

1 The earliest evidence for anatomically modern humans in Europe

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The earliest anatomically modern humans in Europe are thought to have appeared between about 44,000 and 42,000 calendar years before present (44–42 kyr cal BP), by association with Aurignacian sites and lithic assemblages assumed to have been made by modern humans rather than by Neanderthals. However, the actual physical evidence for modern humans is extremely rare, and direct dates reach no farther back than about 41–39 kyr cal BP, leaving a considerable gap to the earlier period. Here we show, using stratigraphic, chronological and archaeological data, that a fragment of human maxilla from the Kent's Cavern site, UK, dates to before the earlier period. The maxilla (KC4), which was excavated in 1927, was initially diagnosed as Upper Palaeolithic modern human¹. In 1989, it was directly radiocarbon dated by accelerator mass spectrometry to 36.4–34.7 kyr cal BP². Using a Bayesian analysis of new ultrafiltered bone collagen dates in an ordered stratigraphic sequence at the site, we show that this date is a considerable underestimate. Instead, KC4 dates to 44.2–41.5 kyr cal BP. This makes it older than any other equivalently dated modern human specimen and directly contemporary with the latest European Neanderthals, thus making its taxonomic attribution crucial. We also show that in 13 dental traits KC4 possesses modern human rather than Neanderthal characteristics; three other traits show Neanderthal affinities and a further seven are ambiguous. KC4 therefore represents the oldest known, anatomically modern human fossil in western Europe, fills a key gap between the earliest dated Aurignacian remains and the earliest human skeletal remains, and demonstrates the wide and rapid dispersal of early modern humans across Europe more than 40 kyr ago.

The dispersal of the first anatomically modern humans (AMH) into Europe has long been associated with the transition from the Middle to the Upper Palaeolithic and linked with the subsequent disappearance of Neanderthals. Numerous sites attest to the change from late Neanderthal Mousterian or transitional industries to Early or proto-Aurignacian technocomplexes, evidenced by the presence of blade-based lithic assemblages and a wide range of bone implements and ornaments. However, the skeletal evidence linking AMH with this earliest phase is extremely fragmentary in comparison with remains from the later Evolved Aurignacian period. The earliest direct date on an AMH bone (42–37.8 kyr cal BP) comes from Peștera cu Oase, Romania, but the dating is imprecise and the human fossils are not associated with any tool industry³.

The site of Kent's Cavern, Torquay, UK, is of great importance because it contains an early, directly dated human maxilla (KC4; Fig. 1A) from a site at the maximal north-westerly range of the European Aurignacian. Stratified sediments ranging from Middle Pleistocene to Holocene in age were excavated in the site, within a

cave earth sealed periodically by stalagmite deposits⁴. The maxilla was found in 1927 at a depth of 10 ft 6 inch (3.23 m) beneath a key 'granular stalagmite' used as a datum during excavations undertaken between 1926 and 1941 by the Torquay Natural History Society⁵. Below it were found two blades similar to those discovered in Aurignacian industries, and deeper still were found two blades that resemble those from Initial Upper Palaeolithic industries of the Lincombian–Ranisian–Jerzmanowician complex, which are tentatively associated with Neanderthals^{6,7}. Keith, who analysed the maxilla, considered it to be of anatomically modern type¹, and interest in the fossil further increased in 1989 when direct dating by accelerator mass spectrometry (AMS) confirmed its early Upper Palaeolithic age (30,900 ± 900 radiocarbon years (yr ¹⁴C) BP; ref. 2). The age fitted then-current views on the dating and modern human associations of the Aurignacian industry in north-western Europe.

However, recent research into the chronology of the Middle to Upper Palaeolithic has suggested that there are severe problems with

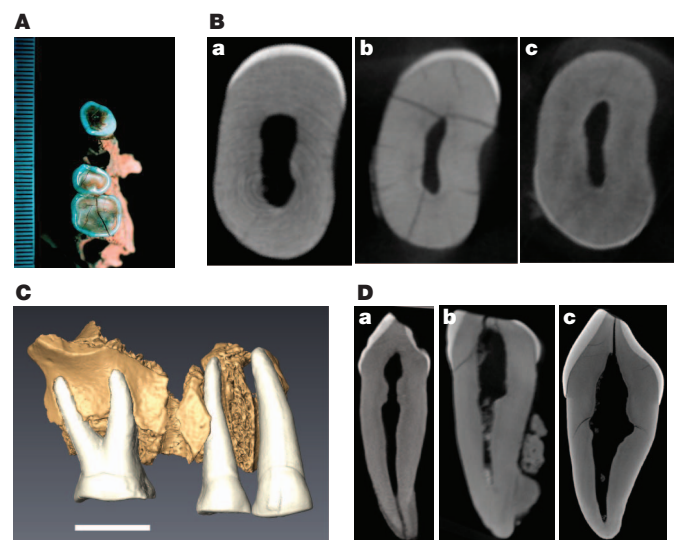


Figure 1 | Morphology of the KC4 maxilla. A, Original dentition within the KC4 maxilla as Keith¹ would have seen it. B, P¹ pulp chamber shape of Neanderthal (a), KC4 (b) and modern human (c). C, Computed-tomography-based three-dimensional model of the KC4 maxilla showing the new reconstruction of the specimen (scale bar, 1 cm). D, Upper canine pulp chamber shapes of Neanderthal (a), KC4 (b) and modern human (c). Neanderthal specimens are from the site at Krapina, Croatia; modern humans are from Gough's Cave, UK. See Supplementary Methods for further details.

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the accuracy of many ^{14}C dates from this period, especially those produced early in the developmental stages of the technique^{8,9}. Contamination problems with many of the existing AMS determinations on bone dating from the Middle and Upper Palaeolithic before 30 kyr ^{14}C BP can be reduced considerably by the use of ultrafiltration during collagen extraction^{9,10}. We used this technique to reinvestigate the age of KC4, first by dating faunal material above and below the maxilla find spot, and then by attempting a direct re-dating of a tooth from the maxilla itself.

Faunal remains from the Torquay Natural History Society excavations that could be matched with the descriptions and contexts given in the *Kent's Cavern Journal* (1926–1932) were selected for radiocarbon dating. AMS dates for fauna from two of the excavation trenches (trenches B and C, eventually linked together by the excavators) are shown in stratigraphic order in increasing depth below the granular stalagmite in Fig. 2 (see also Supplementary Table 1). The results show that the initial AMS determination for the maxilla is too young, probably because of the presence of trace animal glues not effectively removed during chemical pretreatment⁸ (Supplementary Methods). To constrain more precisely the age of the maxilla, we used the new dates and independent stratigraphic depth data to construct a Bayesian model using OXCAL 4.1 software¹¹ and the INTCAL09 ^{14}C calibration curve¹². This approach allows the relative stratigraphic information from the site to be modelled mathematically along with the calibrated radiocarbon

likelihoods (Fig. 2). We are confident that dates corresponding to depths between 12–13 ft and 15 ft stratigraphically precede the age of the maxilla and therefore provide a *terminus post quem* for it. Similarly, our modelling of determinations above the maxilla find spot indicate that they stratigraphically follow it in the sequence. These determinations include a date from a cranial fragment of a woolly rhinoceros found just above KC4 (OxA-13965) and two identical dates from a pair of woolly rhinoceros metacarpals found in articulation (Supplementary Methods). These data constrain the probable age of the maxilla and provide a *terminus ante quem* for it. We used the 'date' function in OXCAL¹¹ to calculate a PDF for its likely age within this modelled sequence, assuming that it was excavated in its originally deposited location. This PDF corresponds to 43,110–41,890 yr cal BP (68.2% probability) and 44,180–41,530 yr cal BP (95.4% probability)—equivalent to the latest part of Greenland interstadial 11 on the NGRIP $\delta^{18}\text{O}$ Hulu-tuned timescale^{13,14} (Supplementary Fig. 2). When we tested the model by varying the priors used, the result for the PDF did not change significantly (Supplementary Methods). We attempted another AMS date from the third premolar (P³) of the KC4 specimen to confirm this age, but too little collagen could be extracted for a reliable AMS date to be determined (Supplementary Table 2).

Comparison of the PDF for KC4 with other direct dates of AMH fossils shows it to be earlier than any other (Fig. 3). However, it overlaps with the remains believed to be earliest dated evidence for

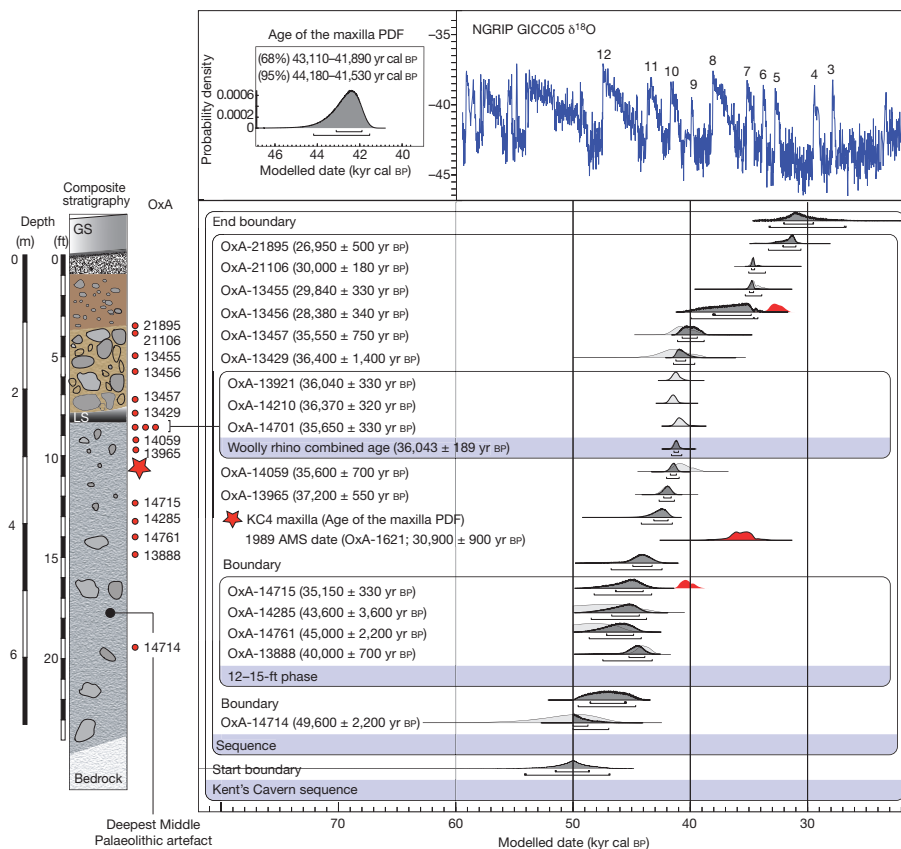


Figure 2 | Bayesian age model for Kent's Cavern. The model incorporates the radiocarbon likelihoods (calibrated probability distributions; brackets under the distributions represent the 68.2% and 95.4% ranges, respectively) within a relative age sequence based on the depths recorded during the excavation of phases and stalagmite deposits throughout the site. This allows a probability distribution function (PDF) for the estimated age of KC4 (age of the maxilla PDF; see inset for magnified view) to be generated. Figures in brackets next to OxA numbers are conventional radiocarbon ages. Dates are calibrated using the INTCAL09 curve¹² and compared against the NGRIP $\delta^{18}\text{O}$ palaeotemperature record¹³ tuned to the Hulu Cave timescale¹⁴ ($\delta^{18}\text{O} = (\delta^{18}\text{O}/$

$\delta^{16}\text{O})_{\text{sample}} / (\delta^{18}\text{O}/\delta^{16}\text{O})_{\text{standard}} - 1$). Numbers on the $\delta^{18}\text{O}$ record represent Greenland interstadials. The three calibrated ages in red are outliers in the model. One of these is the original AMS date of KC4 (OxA-1621), which is shown alongside the new modelled age for the maxilla. It was not included in the Bayesian analysis. The stratigraphic section on the left was adapted from the AR4271 Section Drawing of Vestibule Trench in Ogilvie's excavation archive (Torquay Museum, UK). Location of dated samples by depth is shown: red star, maxilla depth; GS, granular stalagmite, from which depth measurements were recorded; LS, lower stalagmite. Figure generated using OXCAL 4.1¹¹. See Supplementary Methods for details of the modelling and testing.

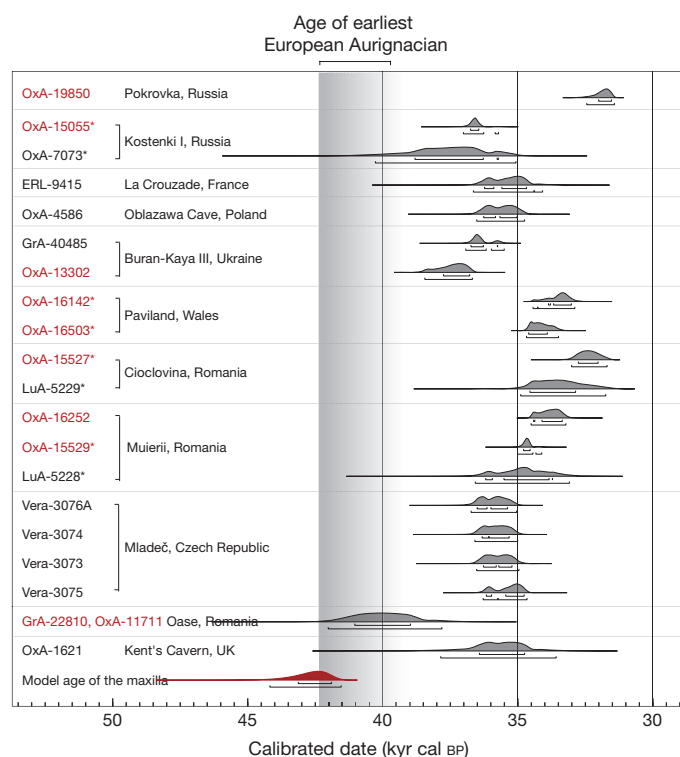


Figure 3 | Comparison of direct radiocarbon determinations of AMH bones from European Palaeolithic sites^{3,9,19–25} with the KC4 model age. Calibrated using the INTCAL09 curve¹². Brackets under the distributions represent the 68.2 and 95.4% probability ranges, respectively. The PDF derived from the Bayesian modelling of KC4 (age of the maxilla PDF, in red) is earlier than the original direct date from Kent's Cavern (OxA-1621) and all others, and overlaps the start of the age range of the earliest European Aurignacian¹⁵, which is widely accepted as being linked with the earliest AMH. Ultrafiltered collagen radiocarbon dates are indicated with red text; non-ultrafiltered dates are in black. Asterisks denote duplicate dates on the same human bone. The Oase date is a mean of two determinations, one ultrafiltered and one not³.

the Aurignacian of Europe¹⁵ and for the latest Neanderthal and Mousterian sites. Thus, it is crucial to determine whether Keith's attribution¹ of the maxilla as modern human is reliable.

Keith's original illustrations¹ show KC4 essentially as it appears today (Fig. 1A), except for increased cracking due to the specimen drying out and the removal of some alveolar bone for the previous AMS determination. Keith reported that three teeth—the canine, second premolar (P^4) and first molar (M^1)—were in place, whereas the sockets for P^3 and the second molar (M^2) were empty. This implies that the specimen had already been reconstructed when Keith received it for study, and may explain why he never questioned the identity of the premolar. He provided basic data on the crown and root dimensions of the three teeth, and the total length of the tooth row as preserved, finding the measurements entirely comparable to those of recent modern humans rather than to those of Neanderthals. However, our study of the specimen shows that P^4 is in fact a right P^3 . To test this re-identification, a virtual three-dimensional model based on a computed microtomography scan of the specimen was generated, and alternative positions for the premolar were tested (Supplementary Methods). This revealed a displaced bone fragment in the P^3 socket, and when this was repositioned virtually, the imaged premolar could be rotated and positioned well into this socket (Fig. 1C). Following virtual testing, a new physical reconstruction was then created.

The wear on the teeth of KC4 is such that all occlusal morphology has been removed. Other aspects of dental morphology and measurement were therefore used to determine whether the specimen is Neanderthal or modern human. To facilitate root and pulp chamber

comparisons, computed tomography was used on modern human fossils from Gough's Cave, UK, and Neanderthal fossils from different sites (Supplementary Methods). The characteristics of each tooth taken individually suggest an identification of Upper Palaeolithic *Homo sapiens*. The premolar is characterized by a low angle of inclination to the vertical of the occlusal part of the buccal surface, small dimensions and a characteristic shape of the pulp chamber and root canals (Fig. 1B), small cervical dimensions and the small size of these relative to the canine and molar, and a narrowness of the root. The canine has a small or absent tuberculum dentale, mild vertical curvature of the buccal side of the root, slight mesial and distal grooves on the root, an absence of buccal and lingual dentine spurs in the root canal, pronounced lingual narrowing of the canal towards the apex and pronounced cervical proportions relative to those of the crown (Fig. 1D). Finally, the molar has a rectangular shape when viewed horizontally, occlusally and at the cervix, and in addition has a less skewed shape in the pulp chamber polygon, an absence of taurodontism, and relative cervical–crown proportions indicative of a modern human (Supplementary Methods).

However, some characteristics of the teeth are ambiguous or more Neanderthal-like. In the canine, there are irregularities in the root canal and the implied presence of tubercle extensions, although the latter are also found in Upper Palaeolithic teeth. Other traits seemingly indicative of non-recent humans are the straight, lingually pointed roots of the first and second molars and the fact that these features are more pronounced in the second molar than in the first.

Nevertheless, in all but three of 16 dental characteristics KC4 shows AMH rather than Neanderthal affinities, whereas seven remain ambiguous (Table 1 and Supplementary Methods). This suggests strongly that this is an early modern human (*H. sapiens*) fossil. The three possible Neanderthal traits may reflect inadequate sampling of modern human variation, the presence of shared primitive features in KC4 and Neanderthals, or indications of gene flow between Neanderthals and early modern humans^{16,17}.

Table 1 | Dental features of the KC4 maxilla suggesting modern human or Neanderthal features

Type	No.	Trait
Traits suggesting modern human affinities	1	Canine tuberculum dentale small or absent
	2	Mild vertical convexity of buccal side of canine root
	3	Vertical grooves on canine root shallow and narrow
	4	No buccal or lingual dentine spurs apical to cervix in canine or P^3 pulp chambers
	5	Pronounced lingual narrowing of canine root canal towards apex
	6	P^3 low angle of inclination of occlusal part of buccal surface relative to vertical axis
	7	Small dimensions and characteristic shape of P^3 pulp chamber and root canals
	8	Rectangular shape of M^1 occlusally and at cervix
	9	Less skewed shape of M^1 pulp chamber polygon
	10	No taurodontism of M^1
	11	Low robusticity of P^3 root
	12	Small actual and relative cervical dimensions of P^3
	13	Relative cervical and crown dimensions of canine and M^1
Traits suggesting Neanderthal affinities	14	Possible tubercle extensions on canine
	15	Irregularities in sides of root canals, especially in the canine
	16	Greater lingual inclination of M^2 lingual root than is found in M^1
Ambiguous traits	17	Crown dimensions and root lengths lie in both Neanderthal and modern human ranges
	18	Canine angle of inclination of occlusal part of buccal surface relative to vertical axis
	19	Mesiobuccal bulge in occlusal outline of canine but not of P^3
	20	Canine root surface smooth
	21	Single-rooted P^3
	22	Dimensions of canine pulp chamber
	23	Height of P^3 pulp chamber roof relative to cervix

Details of the analysis of each trait can be found in Supplementary Methods.

To test further for possible Neanderthal affinities, we attempted the genetic analysis of DNA from the dentine of P³, using previously described techniques for isolating and amplifying DNA from preserved remains¹⁸. PCR amplicons from four positive amplifications were cloned into competent bacterial cells. Analysis of the 72 colonies sequenced from KC4 revealed at least 18 distinct mitochondrial DNA sequences, all of which fell within the range of genetic diversity of AMH. However, given the difficulty of distinguishing between endogenous sequences of modern humans and contamination, we consider these results to be inconclusive regarding the specific identity of KC4. It is not possible to determine whether the specimen is genetically similar to modern humans, or whether the DNA in the sample is so degraded that no endogenous (Neanderthal or otherwise) DNA was recoverable using the methods applied (Supplementary Methods).

The new estimated age for KC4 fills a hitherto unexplained gap between the evidence for the earliest Aurignacian remains and that for the earliest modern human skeletal remains, and adds further strength to the association between the two because of the close correspondence between the age and dates for the earliest European Aurignacian in western Europe¹⁵. Although the Upper Palaeolithic artefacts from the deeper parts of the excavations at Kent's Cavern cannot confidently be assigned a precise cultural attribution, we consider an early Aurignacian association for KC4 to be the most likely. Even if this cannot be established, by confirmation of its attribution as an AMH fossil, KC4 demonstrates the very rapid dispersal of early modern humans across Europe, well before 40 kyr ago.

METHODS SUMMARY

Bone collagen for radiocarbon dating was extracted at the Oxford Radiocarbon Accelerator Unit, University of Oxford, UK, using sequential decalcification, base wash, gelatinization, filtration and ultrafiltration steps to remove low-molecular-mass contaminants. Radiocarbon determinations were obtained using an HVEE accelerator mass spectrometer and calculated conventionally as ages before AD 1950. Calibration was against the INTCAL09 data set, using the OXCAL 4.1 computer program. Bayesian modelling was applied using OXCAL and a relative depth sequence was obtained from the original excavation plans. Outlier detection analysis was used to give less weight to radiocarbon likelihoods in disagreement with the prior information applied. Model sensitivity was tested by varying the priors for the upper parts of the archaeological modelled sequence. New measurements of the morphology of the KC4 teeth were taken from computed tomography scans. Computed microtomography scanning of the teeth and maxilla done using an X-Tek HMX 160 system (X-Tek Systems Ltd). A virtual three-dimensional model of the specimen was created by a combination of thresholding and manual segmentation, and was used for quantitative and qualitative analysis of the specimen. Comparative dimensions and morphological data were obtained for European Neanderthals, European Upper Palaeolithic *H. sapiens* and recent Europeans from the literature, casts in the collection of the Natural History Museum, London, UK, and computed tomography scans available on the NESPOS website (<https://www.nespos.org/display/opensource/home>). The crown measurements of KC4 made by Keith¹ (corrected) were used for comparison, because these were made on the specimen when it had the fewest cracks. Root robusticity, cervical measurements and internal measurements were the principal source for comparisons with these data, owing to the effects of crown wear on the KC4 teeth. All comparative data are listed in Supplementary Methods.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions C.S., R.J., E.T. and T.H. initiated the research. C.S., R.J., T.H. and T.C. designed the research. R.J. determined the spatial and depth locations of the AMS-dated bones, identified the material and analysed the site's lithic remains. T.H. did the AMS dating and Bayesian analysis. T.C. analysed the dental traits. C.F. and S.H. provided comparative dental data. B.S. did the DNA analysis. C.C. reconstructed and conserved the maxilla. B.C. curated the KC4 maxilla. P.O'H. and M.F. did the computed microtomography scanning. F.G. performed the virtual three-dimensional reconstruction of KC4 and prepared the Gough's Cave CTSs. F.G. and T.C. made the KC4 dental measurements. T.H., C.S. and T.C. wrote the initial draft of the paper. All authors contributed to and helped to edit the final manuscript.

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