

The extinction of woolly mammoth (*Mammuthus primigenius*) and straight-tusked elephant (*Palaeoloxodon antiquus*) in Europe

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Abstract

Together with several other megafaunal species in Northern Eurasia, *Mammuthus primigenius* and *Palaeoloxodon antiquus* became extinct in the Last Glacial–Interglacial cycle, but they had very different ecologies, times of extinction and ‘last stands’ in different regions. The dramatic contraction in mammoth range ca. 12 kyr (uncalibrated ^{14}C chronology), after which known populations were confined to Northern Siberia (mainly Taymyr and Wrangel Island), correlates well with the extensive spread of trees in the Allerød phase of the Late Glacial Interstadial. The return of open steppe–tundra in the Younger Dryas cold phase, ca. 10.6–10 kyr, saw a limited re-expansion into NE Europe, followed by retraction and apparent extinction of mainland populations, which can be correlated with the marked loss of open habitats in the early Holocene. In contrast, at the end of the Last Interglacial, the retreat of *P. antiquus* to S. Europe, where it may have survived to ca. 50–34 kyr, can be linked to the loss of woodland habitats elsewhere. Although in both species, climate acting through vegetational changes evidently drove these range shifts, environmental change alone appears insufficient to account for extinctions. However, the possible role of human hunters is also still unclear.

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1. Introduction

Along with several other elements of the Late Pleistocene megafauna of Northern Eurasia, woolly mammoth and straight-tusked elephant went extinct during the Last Glacial–Interglacial cycle, although they had survived the climatic vicissitudes of previous glacial–interglacial cycles of the Middle and Late Pleistocene. Their disappearance should not be viewed in isolation, but as part of a global wave of Late Pleistocene and early Holocene extinctions, mainly affecting terrestrial large mammals (Martin, 1984; Martin and Steadman, 1999). The impact of these extinctions varied widely from one zoogeographical region to another, and was more severe in, for example, North America than in Northern Eurasia (Stuart, 1991, 1999; Martin and Stuart, 1995). However in Northern Eurasia, as in North America, all species in excess of one tonne (proboscideans, rhinos and hippopotamus) were lost, and none was replaced by either its evolutionary descendants or by ecologically similar taxa. Analyses presented by Johnson (2002) indicate that vulnerability to extinction was correlated with low fecundity, not

directly with body size, although large mammals are also slow-breeders.

The key question of the cause or causes of Late Quaternary extinctions has still to be resolved satisfactorily. Losses have been attributed principally to ‘overkill’ by human hunters (Martin, 1984; Martin and Steadman, 1999), or to environmental changes (Camerino Graham and Lundelius, 1984; Lister and Sher, 1995; Guthrie, 2001). Stuart (1991, 1999) proposed that for Northern Eurasia and probably also elsewhere, the final cause was hunting by humans, but only when megafaunal populations were already stressed and reduced in numbers and geographical range by major climatic and vegetational changes.

This paper briefly reviews the Late Quaternary history of the two Pleistocene Eurasian proboscideans, which were very different both in terms of distributional changes and mode of final extinction.

2. *Mammuthus primigenius*

Our knowledge of the Late Quaternary history of woolly mammoth is much better than for any other

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extinct European megafaunal species, partly because its remains are relatively abundant, but probably also because it has an enduring appeal as an icon that epitomises the ‘Ice Age’. The availability of fossil material and the fact that its later history occurred comfortably within the range of radiocarbon dating makes it an ideal subject for studying the process of extinction in the fossil record.

Currently several hundred dates made directly on mammoth material are available from Europe and northern Asia, and several new dates are published each year. However, it is important to carefully evaluate all dates in terms of the pre-treatment methods used. The fraction dated should be purified collagen avoiding contaminants which are likely to give an incorrect value, usually too young. In particular it should be standard practice that any outstanding or unexpected result should be independently checked by another laboratory, ideally with several dates run on the same material (Stuart et al., 2002; Stuart et al., 2004a, b). The dates discussed here are derived from the literature or are Oxford AMS dates from a recent Natural Environment Research Council—funded project (A.M. Lister and A.J. Stuart) ‘Late Quaternary Megafaunal Extinctions in Europe and Northern Asia’ (LQME Project). All radiocarbon dates given here are uncalibrated years BP.

During the Last Cold Stage the woolly mammoth occurred widely across Northern Eurasia, including nearly all of Europe (Kahlke, 1994), mostly in association with regional treeless steppe-tundra vegetation (Allen and Huntley, 2000; Adams, 2002). Radiocarbon-dated finds from ca. 40 kyr (close to or beyond the reliable limit of the method) to ca. 20 kyr (Stuart, 1991; Sulerzhitsky, 1997; Lister and Sher, 2001; Stuart et al., 2004a, b) are similarly widely distributed. However, at ca. 18 kyr during part of the Last Glacial Maximum (LGM), mammoth withdrew entirely from Western Europe, but from ca. 16 kyr reoccupied most of its former range, except Southern Europe (Fig. 1). The reasons for both its LGM retreat and subsequent failure to recolonise Southern Europe are unclear at present.

Shortly before ca. 12 kyr, mammoth disappeared entirely and rather suddenly from Europe and most of northern Asia (Fig. 1) (Stuart, 1991; Sher, 1997; Stuart et al., 2002; Stuart et al., 2004). Significantly, this dramatic event does not correlate with the marked warming and spread of shrub-grassland vegetation over much of Europe, which occurred at the beginning of the Late Glacial Interstadial (LGI) ca. 13–12.6 kyr (earlier in some regions), but does correlate with the major loss of open biomes at the onset of the rather cooler Allerød (later part of the LGI) when boreal birch and pine woodland became widely established (Litt et al., 2003;

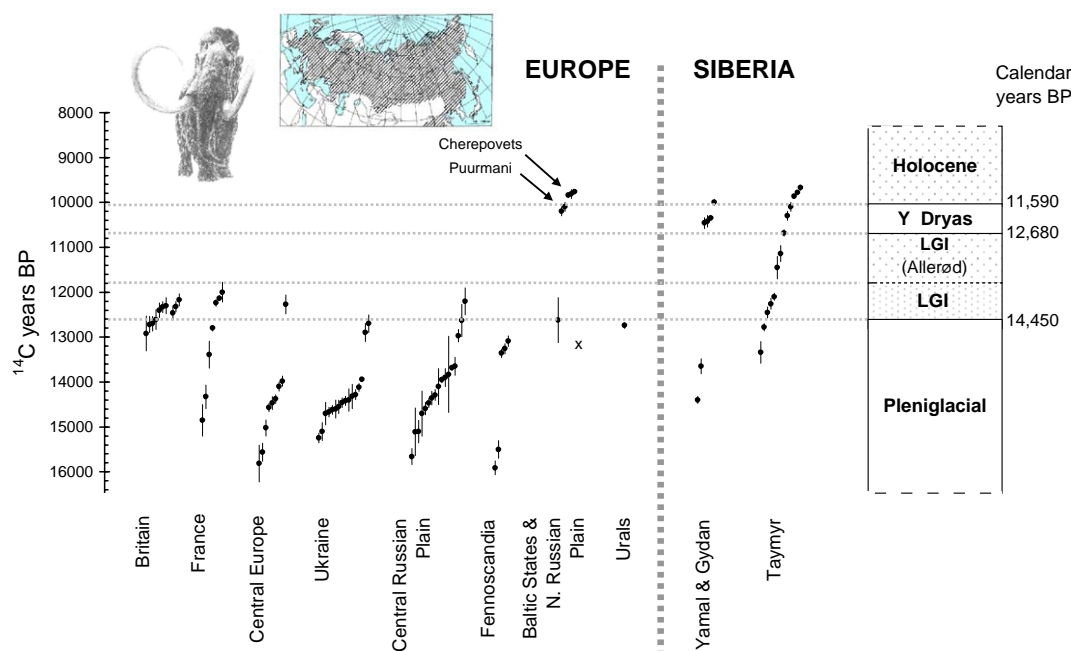


Fig. 1. Chart of radiocarbon dates less than 16 kyr BP (uncalibrated) for woolly mammoth *Mammuthus primigenius* material from Europe, and northwest and north-central Siberia (data from Stuart et al., 2002; Stuart et al., 2004a, b). Inset: overall Last Cold Stage distribution map (Kahlke, 1994). Major phases of vegetational change are indicated schematically in the right hand column (based on Hoek and Bohncke, 2002; Litt et al., 2003; and other sources). LGI, Late Glacial Interstadial; Y Dryas, Younger Dryas. Cold phases with open steppe tundra vegetation over much of Europe are shown blank. Woodland phases (birch and pine) are shown by open stipple, shrub vegetation (earlier part of Late Glacial Interstadial) by closer stipple. Calendar (varve) dates are shown for the major boundaries (Litt et al., 2003). Note the absence of mammoth dates from most of Europe post ca. 12 kyr, and apparent limited re-population from Taymyr in the Younger Dryas.

Hoek et al., 1999; Allen and Huntley, 2000; Lowe, 2001; Adams, 2002; Walker et al., 2003).

As is well known, there is strong evidence (several radiocarbon dates from more than one laboratory) that woolly mammoth populations continued to live in the far north of Siberia on the Taymyr Peninsula for a further two millennia (Sher, 1997; Sulerzhitsky 1997; Vasil'chuk et al., 1997; MacPhee et al., 2002), and an isolated population continued on Wrangel Island to ca. 3.7 kyr (Vartanyan et al., 1993, 1995; Long et al., 1994). Given the vastness of the region it is possible that other Holocene mammoth refugia will be found elsewhere in Siberia.

Although the data are limited at present, there are strong indications that there was a modest re-expansion of range ca. 10–10.5 kyr into the Yamal/Gydan Peninsulas in northwest Siberia and into northeast Europe (Fig. 1). In Europe, two molars from Puurmani, Estonia, have been dated to around the Pleistocene/Holocene boundary: $10,100 \pm 100$ (Hela-423) and $10,200 \pm 200$ (Hela-425) (Lõugas et al., 2002; Stuart et al., 2002), and ribs from a partial mammoth skeleton from Zhidikhovo Peatbog, City of Cherepovets, north of Moscow, gave dates of: 9760 ± 40 BP (GIN-8885c); 9810 ± 100 BP (GIN-8676a); and 9840 ± 50 BP (GIN-8885b) (Stuart et al., 2002). The intention is to cross check these results by submitting further samples to another laboratory as part of the LQME Project.

This limited re-expansion into Europe around the southern margins of the Fennoscandian ice can be correlated to the renewed cold of the Younger Dryas and resulting re-expansion of open steppe-tundra vegetation (Hoek et al., 1999; Allen and Huntley, 2000; Lowe, 2001; Adams, 2002; Litt et al., 2003; Walker et al., 2003). However, it is not at all clear why mammoth did not reoccupy all of the steppe-tundra biome that once again covered most of central and northern Europe. Final extinction of mammoth seems to have occurred in mainland Eurasia (both in Europe and northern Siberia) in the very early Holocene (Stuart et al., 2002). This event occurred soon after, but not coincidentally with the rapid warming that marks the beginning of the Holocene, and can be plausibly correlated with the loss of the steppe-tundra biome and widespread establishment of temperate and boreal forests in mid latitudes and boggy tundra in the far north (Sher, 1997). However, it seems very unlikely that habitats suitable for woolly mammoth were entirely eliminated throughout mainland northern Eurasia at this time, especially in view of the Holocene presence of 'steppe-tundra' on Wrangel Island.

3. *Palaeoloxodon antiquus*

In marked contrast to woolly mammoth, which had its maximum range in the cold stages, straight-tusked

elephant was widely distributed over most of Western Europe (except perhaps Ireland and northern Fennoscandia) in interglacials, including the Eemian ca. 130–117 kyr (Last Interglacial, Marine Isotope Stage 5e) (Stuart, 1991). Comparison with the vegetational sketch map by Van Andel and Tzedakis (1996, Fig. 9) indicates that in most areas it occurred in association with regional temperate forest, although in southern Iberia, Italy and the southern Balkans it was associated with Mediterranean evergreen woodland.

However, its subsequent history is very difficult to interpret with any confidence. Stuart (1991, 1999) inferred that *Palaeoloxodon antiquus*, together with hippopotamus *Hippopotamus amphibius* and extinct rhinoceros *Stephanorhinus hemitoechus*, withdrew from most of Europe at the end of the Eemian, but survived in the south (Iberia, Italy, and probably the Balkans) into the early part of the Last Cold Stage. Such a contraction of range might have been expected in response to climatic cooling at the end of the Eemian and the consequent replacement of forests by treeless steppe-tundra vegetation over most of Europe, while areas of relict deciduous woodland are known to have persisted in Italy and the Balkans (Bennett et al., 1991; Van Andel and Tzedakis 1996, Fig. 14; Adams, 2002; Allen et al., 2000).

The evidence for LCS survival is based mainly on sparse records of *Palaeoloxodon* material from cave sequences in levels with late Mousterian or Aurignacian artefacts, and/or with associated absolute dates. As part of our LQME Project, A.J. Stuart and A.M. Lister attempted direct radiocarbon dates on putatively late *Palaeoloxodon* material from southern Europe, and submitted several specimens to the Oxford AMS laboratory. However, in most cases the dating was unsuccessful because there was no collagen in the submitted material.

A *Palaeoloxodon* molar is recorded from Grotta Guattari, Italy, a well-known Neanderthal site, excavated in 1939, with associated U-series and ESR dates averaging ca. 57 kyr (error 6 kyr) (Schwarcz et al., 1991), but referred to MIS 5a-4 by Caloi and Palombo (1995). It is also recorded from cave deposits at Ingarano, southern Italy (Petronio and Sardella, 1998) in Layer b. The stratigraphic relationship of these sandy clays to the rest of the Late Pleistocene deposits (assigned to MIS 2 and 3) is unclear, but the authors thought an MIS 4 age probable. Other fauna from this level includes *Stephanorhinus hemitoechus*, *Coelodonta antiquitatis*, *Hippopotamus amphibius* and *Panthera leo (spelaea)*, indicating that more than one climatic phase is represented. One specimen resembling a fragment of elephant molar is actually cervid antler, and another molar fragment thought to be *Palaeoloxodon* contained no collagen.

Turning to Iberia, many faunal remains have been recovered from a series of excavations at the Middle

Palaeolithic site of Cova Negra near Valencia south-eastern Spain (Aguirre, 1968/69, Pérez Ripoll, 1977). A *Palaeoloxodon* molar and partial tusk (in the Prehistory Museum in Valencia) recovered from pre 1983 excavations supposedly from layer V (correlated with MIS 4) is probably much older; the stratigraphy is confused because the old excavations cut across the inclined layers (Villaverde, pers. com. 2000). A partial skeleton of *Palaeoloxodon*, recovered from Pleistocene marine deposits on the coast at Cueva de la Silluca (Buelna, Asturias, northern Spain) (Pinto Llona and Aguirre, 1999) gave a radiocarbon date of: $23,575 \pm 1125$ (Ua-13598) (A. Pinto, pers. com.). However, samples of molar and limb bone submitted for dating (LQME Project) contained no collagen. The situation of the marine sediments indicates a high sea level consistent with an MIS 5e or 5c age (Pinto Llona and Aguirre, 1999), so that in the absence of confirmatory evidence the ^{14}C date should be rejected.

An unworn upper molar plate from Foz do Enxarrique Portugal, Level C, has associated U-series dates (on horse teeth) of ca. 33–34 kyr (Cardoso, 1996; Brugal and Raposo, 1999; Sousa and Figueiredo, 2001). A molar plate from cave deposits in the Gruta da Figueira Brava, Portugal with associated radiocarbon and U-series dates of ca. 30–31 kyr, has been attributed either to *Mammuthus* or to *Palaeoloxodon* (Cardoso, 1996; Brugal and Raposo, 1999; Sousa and Figueiredo, 2001).

Palaeoloxodon material is recorded from level 18 in association with Aurignacian artefacts at Cueva del Castillo, northern Spain (Altuna, 1972; Bernaldo de Quiros, 1982). Two deciduous molars (three in total), almost certainly from the same individual gave the following radiocarbon dates (LQME Project): OxA-10187 $42,900 \pm 1,400$ ($\delta^{13}\text{C}$ -19.7), and OxA-10188 $>47,300$ ($\delta^{13}\text{C}$ -22.4). Both these dates and a series of 10 AMS dates on charcoal from this level that are all close to 40 kyr (Cabrera-Valdés et al., 1996) are best regarded as minimum ages. However, ESR dates averaging 70 ± 8 kyr were obtained from underlying Mousterian levels 22 and 23 (Rink et al., 1997), suggesting that the *Palaeoloxodon* material is significantly younger than this.

A major problem is that even where the stratigraphic context appears secure, there is always the possibility that the specimen could be older than its context, having been reworked or brought to the site by Palaeolithic humans, as has been found in several cases with radiocarbon-dated mammoth finds (Stuart et al., 2002). This problem could potentially be overcome by direct dating of *Palaeoloxodon antiquus* remains and/or by discoveries of associated elements of individual elephants in stratigraphically unambiguous post Eemian contexts, thus ruling out reworking by natural or human agency.

A *Palaeoloxodon* molar found by suction dredging near Raalte, Overijssel, Netherlands, gave a radiocarbon date of $32,500 \pm 500$ (UtC-9307) (Bosscha Erdbrink et al., 2001). Other fossils, apparently from the same deposit, include both cold stage elements such as *Rangifer tarandus* and *Ovibos moschatus*, and interglacial taxa such as *Dama dama* and *Capreolus capreolus*. As this is a single date from an unstratified context, and in view of the total lack of other post-Eemian records of *P. antiquus* outside southern Europe, this single date should not be accepted until there is further supporting evidence, including corroborative dates from another laboratory.

To summarize, at present there is reasonable, but not conclusive, evidence for the survival of *Palaeoloxodon antiquus* to 40–50 kyr or perhaps as late as 33–34 kyr in Iberia, significantly later than the Last Interglacial. However, the evidence for late survival in Italy, beyond MIS 5a, is weak. Clearly *Palaeoloxodon* had disappeared from Europe long before the onset of the LGM, ca. 20 kyr. Nothing is known so far about possible late survival in the Balkans, or elsewhere outside Europe.

The ancestor of most small or dwarf elephants reported from several Mediterranean islands was evidently *Palaeoloxodon antiquus* from mainland Europe (Palombo, 2001). In three cases, all from the eastern Mediterranean, these island forms are claimed to have survived much later than on the mainland: on Crete to ca. 18 kyr or later (Symeonides et al., 2001), on Cyprus to ca. 11–10 kyr (Reese, 1999), and on Tilos to after 4 kyr (Theodorou, 1986; Theodorou and Symeonides, 2001), inviting comparison with the similar Holocene survival of woolly mammoth on Wrangel Island. Radiocarbon dating by more than one laboratory is needed to confirm or refute these claims.

4. Discussion

It is very instructive to compare the latest histories of these two proboscideans, with their contrasting ecologies, different times of extinction and ‘last stands’ made in very different regions. *Palaeoloxodon antiquus* was a species of temperate and Mediterranean woodland whereas the cold-adapted *Mammuthus primigenius* was primarily a species of open grassland biomes. Broadly the extinction of the former, in southern Europe, is related to the retreat and near disappearance of woodland early in the Last Cold Stage, whereas conversely the demise of mammoth, making its ‘last stands’ in north eastern Europe, northern Siberia and Wrangel Island, can be linked to the marked decrease in open vegetation, especially steppe-tundra, in the Late Glacial and earliest Holocene. However it should not be overlooked that the histories of the two species also have important features in common. Both species went

extinct, along with other megafauna, during the Last Glacial–Interglacial cycle, but had survived previous cycles of the Middle and Late Pleistocene. Moreover, in both cases final extinction was preceded by a dramatic shrinkage of range.

Clearly climatic changes, acting through vegetational changes were of profound importance in the latest history of both proboscideans. However, if the extinctions of these, and other megafaunal species, were driven solely by environmental change, then why did similar extinctions not occur in previous glacial–interglacial cycles? There are general similarities in the pollen records for successive interglacials from central and north western Europe, and the long pollen records from southern Europe and other proxy records show broadly similar changes over several glacial–interglacial cycles (Tzedakis and Bennett, 1995). Nevertheless, was the last cycle significantly different, in a way that could have caused major extinctions? Some, notably Sher (1997), have argued that it was. According to Sher, in northern Siberia areas of open steppe tundra persisted through previous interglacials, and mammoth extinction occurred early in the Holocene when the last areas of steppe tundra were replaced by boggy tundra, unsuitable for mammoths, in response to changes in circulation of the Arctic Ocean.

However, this hypothesis cannot be used to explain the extinction of other megafauna in Northern Eurasia, including *Palaeoloxodon*, nor of course can it account for the disappearance of so many species from North America. A major problem here is that our knowledge of the pre Last Cold Stage terrestrial record is limited, especially for the cold stages, and there is insufficient information about interglacial floras, faunas and environments for northern Siberia. In particular, largely because of major stratigraphic uncertainties and dating problems, we do not know very much about what happened to mammoths in previous interglacials or to straight-tusked elephants in previous cold stages, even in Europe.

The clear evidence on the one hand of Holocene survival of *Mammuthus* on Wrangel Island in the Arctic Ocean, and on the other the putatively Late Pleistocene and Holocene survival of *Palaeoloxodon* on the Mediterranean islands of Crete, Cyprus and Tilos, is also difficult to reconcile with the hypothesis of extinctions driven solely by climatic and vegetational change. If animals were so vulnerable to environmental changes on the mainland, surely they would have been much more so on islands where they could not respond by migrating elsewhere.

However, the possible role of humans in these extinctions is not clear either, although it is worth restating the circumstantial evidence that the arrival of modern humans (*Homo sapiens*) in Northern Eurasia (from ca. 40 kyr) is the one new factor in the Last

Glacial–Interglacial that was not present before (Stuart, 1991). A possibility to be considered is that the presence of modern human hunters, with better technology and organisation and who occupied a much more extensive geographical range than their predecessors, contributed to the extinction of woolly mammoth, straight-tusked elephant and other megafaunal species by impeding their ‘normal’ migrational responses to climatic and vegetational changes.

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References

- Adams, J., 2002. Global land environments since the last interglacial. Website: <http://members.cox.net/quaternary/>.
- Aguirre, E., 1968/69. Revisión sistemática de los “Elephantidae” por su morfología y morfometría dentaria. Estudios Geológicos, (Madrid) 24, 25.
- Allen, J.R.M., Huntley, B., 2000. Weichselian palynological records from southern Europe: correlation and chronology. Quaternary International 73/74, 111–125.
- Allen, J.R.M., Watts, W.A., Huntley, B., 2000. Weichselian palynostratigraphy, palaeovegetation and palaeoenvironment; the record from Lago Grande di Monticchio, Southern Italy. Quaternary International 73/74, 91–110.
- Altuna, J., 1972. Fauna de mamíferos de los yacimientos prehistóricos de Guipuzcoa. Munibe 24 (1–4), 1–464.
- Bennett, K.D., Tzedakis, P.C., Willis, K.J., 1991. Quaternary refugia of North European trees. Journal of Biogeography 18, 103–115.
- Bernaldo de Quiros, F., 1982. Los Inicios del Paleolítico Superior Cantabro. Centro de Investigación y Museo de Altamira Monografías 8.
- Bosch, Erdbrink, D.P., Brewer, J.G., Mol, D., 2001. Some remarkable Weichselian elephant remains. Deinsea 8, 21–26.

- Brugal, J.-P., Raposo, L., 1999. Foz do Enxarrique (Ródão, Portugal): preliminary results of the analysis of a bone assemblage from a Middle Palaeolithic open site. *Monographie des Römisch-Germanischen Zentralmuseums* 42, 367–379.
- Cabrera-Valdés, V., Valladas, H., Bernaldo De Quiros, F., Gomez, M.H., 1996. La transition Paléolithique moyen-Paléolithique supérieur à El Castillo (Cantabrie): nouvelles datations par le carbone-14. *Compte Rendu Academie des Sciences Paris* 322, 1093–1098.
- Cardoso, J.L., 1996. Les grands mammifères du Pleistocene Supérieur du Portugal. *Essai de Synthèse. Géobios* 29, 235–250.
- Caloi, L., Palombo M.R., 1995. Le principali fauna a grandi mammiferi del Pleistocene superiore dell'Italia centrale. *Studi Geologici Camerti (spec.)* 1994 (B), 515–524.
- Camerino Graham, R.W., Lundelius, E.L., 1984. Coevolutionary disequilibrium and Pleistocene extinctions. In: Martin, P.S., Klein, R.G. (Eds.), *Quaternary Extinctions, a Prehistoric Revolution*. University of Arizona Press, Tucson, pp. 223–249.
- Guthrie, R.D., 2001. Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammal tooth pits, and inside-out Beringia. *Quaternary Science Reviews* 20, 549–574.
- Hoek, W.Z., Bohncke, S.J.P., 2002. Climate and environmental events over the last termination, as recorded in the Netherlands: a review. *Netherlands Journal of Geosciences/Geologie en Mijnbouw* 81, 123–127.
- Hoek, W.Z., Bohncke, S.J.P., Ganssen, G.M., Meijer, T., 1999. Lateglacial environmental changes recorded in calcareous gyttja deposits at Gulickshof, southern Netherlands. *Boreas* 28, 416–432.
- Johnson, C.N., 2002. Determinants of loss of mammal species during the Late Quaternary 'megafauna' extinctions: life history and ecology, but not body size. *Proceedings of the Royal Society of London B* 269, 2221–2227.
- Kahlke, R.D., 1994. Die Entstehungs-, Entwicklungs- und Verbreitungsgeschichte des Oberpleistozänen *Mammuthus-Coelodonta*-Faunencomplexes in Eurasien (Großsäuger). *Abhandlungen Senckenbergischen Naturforschenden Gesellschaft* 546, 1–64.
- Lister, A.M., Sher, A.V., 1995. Ice cores and mammoth extinction. *Nature* 378, 23–24.
- Lister, A.M., Sher, A.V., 2001. The origin and evolution of the woolly mammoth. *Science* 294, 1094–1097.
- Litt, T., Schmincke, H.-U., Kromer, B., 2003. Environmental response to climatic and volcanic events in central Europe during the Weichselian Lateglacial. *Quaternary Science Reviews* 22, 7–32.
- Long, A., Sher, A.V., Vartanyan, S.L., 1994. Holocene mammoth dates. *Nature* 369, 364.
- Lõugas, L., Ukkonen, P., Jungner, H., 2002. Dating the extinction of European mammoths: new evidence from Estonia. *Quaternary Science Reviews* 21, 1347–1354.
- Lowe, J.J., 2001. Climatic oscillations during the Last Glacial cycle—nature, causes and the case for synchronous effects. *Proceedings of the Royal Irish Academy* 101B (1–2), 19–33.
- MacPhee, R.D.E., Tikhonov, A.N., Mol, D., de Marliave, C., van der Plicht, J., Greenwood, A.D., Fleming, C., Agenbroad, L., 2002. Radiocarbon chronologies and extinction dynamics of the Late Quaternary mammalian megafauna of the Taimyr Peninsula, Russian Federation. *Journal of Archaeological Science* 29 (10), 1017–1042.
- Martin, P.S., 1984. Prehistoric overkill: a global model. In: Martin, P.S., Klein, R.G. (Eds.), *Quaternary Extinctions, a Prehistoric Revolution*. University of Arizona Press, Tucson.
- Martin, P.S., Steadman, D.W., 1999. Prehistoric extinctions on islands and continents. In: MacPhee, R.D.E. (Ed.), *Extinctions in Near Time; Causes, Contexts and Consequences*. Kluwer Academic/Plenum Publishers, New York.
- Martin, P.S., Stuart, A.J., 1995. Mammoth extinction: two continents and Wrangel Island. *Radiocarbon* 37, 7–10.
- Palombo, M., 2001. Endemic elephants of the Mediterranean islands: knowledge, problems and perspectives. In: Cavarretta, G., et al. (Ed.), *The World of Elephants*. Consiglio Nazionale delle Ricerche, Rome, pp. 486–491.
- Pérez Ripoll, M., 1977. Los mamíferos del yacimiento musteriano de Cova Negra (Játiva, Valencia). *Monografías del SIP, (Valencia)* 53.
- Petronio, C., Sardella, R., 1998. Remarks on the stratigraphy and biochronology of the Late Pleistocene deposit of Ingarano (Apulia, Southern Italy). *Rivista Italiana di Paleontologia e Stratigrafia* 104, 287–294.
- Pinto Llona, A.C., Aguirre, E., 1999. Presencia del Elefante Antiguo *Elephas (Palaeoloxodon) antiquus* en La Cueva de la Silluca (Buelna, Asturias). In: *Excavaciones Arqueológicas en Asturias 1995–1998, Vol. 4. Principado de Asturias, Consejería de Cultura*, pp. 225–232.
- Reese, D.S., 1999. Pygmy elephant. In: Simmons, A.H. (Ed.), *Faunal Extinction in an Island Society: Pygmy Hippopotamus Hunters of Cyprus*. Kluwer Academic/Plenum Publishers, New York, pp. 161–164.
- Rink, W.J., Schwarcz, H.P., Lee, H.K., 1997. ESR dating of Mousterian levels at El Castillo Cave, Cantabria, Spain. *Journal of Archaeological Science* 24, 593–600.
- Schwarcz, H.P., Bietti, A., Buhay, W.M., Stiner, M.C., Grün, R., Segre, A., 1991. On the re-examination of Grotta Guattari: uranium-series and electron-spin-resonance dates. *Current Anthropology* 32 (3), 313–316.
- Sher, A.V., 1997. Late-Quaternary extinction of large mammals in northern Eurasia: a new look at the Siberian contribution. In: Huntley, B., Cramer, W., Morgan, A.V., Prentice, H.C., Allen, J.R.M. (Eds.), *Past and future rapid environmental changes: The Spatial and Evolutionary Responses of Terrestrial Biota*. Springer, Berlin–Heidelberg–New York, pp. 319–339.
- Sousa, M.F., Figueiredo, S.M., 2001. The Pleistocene elephants of Portugal. In: Cavarretta, G., et al. (Ed.), *The World of Elephants*. Consiglio Nazionale delle Ricerche, Rome, pp. 611–616.
- Stuart, A.J., 1991. Mammalian extinctions in the late Pleistocene of Northern Eurasia and North America. *Biological Reviews* 66, 453–562.
- Stuart, A.J., 1999. Late Pleistocene megafaunal extinctions; a European perspective. In: MacPhee, R.D.E. (Ed.), *Extinctions in Near Time; Causes, Contexts and Consequences*. Kluwer Academic/Plenum Publishers, New York.
- Stuart, A.J., Sulerzhitsky, L.D., Orlova, L.A., Kuzmin, Y.V., Lister, A.M., 2002. The latest woolly mammoths (*Mammuthus Primigenius*) in Europe and Asia: a review of the current evidence. *Quaternary Science Reviews* 21, 1559–1569.
- Stuart A.J., Kosintsev, P.A., Higham, T., Lister, A.M., 2004a. Holocene Extinction of 'Pleistocene' megafauna: new evidence on the Irish elk in comparison with woolly mammoth, in preparation.
- Stuart, A.J., Lister, A.M., et al., 2004b. Distributional changes and extinction of woolly mammoth *Mammuthus primigenius* in the Holarctic, in preparation.
- Sulerzhitsky, L.D., 1997. Patterns of the radiocarbon chronology of mammoths in Siberia and Northern Eastern Europe (as substratum for human dispersal). In: Velichko, A.A., Soffer, O. (Eds.), *Humans settle the Planet Earth*. Institute of Geography, Moscow, pp. 184–202 (in Russian).
- Symeonides, N.K., Theodorou, G.E., Giannopoulos, V.I., 2001. New data on *Elephas chaniensis* (Vamos cave, Chania, Crete). In: Cavarretta, G., et al. (Ed.), *The World of Elephants*. Consiglio Nazionale delle Ricerche, Rome, pp. 510–513.
- Theodorou, G.E., 1986. Pleistocene elephants from Crete (Greece). *Modern Geology* 10, 235–242.
- Theodorou, G.E., Symeonides, N.K., 2001. The excavations of the last ten years at Charkadio cave on Tilos Island, Dodekanese, Greece.

- In: Cavarretta, G., et al. (Ed.), *The World of Elephants*. Consiglio Nazionale delle Ricerche, Rome, pp. 514–518.
- Tzedakis, P.C., Bennett, K.D., 1995. Interglacial vegetation succession: a view from Southern Europe. *Quaternary Science Reviews* 14, 967–982.
- Van Andel, T.H., Tzedakis, P.C., 1996. Palaeolithic landscapes of Europe and environs 150,000–25,000 years ago: an overview. *Quaternary Science Reviews* 15, 481–500.
- Vartanyan, S.L., Arslanov, K.A., Tertychynaya, T.V., Chernov, S., 1995. Radiocarbon evidence for mammoths on Wrangel Island, Arctic Ocean until 2,000 BC. *Radiocarbon* 37 (1), 7–10.
- Vartanyan, S.L., Garrut, V.E., Sher, A.V., 1993. Holocene dwarf mammoths from Wrangel Island in the Siberian Arctic. *Nature* 382, 337–340.
- Vasil'chuk, Y., Punning, J.-M., Vasil'chuk, A., 1997. Radiocarbon ages of mammoths in Northern Eurasia: implications for population development and late Quaternary environment. *Radiocarbon* 39 (1), 1–18.
- Walker, M.J.C., Coope, G.R., Sheldrick, C., Turney, C.S.M., Lowe, J.J., Blockley, S.P.E., Harkness, D.D., 2003. Devensian late glacial environmental changes in Britain: a multi-proxy environmental record from Llanilid, South Wales, UK. *Quaternary Science Reviews* 22, 475–520.