

18. Gauthier, J. in *The Origin of Birds and the Evolution of Flight* (ed. Padian, K.) 1–55 (California Academy of Sciences, San Francisco, 1986).
19. Holtz, T. R. The arctometatarsalian pes, an unusual structure of the metatarsus of Cretaceous Theropoda (Dinosauria: Saurischia). *J. Vertebr. Paleontol.* **14**, 480–519 (1995).
20. Currie, P. J. Allometric growth in tyrannosaurids (Dinosauria: Theropoda) from the Upper Cretaceous of North America and Asia. *Can. J. Earth Sci.* **40**, 651–665 (2003).
21. Holtz, T. R. Jr A new phylogeny of the carnivorous dinosaurs. *Gaia* **15**, 5–61 (2000).
22. Xu, X., Zhou, H. H. & Prum, R. O. Branched integumental structures in *Sinornithosaurus* and the origin of feathers. *Nature* **410**, 200–204 (2001).
23. Carr, T. D. Craniofacial ontogeny in Tyrannosauridae (Dinosauria, Theropoda). *J. Vertebr. Paleontol.* **19**, 497–520 (1999).
24. Hwang, S. H., Norell, M. A., Ji, Q. & Gao, K. New specimens of *Microraptor zhaoianus* (Theropoda: Dromaeosauridae) from northeastern China. *Am. Mus. Novit.* **3381**, 1–44 (2002).
25. Holtz, T. R. The phylogenetic position of the Tyrannosauridae: implications for the theropod systematics. *J. Paleontol.* **68**, 1100–1117 (1994).
26. Xu, X., Norell, M. A., Wang, X. L., Makovicky, P. J. & Wu, X. C. A basal troodontid from the Early Cretaceous of China. *Nature* **415**, 780–784 (2002).
27. Sereno, P. C. The evolution of dinosaurs. *Science* **284**, 2137–2147 (1999).
28. Martin, L. D. & Czerkas, S. A. The fossil record of feather evolution in the Mesozoic. *Am. Zool.* **40**, 687–694 (2000).
29. Spingale, C. *Elephants* (T. & A.D. Poyser, London, 1994).
30. Chen, P. J., Dong, Z. M. & Zhen, S. N. An exceptionally well-preserved theropod dinosaur from the Yixian Formation of China. *Nature* **391**, 147–152 (1998).

Supplementary Information accompanies the paper on www.nature.com/nature.

Acknowledgements We thank T. Holtz, O. Rauhut and X.-C. Wu for critical comments on the manuscript; Z. H. Zhou, Z. L. Tang, Y. Q. Wang, Y. Li, H. J. Wang, Y. L. Huo, H. Q. Shou, X.Z. Liu, Q. Cao, W. Chen, J. C. Lu and C. Li for their contribution in the field; H. J. Wang, J. M. Yang, G. H. Cui and X. Q. Ding for preparing the specimens; and R. S. Li, J. L. Huang and M. W. Yang for illustrations. The study was supported by the Special Funds for Major State Basic Research Projects of China, the National Natural Science Foundation of China, the National Geographic Society, the Chinese Academy of Sciences, the National Science Foundation of the USA and the American Museum of Natural History.

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to X.X. (xu@amnh.org or xingxu@vip.sina.com) or M.A.N. (norell@amnh.org).

Pleistocene to Holocene extinction dynamics in giant deer and woolly mammoth

A. J. Stuart¹, P. A. Kosintsev², T. F. G. Higham³ & A. M. Lister¹

¹Department of Biology, University College London, London WC1E 6BT, UK

²Institute of Plant and Animal Ecology, 620144 Ekaterinburg, Russia

³Oxford Radiocarbon Accelerator Unit, University of Oxford, Oxford OX1 3JQ, UK

The extinction of the many well-known large mammals (mega-fauna) of the Late Pleistocene epoch has usually been attributed to ‘overkill’ by human hunters, climatic/vegetational changes or to a combination of both^{1,2}. An accurate knowledge of the geography and chronology of these extinctions is crucial for testing these hypotheses. Previous assumptions that the mega-fauna of northern Eurasia had disappeared by the Pleistocene/Holocene transition² were first challenged a decade ago by the discovery that the latest woolly mammoths on Wrangel Island, northeastern Siberia, were contemporaneous with ancient Egyptian civilization^{3,4}. Here we show that another spectacular mega-faunal species, the giant deer or ‘Irish elk’, survived to around 6,900 radiocarbon yr BP (about 7,700 yr ago) in western Siberia—more than three millennia later than its previously accepted terminal date^{2,5}—and therefore, that the reasons for its ultimate demise are to be sought in Holocene not Pleistocene events. Before their extinction, both giant deer and woolly mammoth

underwent dramatic shifts in distribution, driven largely by climatic/vegetational changes. Their differing responses reflect major differences in ecology.

The giant deer, *Megaloceros giganteus* Blumenbach, with a maximum shoulder height of 2.1 m and an antler span of up to 3.6 m, is one of the most striking and evocative extinct animals of the Palaearctic. First appearing about 0.4 Myr ago⁶, the overall distribution of *M. giganteus* during the Last Cold Stage extended across the middle latitudes of Eurasia from Ireland to east of Lake Baikal⁷. 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 antler growth in males^{6,8}. On the other hand, it is likely that the huge antlers would have excluded males from even moderately dense woodland, at least for part of the year.

The giant deer was a key element in the relatively restricted set of Late Pleistocene extinctions in northern Eurasia, but unlike the mammoth it was not a species of the treeless ‘steppe-tundra’. Theories of its extinction formerly invoked the ‘maladaptation’⁹, or more recently the seasonal nutrient requirements⁸, of the huge antlers, and have focused on the well-studied Irish population of the Allerød phase around 12–10.6 kyr (12,000 to 10,600 uncalibrated radiocarbon yr BP; all dates hereafter are radiocarbon yr BP, unless stated otherwise. See Supplementary Information for calibrated calendar equivalents). Ireland has yielded most of the best-preserved specimens, including near-complete skeletons, from calcareous lake sediments ideal for the preservation of bone^{10,11}. The absence of specimens from deposits of the succeeding Younger Dryas phase (about 10.6–10 kyr) has led to an extrapolated assumption of global extinction at the onset of this severe cold episode^{5,9,10}.

Fortunately, most Late Quaternary extinctions occurred well within the range of radiocarbon (¹⁴C) dating, and we use direct dating of megafaunal remains, thereby minimizing any uncertainties of stratigraphical context. So far we have obtained 43 new radiocarbon accelerator mass spectrometry (AMS) dates from the Oxford Radiocarbon Accelerator Unit (ORAU) directly from *M. giganteus* material from western Europe, the Urals and Siberia, to which have been added 49 previously published direct dates (ORAU and other laboratories) (see Supplementary Information). This direct-dating approach has allowed us to track the fate of the species through climatic episodes leading up to extinction across its geographic range and in relation to changing palaeoenvironments.

During the Last Cold Stage, until around 20 kyr, the giant deer was widespread across western Europe (Fig. 1a), although the records are sporadic, and to the north of the Mediterranean region its occurrence may have been restricted to warmer (interstadial) phases with suitable vegetational growth. Indirectly dated records suggest that the species was probably also present in southeastern Europe and central Asia¹² during this time, and there are two dates around 39 kyr and 41 kyr (close to or beyond the reliable limit of ¹⁴C dating) from Kamenka Buryatia, Transbaikalia (Supplementary Information). However, there are no known occurrences before 20 kyr from the Urals and the adjacent part of western Siberia.

Our data so far indicate a striking absence of dates for giant deer within the long interval around 20–12.5 kyr, implying that it had withdrawn entirely from western and central Europe. This period corresponds broadly to the Last Glacial Maximum (LGM), when the Scandinavian and Alpine ice sheets expanded, and elsewhere open treeless steppe-tundra vegetation predominated. Indirectly dated records¹² suggest that refugia for *Megaloceros* at this time (Fig. 1b) included parts of southeastern Europe and south central Asia, probably in areas where tree and shrub vegetation persisted. So far there are no records for giant deer, ¹⁴C-dated or otherwise, from Mediterranean Europe for the LGM period, although in view of the known persistence of woodland¹³ (Supplementary Information) this region presumably would have provided suitable refugia for this animal.

Many dates and abundant secure stratigraphic evidence^{5,10,14–16} show that after the LGM, *Megaloceros* re-occupied part of north-western Europe. The earliest good evidence that we have for this re-occupation (discounting an old date with a large error from Britain) is a date of $12,455 \pm 65$ (Oxford laboratory number OxA-11687) from the Isle of Man, as well as a series of dates clearly indicating extensive recolonization of the Isle of Man and Britain by around 12.2 kyr, and of Ireland, southern Scandinavia and northern Germany by about 12 kyr (Figs 1c and 2). Whether or not these apparent differences in timing are real, needs to be tested by further dating. This Late Glacial recolonization by giant deer and its persistence for some one and a half millennia (Figs 1d and 2) can be correlated with the Late Glacial Interstadial (LGI), a warm phase that began around 13–12.6 kyr. The rather rapid warming at the onset of the LGI resulted in the replacement of steppe–tundra with a more productive grass and sedge vegetation with shrubs and some birch trees^{17,18} (Supplementary Information).

However, there is no evidence that giant deer returned to central or southern parts of western Europe. There are very few published accounts of *Megaloceros* from putatively Late Glacial contexts in these areas. Most of the specimens that we were able to trace proved to have been misidentified, and the only two that are definitely giant deer did not give a ¹⁴C date.

The apparent restriction of *Megaloceros* within Europe to part of the northwest in the LGI (Fig. 1c, d) is intriguing. In the generally cooler, later part of the LGI (Allerød), birch and pine woodland colonized much of Europe, whereas more open herbaceous veg-

etation with birch trees was present in the north-west; therefore, the distribution of giant deer at this time plausibly correlates to a marked north–south vegetational gradient (Supplementary Information). But this cannot explain the same distribution pattern in the early LGI when similar open vegetation occurred across both northwestern and central Europe. A recent analysis of the ¹⁴C-dated archaeological record¹⁹ indicates that after a major contraction in range during the LGM, humans progressively repopulated central and northwestern Europe from the south, and had reached northern Germany and Britain—albeit in low population densities—by around 14 kyr, well before the reappearance of giant deer in this region. Therefore there is no indication of human interference with giant deer recolonization of northwestern Europe in the Late Glacial. However, it is possible that denser human populations further south, shown by significantly higher numbers of occupation sites (C. Gamble and W. Davies personal communication), may have inhibited recolonization of central and southern Europe by *Megaloceros* after the LGM.

The subsequent dramatic collapse of the northwestern European population of *Megaloceros*, which occurred around 10.7 kyr, inferred both from the pattern of ¹⁴C dates and abundant stratigraphic evidence of its absence from Younger Dryas sediments^{5,10,11,14,15}, can be correlated with the marked deterioration in vegetation in this cold phase, when open steppe–tundra returned¹⁸ (Supplementary Information). However, dates of $10,585 \pm 65$ (OxA-11498) and $10,257 \pm 75$ (Arizona laboratory number, AA-51350) (Fig. 2) on an antler from the River Cree, southwestern

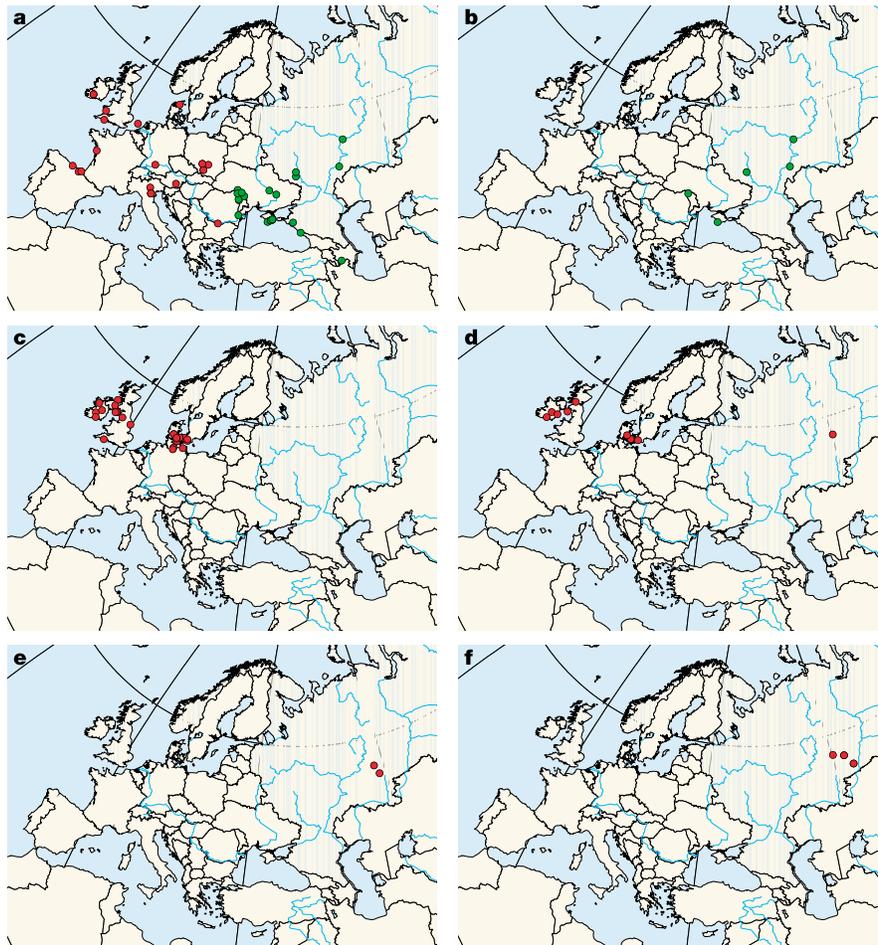


Figure 1 Radiocarbon dated (red dots) *M. giganteus* finds, showing chronological changes in distribution. Green dots indicate indirectly dated records for eastern Europe¹². Dates are uncalibrated. **a**, 20 kyr and older. **b**, Around 20–13 kyr, indicating possible

refugia during the LGM. **c**, 12.9–11 kyr. **d**, 10.9–10.5 kyr. **e**, 10.4–9.9 kyr. **f**, 8.0–6.9 kyr Shigir (Urals), Kamyshlov, Redut (western Siberia).

Scotland, may indicate persistence into the early part of the Younger Dryas in northwestern Britain. In both Ireland and the Isle of Man (probably connected to mainland Britain) extirpation was almost certainly due solely to climatic/vegetational change because there is no evidence of humans from these areas until the early Holocene epoch, around 9 kyr (ref. 20).

Claims of Holocene survival in northwestern Europe have not been substantiated. Two recent ¹⁴C dates obtained directly on antlers seemed to demonstrate that giant deer had persisted through the Younger Dryas and into the earliest Holocene in the Isle of Man and southwestern Scotland²¹, but further investigation indicates that these specimens actually date from the Late Glacial (see Methods and Supplementary Information). We have been unable to locate *Megaloceros* remains found by workmen at Theresienhof (northern Germany) and said to have come from a Younger Dryas/Preboreal horizon²². Suggestions of Holocene survival in Ireland²³ are based on specimens of very dubious provenance¹⁰.

However, a series of new AMS dates presented here indicates that giant deer did persist long into the Holocene in a very different area, on the boundary between Europe and Asia in the Urals/western Siberia region. The earliest record that we have from this region is about 10.8 kyr, during the late Allerød or early Younger Dryas (Figs 1d and 2; Table 1). The appearance of giant deer here probably represents colonization from southeastern Europe or west central Asia, rather than from northwestern Europe, which is considerably further away. A date from Kulmetovsk cave (Table 1; Figs 1e and 2), on the eastern side of the southern central Urals, falls within the Younger Dryas; another, from Grotto Bobylek, is close to the transition from the Younger Dryas to the Holocene. This is followed by a date of around 8 kyr from the Shigir Mesolithic site (Fig. 1f). The two youngest records of *Megaloceros* (around 6.9 and 7.0 kyr) known so far from anywhere are, respectively, on a largely complete

antler-bearing male skeleton from Kamyshlov mire (Supplementary Fig. 1) and a male skull with associated cervical vertebrae from the Redut river, in the adjacent part of western Siberia. These were each independently AMS dated by the Kiel (KIA) and Oxford laboratories, and the dates are statistically indistinguishable (Table 1 and Fig. 2). The validity of Holocene survival is supported not only by records from two separate sites and replicate results from two laboratories, but also by the fact that they are linked to their Late Pleistocene predecessors by a series of intermediate dates.

There are two crucial questions. First, why did *Megaloceros* survive through the Younger Dryas in the Urals and western parts of Siberia, but not in western Europe? Palaeobotanical data indicate that in contrast to the harsh conditions of the Younger Dryas in Europe, on the eastern slopes of the Urals this period saw the persistence of grass–shrub vegetation and open woodland with larch, spruce, pine and birch trees²⁴—apparently good habitat for *Megaloceros*—whereas less suitable, dry steppe–tundra with dwarf birch and dwarf willow occupied the adjacent West Siberian Plain. Subsequently, in the Early Holocene, the spread of closed forest in the mountains probably excluded giant deer, but it survived in the forest–steppe of western Siberia²⁴. In view of the limited available data for large areas of its known distribution, it is possible that further work will reveal other areas in eastern Europe and Asia (for example, southern Siberia) where *Megaloceros* survived into the Holocene. A single new *Megaloceros* date of 10,055 ± 45 (OxA-13026) from the Chernigovo open cast coal mine, Kuznetsk basin in southwestern Siberia²⁵, suggests that the giant deer persisted through the Younger Dryas in this region, raising the possibility that it may also have survived into the Holocene.

The second important question is what caused its extinction in the Holocene? Given the comparative rarity of *Megaloceros* material, the Redut and Kamyshlov individuals may not have been among the

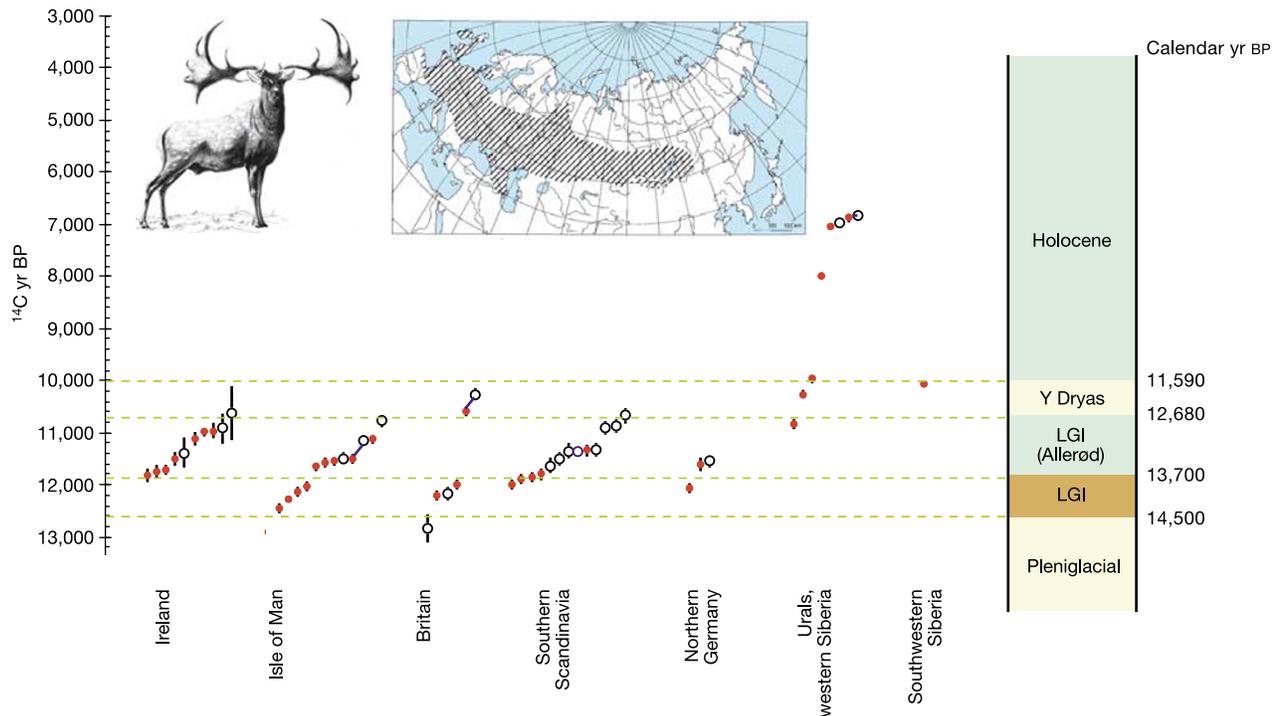


Figure 2 Chart of Late Glacial and Holocene ¹⁴C dates for *M. giganteus*. Inset: overall Last Cold Stage distribution⁷. Error bars are ± 1 s.d. Connected points are dates made on the same material. Oxford AMS dates are shown in red (Supplementary Information), other laboratories are open circles^{5,14–16,21}. Calendar (varve) dates are indicated for major

boundaries¹⁸. Major climatic/vegetational phases are shown schematically^{17,18} (Supplementary Information). LGI, Late Glacial Interstadial; Y Dryas, Younger Dryas. Predominant vegetation: steppe–tundra, yellow; shrub vegetation, brown; trees and shrubs, green.

Table 1 ¹⁴C-dated *Megaloceros* finds from the Urals (UR) and western Siberia (WS)

Locality	Co-ordinates	Provenance	Element	Laboratory number	¹⁴ C date	δ ¹³ C†
Kamyshlov mire WS	62.73° E 56.92° N	Peat bog	Rib (associated skeleton)	KIA-5669	6816 ± 35	-21.46
Kamyshlov mire WS	62.73° E 56.92° N	Peat bog	Skull (associated skeleton)	OxA-13015	6881 ± 38	-19.5
Redut*, Miass river WS	64.23° E 55.48° N	Peat bog	Cervical vertebra (skull and vertebrae)	KIA-5668	6968 ± 33	-20.16
Redut, Miass river WS	64.23° E 55.48° N	Peat bog	Cervical vertebra (skull and vertebrae)	OxA-13014	7034 ± 34	-19.0
Shigir WS	60.17° E 57.37° N	Mesolithic site	Antler	OxA-11064	7990 ± 45	-19.7
Grotto Bobylek UR	57.65° E 56.32° N	Cave	Tooth root	OxA-11063	9960 ± 55	-19.6
Kulmetovsk UR	58.47° E 55.15° N	Cave	Maxilla	OxA-10676	10260 ± 55	-19.5
Neviansk WS	60.20° E 57.50° N	Alluvium	Skull	OxA-11065	10825 ± 65	-19.7

*The duplicate dates from Kamyshlov and Redut are in each case from the same individual.
 †δ¹³C = [(¹³C/¹²C)_{sample} / (¹³C/¹²C)_{standard}] - 1 × 1,000

last of their line, even in the Urals/western Siberia region; however, the spread of dry steppe over western Siberia around 7 kyr while closed forest persisted in the mountains²⁴ may have resulted in or contributed to the extirpation of this population.

A full evaluation of the possible role of humans in the processes of range reduction and ultimate extinction will require further data from across the Siberian part of the range of *Megaloceros*, both in terms of radiocarbon chronology and the archaeological record. In the Urals/western Siberia region, known Mesolithic and Neolithic settlements are largely located on the banks of rivers and lakes²⁶ (Supplementary Information). It is possible that while *Megaloceros* survived in the Ural foothills it was relatively safe from human predation, but when forced onto the plain by vegetational changes, it became critically vulnerable to increased hunting pressure.

Previous studies have suggested that the nutrient requirements of antler growth proved critical at times of environmental stress, and that the latest (Allerød) populations from the westernmost margin of the species' range may have suffered reduction in body and antler size^{8,11,21}. However, the Kamyshlov skeleton—a large male with an antler span of 2.56 m (ref. 27; Supplementary Fig. 1)—shows no evidence of reduction in antler or body size. Although it is only a single specimen, its antler, skull and limb bone dimensions fall in the middle of the range of variation of the Irish Late Glacial sample, itself composed largely of males^{6,9,11,27}. The Redut specimen, a skull with neck vertebrae, was unfortunately not available for measurement.

The striking contrast in the histories of giant deer and woolly mammoth, *Mammuthus primigenius* Blumenbach, can be plausibly linked to the differing ecologies of the two species. *Megaloceros* shows a much larger apparent LGM gap in Europe, around 20–12.5 kyr compared with 18–16 kyr for mammoth (Fig. 3). Giant deer did not re-expand until the onset of the LGI when increased warmth probably resulted in increased plant productivity¹⁷, and it apparently became particularly abundant when open habitats were invaded by trees and shrubs in the Allerød. In contrast, only about 0.5 kyr after the reappearance of *Megaloceros* in northwestern Europe, mammoth disappeared from most of northern Eurasia, and available data indicate that after 12 kyr—when forests spread at the onset of the Allerød interstadial—it became restricted to the far north of Siberia where open steppe-tundra environments persisted³ (Supplementary Information). The latest available mainland records (Taymyr Peninsula) are around 9.6 kyr (ref. 3; Supplementary Information). A series of ¹⁴C dates, from more than one laboratory, demonstrates that mammoth survived to around 3.7 kyr (about 4,000 yr ago) on Wrangel Island, northeastern Siberia, where steppe-tundra vegetation occurs at the present day⁴ (Supplementary Information), and recently it has been shown that it survived to around 8 kyr on St Paul Island (Pribilofs)

in the Bering Sea²⁸. The contrasting patterns of giant deer compared with woolly mammoth (Fig. 4) highlight the profound impact of climate and vegetation on the range fluctuations of these two species before their extinction. Their complementary chronological distribution also strongly suggests that the pattern of presence and absence in each is not due to taphonomic or other extraneous effects.

The complex history of the last approximately 30 kyr of woolly mammoth and giant deer (Irish elk), emphasizes the 'ragged' nature of the so-called 'end Pleistocene' megafaunal extinctions in northern Eurasia, in which different species went extinct at different times, and had their 'last stands' in different regions². Our perspective on the extinction of both species has shifted radically with the realization that we have to consider Holocene as well as Late Pleistocene events in seeking the cause or causes of their demise, with the important corollary that there were no major climatic/vegetational changes in the Holocene compared with those of the Last Cold Stage. Widely distributed before about 20 kyr, both giant deer and woolly mammoth underwent successive contractions in

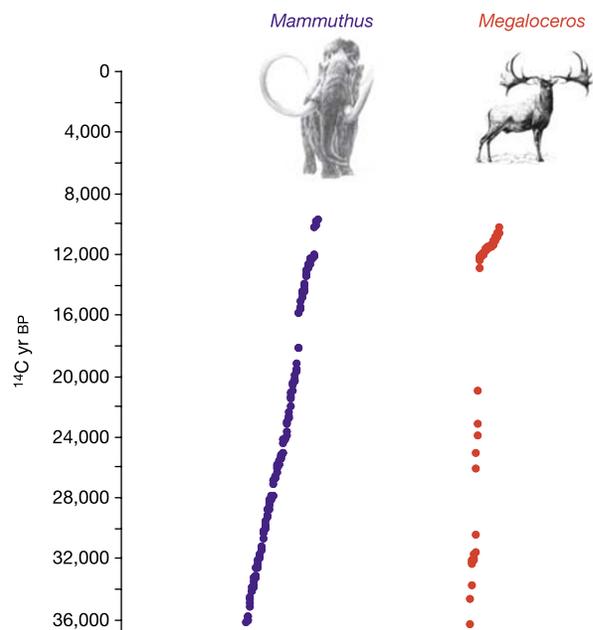


Figure 3 Chart of ¹⁴C dates <36 kyr for *Mammuthus primigenius* and *Megaloceros giganteus* in western Europe. Note much larger LGM gap for giant deer than for mammoth (refs as Fig. 2, and refs 3, 29; Supplementary Information).

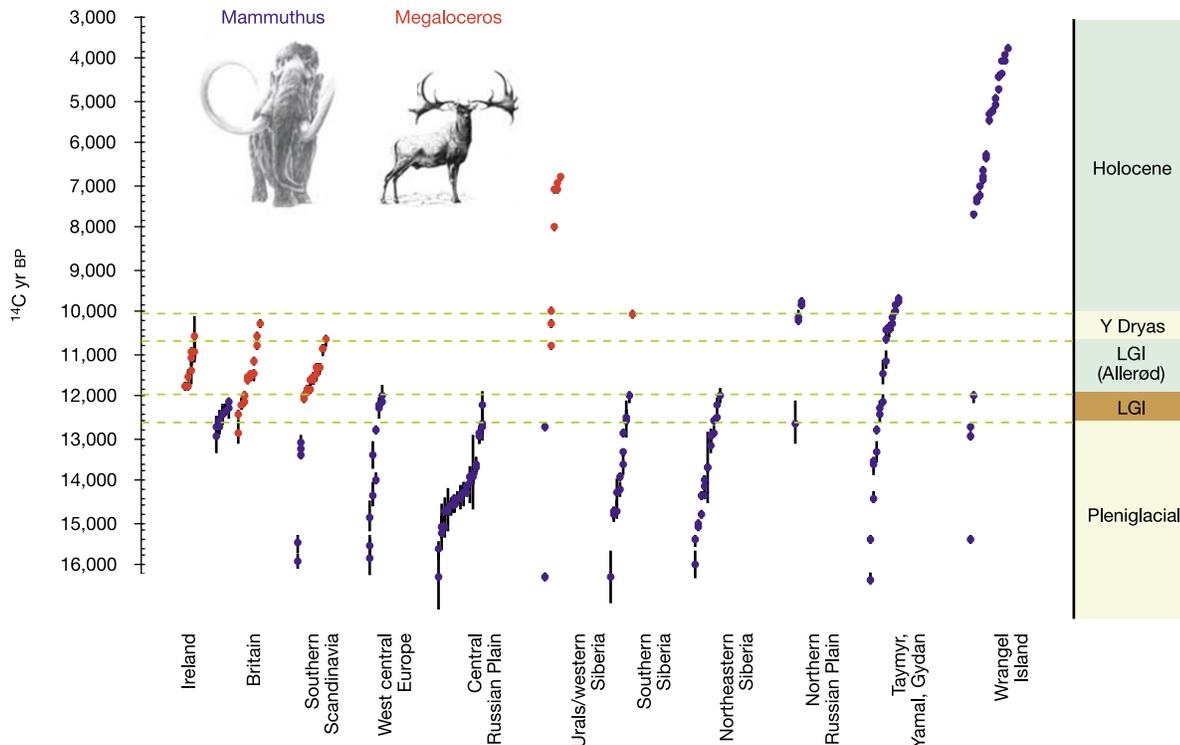


Figure 4 Chart of ^{14}C dates <16 kyr for *Megaloceros giganteus* (red) and *Mammuthus primigenius* (blue) in Europe and selected areas of Siberia^{3,4,9–13,29} (and refs as Fig. 2). Error bars are ± 1 s.d. Climatic/vegetational phases as in Fig. 2. For clarity, Isle of Man dates are grouped with Britain, and northern Germany with southern Scandinavia. Note the increased records for giant deer in Europe around 12–11 kyr, after the disappearance

of mammoth. Note also the termination of most mammoth dates around 12 kyr (Allerød), except for parts of Siberia, and outlying mammoth dates around 10 kyr in northeastern Europe, probably representing brief repopulation from northern Siberia during the Younger Dryas^{3,29}.

range (although at different times), from each of which they made only partial recoveries. Finally, in the Holocene, both were confined to one or more relatively small areas before becoming extinct. Comparison of our data set with proxy records indicates that the marked shifts in the distributions of both species were driven by climate acting through vegetational changes. However, giant deer had survived previous Pleistocene cold episodes, and unlike the mammoth—which presumably survived previous interglacials in Siberian refugia—had expanded its European range and thrived during previous interglacials. Why, then, didn't giant deer re-expand its range in the Holocene as in previous interglacials with putatively similar climate and vegetation¹³? The possible role of modern humans (not present in previous interglacials) needs further investigation. Future work will need to target other possible Holocene refugia, and further analyse the spatio-temporal pattern of extinction in comparison with vegetational change and human activity. □

Methods

Sample selection

Careful attention was given to specimen identification in view of the frequent past misidentification of red deer, elk/moose or large bovids such as *Megaloceros*. The direct-dating approach is crucial in avoiding stratigraphical uncertainty, as is replicate dating of key samples.

Radiocarbon dating

Bone samples were prepared for AMS ^{14}C dating at the ORAU using routine collagen extraction procedures (Supplementary Information). An additional ultrafiltration pre-treatment step was used to further purify the bone gelatin and retain only the >30-kD molecular weight fraction for ^{14}C assay. Lyophilized gelatin samples were combusted using a Roboprep CHN sample converter unit and mass spectrometrically analysed using a Europa Scientific 20-20 mass spectrometer, operating in continuous flow mode. Graphite was prepared using routine methods (Supplementary Information). Bone collagen

preservation was evaluated using the carbon to nitrogen atomic ratio (C:N) and the per cent weight collagen was extracted from the bone. The addition of exogenous carbon atoms increases the C:N ratio and, depending upon the age and size of the contaminant, may result in errors in the AMS determinations. All of the *Megaloceros* bones dated at ORAU were within the acceptable C:N range of 2.9–3.5. All dated samples exceeded 1% wt collagen, which is the minimum threshold for acceptance.

When dating duplicate samples of bone, ORAU AMS determinations often yielded slightly older results compared with other laboratories (Fig. 2 and Table 1). We attribute this to the removal of low molecular weight (<30 kD) components, including potential contaminants, by ultrafiltration. These particles include degraded and broken up collagen, salts, sediment particulates and sometimes contaminants of different, usually more modern, ^{14}C age. Low-collagen-yield bones (pre-treatment yield < approximately 20 mg) must be treated with care during ultrafiltration to ensure that humectants (glycerin) designed to keep the ultrafilters moist are removed completely before use. Failure to do this has resulted in small amounts (approximately 20–30 μg) of glycerin becoming incorporated into gelatin, affecting accuracy in dating low-collagen-yield bones of Holocene age, because the glycerin is 30 kyr in age. ORAU therefore implements a rigorous cleaning protocol of all ultrafilters before use, to ensure removal to background levels (Supplementary Information). None of the dated samples was of low enough pre-treatment yield to be affected by this contaminant.

The young Redut and Kamyshlov specimens were dated both at the Leibniz Labour AMS laboratory (Kiel) and in Oxford (Table 1). The Kiel bone samples were prepared to filtered collagen using a similar method to that used at ORAU, but without ultrafiltration. As a test of the presence of potential contaminants, both filtered collagen and insoluble residue fractions from both bones were dated. The age difference between the KIA-5668 residue and collagen suggests that the bone was not significantly contaminated with exogenous carbon. Similarly, the results are identical to the date of OxA-13014, obtained from the same bone. The Kamyshlov sample (KIA-5669) yielded a much younger age for the removed insoluble residue, suggesting the bone has been contaminated, but that this has been effectively removed by the pre-treatment chemistry applied to the bone. The ORAU ultrafiltered AMS result was again statistically indistinguishable from the Kiel filtered collagen date. In a previous study²¹, remains of *M. giganteus* from Ballaugh, Isle of Man and the River Cree, southwestern Scotland, were dated to the early Holocene (around 9.4–9.2 kyr). Re-dating of duplicate samples at ORAU by the above methods (Supplementary Information), and separately by the University of Arizona NSF Radiocarbon Laboratory, have produced ages within the Late Glacial, and these ages are accepted here (Fig. 2 and Supplementary Information).

Received 26 August 2003; accepted 27 July 2004; doi:10.1038/nature02890.

1. Martin, P. S. in *Quaternary Extinctions: A Prehistoric Revolution* (eds Martin, P. S. & Klein, R. G.) 364–403 (Univ. Arizona Press, Tucson, 1984).
2. Stuart, A. J. Mammalian extinctions in the late Pleistocene of northern Eurasia and North America. *Biol. Rev.* **66**, 453–562 (1991).
3. Stuart, A. J., Sulerzhitsky, L. D., Orlova, L. A., Kuzmin, Y. V. & Lister, A. M. The latest woolly mammoths (*Mammuthus primigenius*) in Europe and Asia: a review of the current evidence. *Quat. Sci. Rev.* **21**, 1559–1569 (2002).
4. Vartanyan, S. L., Garrut, V. E. & Sher, A. V. Holocene dwarf mammoths from Wrangel Island in the Siberian Arctic. *Nature* **382**, 337–340 (1993).
5. Barnosky, A. D. Big game extinction caused by late Pleistocene climatic change: Irish elk (*Megaloceros giganteus*) in Ireland. *Quat. Res.* **25**, 128–135 (1986).
6. Lister, A. M. The evolution of the giant deer, *Megaloceros giganteus* (Blumenbach). *Zool. J. Linn. Soc.* **112**, 65–100 (1994).
7. Kahlke, R. D. Die Entstehungs-, Entwicklungs- und Verbreitungsgeschichte des Oberpleistozänen *Mammuthus-Coelodonta*-Faunencomplexes in Eurasien (Großsäuger). *Abh. Senckenb. Natf. Ges.* **546**, 1–64 (1994).
8. Moen, R. A., Pastor, J. & Cohen, Y. Antler growth and extinction of Irish Elk. *Evol. Ecol. Res.* **1**, 235–249 (1999).
9. Gould, S. J. The origin and function of 'bizarre' structures: antler size and skull size in the 'Irish Elk', *Megaloceros giganteus*. *Evolution* **28**, 191–220 (1974).
10. Mitchell, G. F. & Parkes, H. M. The giant deer in Ireland. *Proc. R. Ir. Acad. B* **52**, 291–314 (1949).
11. Barnosky, A. D. Taphonomy and herd structure of the extinct Irish Elk *Megaloceros giganteus*. *Science* **228**, 340–344 (1985).
12. Markova, A. K. et al. Late Pleistocene distribution and diversity of mammals in northern Eurasia. *Paleont. Evol.* **28–29**, 5–143 (1995).
13. Tzedakis, P. C. & Bennett, K. D. Interglacial vegetation succession: a view from southern Europe. *Quat. Sci. Rev.* **14**, 967–982 (1996).
14. Kaiser, K., De Klerk, P. & Terberger, T. Die "Riesenhirsch Fundstelle" von Endingen: geowissenschaftliche und archäologische Untersuchungen an einem spätglazialen Fundplatz in Vorpommern. *Eiszeit. Ggw.* **49**, 102–122 (1999).
15. Aaris-Sørensen, K. & Liljegren, R. Late Pleistocene remains of giant deer (*Megaloceros giganteus* Blumenbach) in Scandinavia – chronology and environment. *Boreas* **33**, 61–73 (2004).
16. Woodman, P., McCarthy, M. & Monaghan, N. The Irish Quaternary fauna project. *Quat. Sci. Rev.* **16**, 129–159 (1997).
17. Hoek, W. Z. Vegetation response to the 14.7 and 11.5 ka cal. BP climate transitions: is vegetation lagging climate? *Global Planet. Change* **30**, 103–115 (2001).
18. Litt, T., Schmincke, H.-U. & Kromer, B. Environmental response to climatic and volcanic events in central Europe during the Weichselian Lateglacial. *Quat. Sci. Rev.* **22**, 7–32 (2003).
19. Gamble, C., Davies, W., Paul Pettitt, P. & Richards, M. Climate change and evolving human diversity in Europe during the last glacial. *Phil. Trans. R. Soc. Lond. B* **359**, 243–254 (2004).
20. Woodman, P. C. in *The Quaternary History of Ireland* (eds Edwards, K. & Warren, W.) 251–278 (Academic, Orlando and London, 1985).
21. Gonzalez, S., Kitchener, A. C. & Lister, A. M. Survival of the Irish Elk into the Holocene. *Nature* **405**, 753–754 (2000).
22. Guenther, E. W. Funde von Ren und Riesenhirsch in nacheiszeitlichen Schichten aus der Nähe von Theriesenhof bei Plön. *Schrift. Naturwiss. Ver. Schleswig-Holstein* **30**, 79–81 (1960).
23. Vereshchagin, N. K. & Baryshnikov, G. F. in *Quaternary Extinctions: A Prehistoric Revolution* (eds Martin, P. S. & Klein, R. G.) 483–516 (Univ. Arizona Press, Tucson, 1984).
24. Panova, N. K. *The Forest Development Process in Urals and Trans-Urals* [in Russian] 26–49 (Uralskoye Otdelenie Rossijskoi Akademii Nauk, Ekaterinburg, 1996).
25. Foronova, I. V. *Quaternary Mammals of the South-East of Western Siberia (Kuznetsk Basin): Phylogeny, Biostratigraphy, and Palaeoecology* [In Russian] 243 (United Institute of Geology Transactions 848, Publishing house of SB RAS Branch "GEO", Russian Academy of Sciences, Siberian Branch, Novosibirsk, 2001).
26. Serikov, Y. B. *Paleolithic and Mesolithic of the Middle Trans-Urals* [in Russian] 351 (Izdatelstvo Nizhne-Tagil'skogo Pedagogicheskogo Instituta, Nizhny Tagil, 2000).
27. Pavlova, M. V. Etudes sur l'Histoire paléontologique des Ongulés, IX Sélénodontes post tertiaires de la Russie. *Mem. Acad. Sci. St Petersburg* **20**, 1–95 (1906).
28. Guthrie, R. D. Radiocarbon dating evidence of Holocene mammoths on an Alaskan Bering Sea island. *Nature* **429**, 746–748 (2004).
29. Stuart, A. J. The extinction of woolly mammoth (*Mammuthus primigenius*) and straight-tusked elephant (*Palaeoaloxodon antiquus*) in Europe. *Quat. Int.* (in the press).

Supplementary Information accompanies the paper on www.nature.com/nature.

Acknowledgements The research was funded by the Natural Environment Research Council. We thank the following for their help in providing specimens and/or data: K. Aaris-Sørensen, J. Altuna, N. Benecke, P. Boscato, M. Breda, C. Bronk Ramsey, V. Cabrera, A. Currant, W. Davies, P. Doughty, I. V. Foronova, C. Gamble, M. Germonpré, S. Gonzalez, K. Hawkins, R. Hedges, B. Huntley, R. Jacobi, K. James, L. Kaagan, R. Kahlke, A. Kitchener, Y. V. Kuzmin, J. van der Made, A. K. Markova, D. Mol, D. Nagel, L. Niven, M. Palombo, M. Patou, P. Pettitt, A. Pinto, B. Sala, M. Street, A. Tagliacozzo, P. Tomlinson, E. Turner, A. A. Vorobiev and P. Wojtal. Special thanks to I. V. Foronova for agreeing to publication of the Chernigovo date in advance of further collaborative work on Siberian *Megaloceros*, and to P. Grootes for AMS radiocarbon dating of the Kamyshev and Redut specimens. We are grateful to A. Mangione, B. Sala and Superintendenza per i Beni Archeologici dell'Umbria for permission to use the *Megaloceros* illustration in Figs 2, 3 and 4.

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to A.J.S. (Tony@megafauna.freeserve.co.uk).

Photosynthetic architecture differs in coastal and oceanic diatoms

Robert F. Strzepek^{1*} & Paul J. Harrison^{2*}

¹Department of Botany, University of British Columbia, Vancouver BC Canada V6T 1Z4

²Department of Botany and Department of Earth and Ocean Sciences, University of British Columbia, Vancouver BC Canada V6T 1Z4

* Present addresses: NIWA Centre for Chemical and Physical Oceanography, Department of Chemistry, University of Otago, PO Box 56, Dunedin, New Zealand (R.F.S.); Atmospheric, Marine & Coastal Environment (AMCE) Program, Hong Kong University of Science and Technology, Clear Water Bay, Hong Kong (P.J.H.)

Diatoms are a key taxon of eukaryotic phytoplankton and a major contributor to global carbon fixation¹. They are ubiquitous in the marine ecosystem despite marked gradients in environmental properties, such as dissolved iron concentrations, between coastal and oceanic waters. Previous studies have shown that offshore species of diatoms and other eukaryotic algae have evolved lower iron requirements to subsist in iron-poor oceanic waters, but the biochemical mechanisms responsible for their decreased iron demand are unknown^{2,3}. Here we show, using laboratory-cultured model species, a fundamental difference between a coastal and an oceanic diatom in their photosynthetic architecture. Specifically, the oceanic diatom had up to fivefold lower photosystem I and up to sevenfold lower cytochrome *b₆f* complex concentrations than a coastal diatom. These changes to the photosynthetic apparatus markedly decrease the cellular iron requirements of the oceanic diatom but not its photosynthetic rates. However, oceanic diatoms might have also sacrificed their ability to acclimate to rapid fluctuations in light intensity—a characteristic of dynamic and turbid coastal waters. We suggest that diatoms, and probably other eukaryotic algal taxa, exploited this difference in the underwater light climate between oceanic and coastal waters, enabling them to decrease their iron requirements without compromising photosynthetic capacity. This adaptation probably facilitated the colonization of the open ocean by diatoms, and contributes to their persistence in this iron-impooverished environment.

It has been well established that diatoms and other eukaryotic algae from oceanic waters are less susceptible to iron limitation than coastal species^{2–6}. This trend was supported by growth rate data from two closely related model diatom species cultured over an ecologically relevant range of iron concentrations and light intensities (Fig. 1). In iron-replete medium, the two diatoms grew at comparable rates (Fig. 1a). However, the oceanic centric diatom, *Thalassiosira oceanica*, maintained high growth rates (about 80% of those in iron-replete conditions) in low-iron media that restricted the growth of the coastal diatom, *Thalassiosira weissflogii*, to about 20% of iron-replete growth rates (Fig. 1c). Previous studies have shown that oceanic species of diatoms and other eukaryotic algae are unusual in that they maintain these high growth rates despite having very low cellular iron concentrations^{2,3,6}. We therefore conducted the first investigations at the biochemical level to determine how an oceanic diatom has decreased its dependence on iron.

Theoretical calculations predict that most of the iron required by phytoplankton is used for photosynthetic electron transport. Iron is an essential component of the cytochrome and iron-sulphur protein cofactors of the major photosynthetic complexes: photosystem II (PSII), the cytochrome (Cyt) *b₆f* complex and photosystem I (PSI)^{7,8}. Although the iron content of the complexes is evolutionarily conserved, there is some flexibility in iron requirements because the cellular abundance of the complexes themselves

21. Craxton, M. Genomic analysis of synaptotagmin genes. *Genomics* **77**, 43–49 (2001).

22. Mackler, J. M. & Reist, N. E. Mutations in the second C2 domain of synaptotagmin disrupt synaptic transmission at *Drosophila* neuromuscular junctions. *J. Comp. Neurol.* **436**, 4–16 (2001).

23. Chapman, E. R., Desai, R. C., Davis, A. F. & Tornehl, C. K. Delineation of the oligomerization, AP-2 binding, and synprint binding region of the C2B domain of synaptotagmin. *J. Biol. Chem.* **273**, 32966–32972 (1998).

24. Rickman, C. *et al.* Synaptotagmin interaction with the syntaxin/SNAP-25 dimer is mediated by an evolutionarily conserved motif and is sensitive to inositol hexakisphosphate. *J. Biol. Chem.* **279**, 12574–12579 (2004).

25. Grass, I., Thiel, S., Honing, S. & Haucke, V. Recognition of a basic AP-2 binding motif within the C2B domain of synaptotagmin is dependent on multimerization. *J. Biol. Chem.* **279**, 54872–54880 (2004).

26. Nakhost, A., Houeland, G., Blandford, V. E., Castellucci, V. F. & Sossin, W. S. Identification and characterization of a novel C2B splice variant of synaptotagmin I. *J. Neurochem.* **89**, 354–363 (2004).

27. Reenan, R., Hanrahan, C. & Ganetzky, B. The mle(napts) RNA helicase mutation in *Drosophila* results in a splicing catastrophe of the *para* Na⁺ channel transcript in a region of RNA editing. *Neuron* **25**, 139–149 (2000).

28. Aruscavage, P. & Bass, B. A phylogenetic analysis reveals an unusual sequence conservation within introns involved in RNA editing. *RNA* **6**, 257–269 (2000).

29. Kung, S. S., Chen, Y. C., Lin, W. H., Chen, C. C. & Chow, W. Y. Q/R RNA editing of the AMPA receptor subunit 2 (GRIA2) transcript evolves no later than the appearance of cartilaginous fishes. *FEBS Lett.* **509**, 277–281 (2001).

30. Wheeler, W. C., Whiting, M., Wheeler, Q. D. & Carpernter, J. M. The phylogeny of the extant hexapod orders. *Cladistics* **17**, 113–169 (2001).

Supplementary Information accompanies the paper on www.nature.com/nature.

Acknowledgements I thank L. Reenan for discussions; B. Hoopengardner, T. Bhalla and A. Das for comments on the manuscript; B. Hoopengardner for sharing certain genomic DNA templates and for assistance with S2 cell culture; UCHC Molecular Core Facility staff for diligent sequencing efforts; and M. Lalande for his encouragement. This work was supported by grants from the National Science Foundation and National Institutes of Health (R.A.R.).

Competing interests statement The author declares that he has no competing financial interests.

Correspondence and requests for materials should be addressed to R.A.R. (reenan@neuron.uchc.edu).

erratum

Pleistocene to Holocene extinction dynamics in giant deer and woolly mammoth

A. J. Stuart, P. A. Kosintsev, T. F. G. Higham & A. M. Lister

Nature **431**, 684–689 (2004).

In Fig. 4 of this Letter, some of the data were not properly aligned with their location labels. The corrected figure is shown here. □

