrafiltered date (KIA-5670) could extend its chronological range in the Urals by up to ca 700 years, suggesting disappearance at some time within GI-1e or at the onset of the Allerød. Orlova et al. (2008) and Kuzmin (2010), accepting SOAN-4747 (SI Table 2), suggested a later, Younger Dryas extinction, with the Ural region as the terminal refugium of the species. In north-east Siberia a cluster of several dates with 95% ranges close to the end of the interstadial provide firm evidence that in this region *C. antiquitatis* survived through much of GI-1d,e and probably went extinct at or close to the onset of GI-1c (Allerød) ca 13.9 ka BP. The timing of the final extinction of woolly rhino could be related to the fact that the Lateglacial interstadial was significantly warmer than any other event in the previous 50 millennia and was accompanied by more profound changes in vegetational cover. However, as with other megafaunal extinctions, we are inferring the time of extinction from the youngest available dates, so the possibility of later survival cannot be ruled out.

Although figured in Palaeolithic art, there appears to be no compelling evidence that woolly rhinoceros – a large, formidable and dangerous animal – was hunted by humans, although presumably this might have happened occasionally. The rare occurrence of their remains in archaeological cave and open sites could well represent material collected after death. Lorenzen et al. (2011, Fig. 4) noted very limited geographical overlap between Palaeolithic humans and woolly rhinoceros in Europe and Siberia after 20 ka BP. In a literature review they found *C. antiquitatis* in fewer than 11% of Siberian archaeofaunal sites during this time, and concluded that it was not a common prey species for humans, so that overhunting is an unlikely explanation for its extinction in Siberia.

In conclusion, the dynamics of range change in the woolly rhinoceros, in the millennia leading to its extinction, appear to relate largely to climatic and/or vegetational changes. Final extinction probably correlates with the widespread Lateglacial change to shrubs and trees at the expense of grasses and herbs. Another probable factor is increased precipitation resulting in wetter ground, and especially increased snowfall which would have been detrimental to woolly rhinoceros (Guthrie, 1990; Sher, 1997). In a simulation of the palaeovegetation of northern Eurasia and Alaska using the LPJ-GUESS dynamic vegetation model, Allen et al. (2010) concluded that "a marked and rapid decrease in aNPP (annual net primary productivity) of mesophilous herbs began shortly after the Last Glacial Maximum, especially in western Eurasia. This is likely implicated in extinction of several large herbivorous mammals during the latter part of the glacial stage and the transition to the Holocene". The survival of woolly rhinoceros in north-eastern Siberia when it had disappeared further west may relate to the later persistence of open vegetation in that region as also shown by Allen et al. (2010).

The radiocarbon record of *C. antiquitatis* is still poor in some potentially important areas, and further work will corroborate or reject the hypotheses of regional 'gaps' in occurrence' noted above, and might possibly reveal currently unsuspected later survival.

6. Absence of *Coelodonta* in North America

Many species present in Western Beringia succeeded in crossing into North America during the Last Glacial or earlier, via the Chukotka Peninsula (extreme north-east Siberia) and Alaska, e.g. cave lion *Panthera spelaea*, musk ox *Ovibos moschatus*, saiga antelope *Saiga tatarica*, reindeer or caribou *Rangifer tarandus*, and 'steppe bison' *Bison priscus.* Similarly, there are beetle species that were common to both sides of the Land Bridge, although others occurred only on one or the other (Elias et al., 1996; Elias and Crocker, 2008). It therefore seems remarkable that no fossils of *Coelodonta* are known from North America, especially when there are records from western Chukotka within a few hundred kilometres of the present Bering Strait (Tikhonov et al., 1999; Boeskorov, 2001). It is also remarkable that several species known from Alaska/Yukon failed to cross in the opposite direction to north-east Siberia. Some of the latter, such as mastodon *Mammut americanum*, and ground sloth *Megalonyx jeffersoni*, are probably of interglacial age (Harington, 2011), when the Bering Straits would have been flooded due to high sea levels, but others such as short-faced bear *Arctodus simus*, sabretooth *Homotherium serum* and helmeted musk ox *Bootherium bombifrons* are from the Last Glacial, within radiocarbon dating range (Fox-Dobbs et al., 2008). A simulation by Hu et al. (2010), suggests that the Bering Land Bridge was in existence between 35 and 11 ka, and also intermittently in the intervals ca 70–60 ka and 45–35 ka, potentially providing many opportunities for woolly rhinoceros to cross into North America. There are several dates on *C. antiquitatis* from Wrangel Island and western Chukotka between ca 52 ka and 16.5 ka (Supplementary Table 1, Fig. 1) providing strong evidence that it was present in the region over a long period when the Strait was above sea level.

Fossil beetle assemblages from lowland organic deposits suggest that during the Last Glacial much of the Bering Land Bridge experienced a mesic climate and was covered by shrub tundra vegetation, whereas inland areas of both Western Beringia (northeast Siberia) and Eastern Beringia (Alaska/Yukon) had arid ‘steppe-tundra’ environments dominated by herbaceous vegetation (Elias and Crocker, 2008). Guthrie (2001) envisaged the Land Bridge as a ‘mesic buckle’ connecting the more arid regions to the west and east. It appears very probable that the Land Bridge acted as a filter during the Last Glacial (Guthrie, 2001; Kuzmina et al., 2010), allowing some species such as musk ox and woolly mammoth to cross while barring others including woolly rhinoceros. Elias and Crocker (2008) postulate that species such as mammoth and musk ox arrived at the land bridge early when conditions were favourable, whereas *C. antiquitatis* was somehow prevented from reaching the area until some time in the Last Glacial, by which time, they propose, the land bridge had become too wet and boggy for this long-haired and short-legged animal to cross. Clearly further work is needed to confirm or refute these ideas.

There is an interesting contrast between woolly rhino and woolly mammoth in that the overall range of the latter was much more extensive, including Ireland, northern Scandinavia, the Taimyr Peninsula and of course North America. Moreover, mammoth survived for many millennia after the disappearance of woolly rhino. Evidently the woolly mammoth had significantly wider ecological tolerances than woolly rhinoceros, and this difference may supply the key to why one successfully colonized the New World whereas the other did not.

7. Other megafaunal extinctions in northern Eurasia

A striking feature of extinctions in northern Eurasia is that the losses of different species were staggered over many millennia (Fig. 3), and moreover there were important differences in timing of the extirpation of individual species in different geographical areas. The youngest available dates (including calibrations) for a range of mainland species are listed in Table 2. Below, we summarise knowledge of the extinction chronology of these species. The addition of island taxa, mainly in the Mediterranean (Van der Geer et al., 2010), would emphasise the substantial losses of large mammal species in northern Eurasia, and the time-transgressive nature of their extinctions.

7.1. Early last cold stage ca 117–40 ka

This first wave of extinctions occurred mostly beyond the range of reliable radiocarbon dating, so that the chronology is poorly known. During the Last Interglacial (MIS 5e, ca 130–117 kyr) the range of *Hippopotamus amphibius* (hippopotamus) extended from Africa to Mediterranean Europe and Iberia northwards to Britain. Intolerant of cold it is likely to have been extirpated from Europe at the beginning of the Last Glacial (Stuart and Lister, 2007). *Palaeoloxodon antiquus* (straight-tusked elephant) was widespread in Europe in the Last Interglacial in association with regional temperate and Mediterranean forests, but seems to have retreated south of the Pyrenees and Alps in the early part of the Last Glacial in response to cooler temperatures and spread of open vegetation (Stuart, 2005). *P. antiquus* was probably extinct well before the LGM

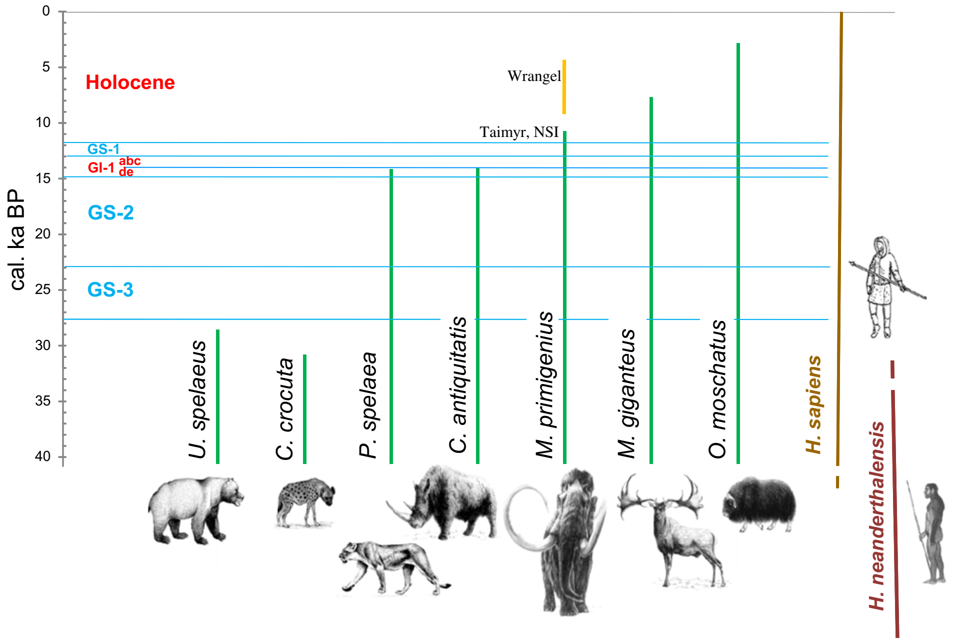

Fig. 3. Summary megafaunal extinctions chart for northern Eurasia. Green bars show the known time-span (from 40 ka BP) of a range of species with good radiocarbon dated records. *C. crocuta* survives today in Africa and *O. moschatus* in Greenland, and the far north of Canada and Alaska; the other species are globally extinct. Time-ranges for Neanderthals *Homo neanderthalensis* and modern humans *H. sapiens* are also shown. Greenland stadials and interstadials are indicated; cold phases in blue, warm phases red. Latest survivals for woolly mammoth shown: NSI, New Siberian Islands, Wrangel, Wrangel Island.

Table 2
Radiocarbon dates for extinct megafauna in northern Eurasia. Latest date shown, ultrafiltered where available; also non-ultrafiltered date if younger. The mammoth from New Siberian Islands is the youngest for Eurasia outside Wrangel Island.

Youngest dates	Location	Lab number	^{14}C date	Error	cal from	cal to	cal median	Material dated	Reference	Ultrafiltered
Ursus spelaeus	Sirgenstein Cave, Germany	OxA-12013	25,560	130	29,753	30,823	30,413	Upper incisor 3	1	+
Ursus spelaeus	Vindija Cave, Croatia	Beta-156100	23,780	120	28,055	29,054	28,540	Bone, aDNA	1	
Palaeoloxodon naumanni	Aomori, Honshu, Japan	IAAA-53431	23,600	130	27,963	28,681	28,337	Molar	2	
Crocuta crocuta	Grotta Paglicci, Italy	OxA-10523	26,120	330	30,328	31,221	30,813	Lower incisor 3	3	+
Panthera spelaea	Zigeunerfels Cave, Germany	OxA-17268	12,375	50	14,075	14,915	14,413	Upper canine	4	+
Panthera spelaea	Le Closeau, France	AA-41882	12,248	66	13,873	14,831	14,124	Metacarpal 4	4	
Megaloceros giganteus	Kamyshlov Mire, W. Siberia	KIA-5669/OxA-13015	6846	26	7615	7728	7674	Skeleton: skull, rib	5	+
Coelodonta antiquitatis	Lena-Amga, NE Siberia	AAR-11027/OxA-18602	12,155	37	13,851	14,156	13,999	Humerus/aDNA	6	+
Mammuthus primigenius	New Siberian Islands	GIN-11874	9470	40	10,581	11,065	10,713	Tusk	7	
Mammuthus primigenius	Wrangel Island, Siberia	OxA-11181	4091	36	4444	4813	4602	Molar	6	+
Mammuthus primigenius	Wrangel Island, Siberia	Ua-13366	3685	60	3854	4225	4024	Molar	8	
Bison priscus	Taimyr Peninsula, Siberia	Beta-148623	8810	40	9684	10,148	9845	Horn sheath	9	
Ovibos moschatus	Taimyr Peninsula, Siberia	OxA-17062	2756	27	2778	2925	2844	Skull	10	+
Single date										
Spiroceros kiakhtensis	Tunka Rift Valley, S. Siberia	OxA-19193	32,570	340	36,520	38,390	37,163	Metatarsal	6	+

1. Pacher and Stuart 2009, 2. Iwase et al., 2012, 3. Stuart and Lister 2007, 4. Stuart and Lister 2011, 5. Stuart et al., 2004, 6. this paper, 7. Nikolskiy et al., 2011, Sulerzhitsky and Romanenko 1997, 8. Vartanyan et al. 2008, 9. Macphee et al., 2002, 10. Campos et al. 2011.

and perhaps survived in Iberia to ca 70–50 ka (Stuart, 2005; Stuart and Lister, 2007). This interpretation is at odds with two radiocarbon dates in the range ca 37–40 ka obtained on *P. antiquus* molars from the Netherlands and North Sea (Bosscha Erdbrink et al., 2001; Mol et al., 2007). While intriguing, these dates are best viewed with caution until corroborative evidence is forthcoming given their closeness to the limit of radiocarbon dating and the lack of other post-Eemian records outside southern Europe. *S. hemitoechus* (narrow-nosed rhino) was also widespread during the Last Interglacial, and seems to have survived into the early part of the Last Glacial in southern Europe, to perhaps ca 45 ka (Stuart and Lister, 2007).

There are a few megafaunal species where available information is inadequate to infer time of extinction. According to Titov (2008), in the Late Pleistocene *Camelus knoblochi* (a large extinct camel) ranged from the Urals to north-eastern China. No stratigraphic details or radiocarbon dates are available to estimate when it became extinct. The extinct antelope *Spiroceros kiakhtensis* was confined to central and Eastern Siberia and Mongolia in the Late Pleistocene (Kahlke, 1999). We submitted a single sample of a *S. kiakhtensis* metatarsal from the Baikal region of southern Siberia which gave a date (ultrafiltered) of ca 37 ka (Tables 1 and 2) confirming that this species went extinct in the late Quaternary. Of the few available dates on the giant deer *Sinomegaceros yabei*, from China and Japan, the youngest (Japan) is ca 44.6 ka (Iwase et al., 2012).

Extinction chronologies for species with the best radiocarbon-dated records are shown schematically in Fig. 3.

7.2. Extinctions close to the onset of the LGM, ca 30–27 ka

The extinction of the cave bear *Ursus spelaeus* probably occurred ca 30.5–28.5 ka BP (Pacher and Stuart, 2009). Since it appears to have been mostly vegetarian its demise probably can be linked to decreased temperatures and concomitant deterioration in vegetational quality and productivity around the onset of Greenland Stadial GS-3 (ca 27.5 ka BP: start of 'LGM'). Spotted hyaena *Crocuta crocuta*, which still occurs in sub-Saharan Africa today, seems to have disappeared a little earlier ca 30.8 ka (Stuart and Lister, 2007), perhaps because of a decrease in available prey and scavenging opportunities. Other species, such as cave lion *P. spelaea* and giant deer *M. giganteus*, withdrew from Europe in the LGM, but survived further east and later returned (Stuart et al., 2004; Stuart and Lister, 2011). A series of direct dates on Naumann's elephant *Palaeoloxodon naumanni* from Japan terminates at ca 28 ka, so it may also have disappeared at the onset of the LGM (Iwase et al., 2012). The recent claim of Holocene survival of *Palaeoloxodon* in China (Li et al., in press) is based on molars in our opinion referable to *Elephas maximus*, and on bronze representations of elephants too stylised to be reliable taxonomic indicators. A sensational date of ca 32 ka on a mandible of sabretooth cat *Homotherium latidens* dredged from the North Sea bed (Reumer et al., 2003) needs to be corroborated by other dated finds. Otherwise all the latest sabretooth records from Europe are Middle Pleistocene. As has been pointed out by several authors, the demise of Neanderthals *Homo neanderthalensis* should be seen as part of the overall phenomenon of late Quaternary megafaunal extinction. The chronology of their extinction is highly controversial; as are the possible reasons, but broadly Neanderthals seem to have survived in western and central Europe and part of south-west Asia until about the time that modern humans arrived in these areas, ca 40 ka. Neanderthal extinction seems to have begun in the north of its European range, with the last populations in southern refugia such as Iberia, the Balkans, and possibly the Levant (Stewart and Stringer, 2012). On the basis of Middle Palaeolithic artefacts Neanderthals are claimed to have survived latest in Gibraltar, to ca 28 ka (Finlayson et al., 2006; Jennings et al., 2011).

7.3. Lateglacial and early Holocene ca 15–4 ka

As described above, woolly rhino *C. antiquitatis* was widespread until ca 35 ka, then its range contracted progressively eastward and the last dated records are ca 14 ka from NE Siberia. Cave lion *P. spelaea* also went extinct in the Lateglacial at about 14 ka, although the latest known northern Eurasian dates are from Europe (Tables 1 and 2; Stuart and Lister, 2011). However, it survived a little later, to ca 13.8 ka, in Alaska, where *Coelodonta* did not reach. The disappearance of both species was probably in response to increased temperatures and the accompanying replacement of vast areas of open, herb-dominated vegetation ('mammoth steppe') by shrubs and trees which began ca 14.7 ka. In the case of the cave lion there was probably a concomitant reduction in abundance of suitable prey. The range of *Mammuthus primigenius* (woolly mammoth) was also drastically reduced at this time, but it survived into the early Holocene in restricted areas of northern Siberia, to ca 11.1 ka in Taimyr and to ca 10.7 ka in the New Siberian Islands (Tables 1 and 2). Vartanyan et al. 1993 published their sensational finding, substantiated by many radiocarbon dates, that woolly mammoths had survived well into the Holocene, many millennia later than previously thought, on Wrangel Island off north-east Siberia. The youngest date obtained is ca 4.0 ka (contemporary with early Egyptian civilization). Attempts to find similar late records from mainland Siberia have been unsuccessful so far. In an interesting parallel to the Holocene survival on Wrangel Island, dated finds indicate that *M. primigenius* also survived on St Paul Island in the Bering Sea off Alaska until ca 6.5 ka (Guthrie, 2004; Veltre et al., 2008). There are rather few available dates for northern Eurasian *Bison priscus* ('steppe bison') but it evidently survived into the Lateglacial in Siberia and European Russia and to the earliest Holocene in Taimyr (Tables 1 and 2; Macphee et al., 2002).

Another surprising discovery in the last few years was that giant deer or 'Irish elk' *Megaloceros giganteus* had survived well into the Holocene. It disappeared from Western Europe soon after the onset of the Younger Dryas cold phase ca 12.9 ka and previously was thought to have gone extinct at that time. However, it is now known that it persisted until at least 7.7 ka in western Siberia and European Russia (Stuart et al., 2004). In contrast to species such as woolly rhino and mammoth, giant deer clearly favoured mesic environments. Its anatomy and distribution suggest it was a mixed feeder, requiring both to browse and to graze in a productive environment – especially necessary to sustain the annual growth of the enormous antlers in males.

7.4. Later extinctions ca 4 ka to present

During the Last Glacial, musk ox *Ovibos moschatus*, now restricted naturally to Arctic North America and Greenland, ranged from Iberia, Ireland and Britain in the west, eastwards across northern Asia into Alaska/Yukon and as far south as the Great Lakes region. It survived until at least 2.8 ka in the tundra of northern Siberia (Taimyr) (Campos et al., 2011). The 'European ass' *Equus hydruntinus* had a much more restricted distribution in the Last Glacial, from southern Europe to south-west Asia. A compilation by Jennifer Crees (pers. comm.) shows that in the Holocene its area of distribution progressively shrank, with the latest probable records approximately 3.0–3.5 ka from the Caucasus and Iran.

Other species have disappeared within the last few hundred years, almost certainly due to hunting by humans. The last recorded individual of *Bos primigenius* (aurochs), the wild ancestor of domestic cattle, died in 1627 in the Jaktorów Forest, Poland (Grubb, 2005). *Panthera leo* (lion) had probably gone from its foothold in south-east Europe by 2000 years ago, although it was still present within the last 200 years in the Middle East and North Africa (Stuart and Lister, 2011).

8. Discussion

The pattern of northern Eurasian extinctions, summarised in Fig. 3, is based on a substantial dataset of radiocarbon dates made directly on megafaunal material. It is conspicuously staggered (Stuart, 1991; Stuart and Lister, 2007), contrasting with North America where, based on available radiocarbon evidence, many or most extinctions seem to have occurred in the Lateglacial, perhaps within less than one thousand years (e.g. Martin and Steadman, 1999; Barnosky et al. 2004; Koch and Barnosky, 2006; Haynes, 2010). Much more dating evidence for North America is needed to confirm this interpretation, or whether a significant number of species went extinct earlier in the Last Glacial, as in northern Eurasia.

In northern Eurasia, each megafaunal species exhibits a unique and complex pattern of distributional shifts, culminating in extinction for some species and survival in others. Comparing woolly mammoth and giant deer, Stuart et al. (2004) and Lister and Stuart (2008) noted their differing, at times inverse, responses to environmental change, which are probably related to their different ecologies. Both, however, suffered range contraction during the LGM, followed by partial re-expansion, but eventual restriction to smaller terminal refugial areas, where they remained for several millennia before extinction, although the geographical locations for each species were very different. A third megaherbivore, the woolly rhinoceros, shows yet another pattern, with complex range shifts at various times, less marked response to the LGM, and a progressive contraction of range culminating in extinction without, thus far, evidence of long-term refugial survival.

It is generally accepted that modern humans arrived in Europe from Africa via the Middle East ca 40 ka. Significantly, most megafaunal extinctions in the region occurred many millennia after the arrival of modern humans, precluding a simple 'Blitzkrieg' model. There is abundant evidence that climatic and vegetational changes had major impacts on species' ranges, which must at the very least have predisposed them to extinction. Moreover, the strongly differing timescales and geographical patterns of species' range contractions are more consistent with environmental drivers in relation to their differing ecologies, than any obvious pattern of human expansion or exploitation. Nonetheless, the possible role of humans in this process, especially in inhibiting natural range expansion, and in precipitating the extinction of terminal populations, has still to be satisfactorily explored.

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Appendix A. Supplementary material

Supplementary material associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.quascirev.2012.06.007.

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