Age estimates for hominin fossils and the onset of the Upper Palaeolithic at Denisova Cave

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Denisova Cave (Siberian Altai, Russia) is a key site in understanding the complex relationships between hominin groups inhabiting Eurasia in the Middle and Late Pleistocene. DNA sequenced from human remains found here has shown the presence of a hitherto unknown hominin, the "Denisovans"[1,2] **and high coverage genomes from both Neanderthal and Denisovan fossils provide evidence for admixture between the two groups**[3]**. Determining the age of these fossils is important if we are to understand the nature of hominin interaction, and aspects of their cultural and subsistence adaptation. Here, we present 50 new radiocarbon determinations from the late Middle and Upper Palaeolithic parts of the site. We also report three newly-discovered directly-dated hominin fossil fragments, and obtain a mitochondrial DNA sequence for one of them. To calculate probabilistically the age of the human fossils at the site, we apply a novel Bayesian age modelling approach that combines chronometric (radiocarbon, uranium-series and optical ages), stratigraphic and genetic data. Our modelled age estimate for the oldest Denisovan fossil suggests that this group was present at the site as early as 195,000 years ago (at 95.4% probability). All Neanderthal fossils, as well as *Denisova 11*, the daughter of a Neanderthal and a Denisovan**[4]**, date between 80,000 and 140,000 years ago. The youngest Denisovan dates up to 51,000 years ago. Direct radiocarbon dating of Upper Palaeolithic tooth pendants and bone points yielded the earliest evidence for the production of such artefacts in northern Eurasia, at *c.* 43,000–49,000 years cal BP. Based on present archaeological evidence, it may be assumed that these artefacts are associated with the Denisovans. Whether anatomically modern humans were involved in their production is not possible to determine at present since their remains have not yet been identified in the Altai region.**

Denisova Cave preserves the longest and most notable Palaeolithic sequence in northern Asia. It consists of three chambers: Main, East and South (Supplementary Information 1). Excavations at the site have so far yielded the remains of 12 hominins (Extended Data Fig. 1, Supplementary Information 3), most of which are small and highly fragmentary. Despite this, the preservation of DNA in some of these remains is very good, and has enabled genome-wide data to be obtained from both Neanderthal and Denisovan human remains, as well as from cave sediments[1-8].

A key unresolved issue remains the chronology of the site and the age of the recovered human remains. Previous attempts at building a chronology at Denisova Cave have employed radiocarbon dating in the uppermost sections, and thermoluminescence dating of the older layers[9]. More recently, radiocarbon dating from the uppermost Pleistocene layers in the East Chamber revealed some age variations that were ascribed to taphonomic mixing and carnivore bioturbation[2]. A new set of optical ages[10] has been obtained from Pleistocene sedimentary layers in all three chambers.

Here we report 50 new radiocarbon determinations from 40 samples collected from the upper parts of the Pleistocene sequence (layers 9–12) in the Main and East Chambers (Fig. 1 and Extended Data Table 1). A further 23 samples were processed, but did not yield sufficient carbon for dating (Supplementary Information 2). We selected samples of charcoal, humanly-modified bone and artefacts (Supplementary Information 2 and Extended Data Fig. 2) from locations deemed undisturbed during excavation. The samples were prepared using, where possible, robust decontamination protocols, including collagen ultrafiltration and single amino acid extraction of hydroxyproline from bones and teeth, and ABOx-/AOx-SC for charcoal (Supplementary Information 2).

All samples from layers 11.3, 11.4 and 12 in the East Chamber, as well as the directly-dated *Denisova 11*[13], predate the radiocarbon age limit. In layer 11.2, we found two age clusters: three samples, including two humanly-modified bones collected from the same square, sector and year of excavation as the *Denisova 3* phalanx, have infinite ages, and three samples have finite calibrated ages (Extended Data Table 1). A horse tooth from layer 9.2 gave a result of 45,720–50,000 cal BP (OxA-29859). This age is statistically indistinguishable from the group of finite ages (treated with ultrafiltration and ABOx) from layer 11.2.

In the Main Chamber, the new radiocarbon ages reveal a depositional hiatus between layers 12 and 11.4. Samples from layer 12, at the end of the Middle

Palaeolithic, all gave infinite radiocarbon ages compared to samples from layer 11.4, which have ages between ~35,000 and 40,000 cal BP (Fig. 1).

Four pendants made from red deer (*Cervus elaphus*) and elk (*Alces alces*) teeth, often associated with Upper Palaeolithic technocomplexes, provided results of ~32,000, ~40,000 and ~45,000 cal BP (Fig. 1 and Extended Data Fig. 2). The oldest of these ages (OxA-30963) is corroborated by a charcoal date (OxA-31506) from the same stratigraphic location and year of excavation, and is the earliest direct date for an artefact of this type. The younger determinations for some of these artefacts may be considered minimum ages due to small sample sizes and marginal collagen yields (~1% wt. collagen), which prevented the application of robust chemical pretreatment methods. Two bone points were dated to 42,660–48,100 and 41,590–45,700 cal BP (Fig. 1 and Extended Data Fig. 2), also representing the earliest occurrence of such objects in northern Eurasia.

The radiocarbon ages for the oldest Denisova pendants and the bone points overlap with the directly dated modern human femur from Ust'-Ishim in western Siberia[14] (43,200–46,880 cal BP)(Fig. 2). This raises the possibility of a connection between the spread of modern humans and the emergence of innovative behaviours and symbolic artefacts across northern Eurasia at the start of the Initial Upper Palaeolithic, by 43,000**–**48,000 cal BP.

In an attempt to retrieve further human fossils from the site, we applied collagen peptide mass spectrometry fingerprinting (or ZooMS) to 2,212 non-diagnostic bone fragments and identified three new specimens that contained peptides consistent with the Hominidae (Supplementary Information 8). The bones come from layers 9.3 (*Denisova 14*, DC 3758) and 11.4 (*Denisova* 15, DC 3573) in the East Chamber, and layer 9.1 (*Denisova 16*, DC 4114) in the Main Chamber (Extended Data Fig. 3). *Denisova 14* and *Denisova 15* were directly dated and genetically analysed. The radiocarbon ages are close to, or beyond, the radiocarbon limit (Fig. 1 and Extended Data Table 1). No ancient hominin DNA was retrieved from *Denisova 14*, but *Denisova 15* carries a mitochondrial genome of the Neanderthal type (Supplementary Information 5). *Denisova 16* was too small for radiocarbon dating and aDNA analyses are ongoing.

All directly dated human remains yielded infinite radiocarbon ages and are associated, in most cases, with layers that are beyond the limit of the method. Using optical dating finite ages for layers containing human remains have been obtained[10], but the association between the sediment samples and human fossils is inferred, and the dated sediments do not immediately surround the fossils. Age estimates based on branch shortening of the nuclear genome have been published for *Denisova 3, Denisova 5* and *Denisova 11*[3-5](Supplementary Information 4) but these are sensitive to sequencing error and the human/chimpanzee divergence date, which is under discussion. To exploit the different types of information available for Denisova Cave derived from radiocarbon and optical dating, stratigraphy and genetic analyses, we developed a novel Bayesian approach to generate robust age estimates for the human remains and ameliorate the shortcomings of each technique and line of evidence when used individually.

We used OxCal 4.3 software[11] to build a Bayesian model consisting of several types of prior information; the stratigraphic position of all specimens (Fig. 3), the relative genetic ages for seven human remains (*see below*, Extended Fig. 4), the finite radiocarbon age for *Denisova 14*, a *terminus ante quem* boundary for the radiocarbon ages (>50,000 BP), optical ages for layers 22.1 (n=2) and 21 (n=3) in the Main Chamber and layers 12.3 (n=3) and 11.2 (n=3) in the East Chamber (Supplementary Information 6) and a minimum uranium-series age of 67,500 ± 2500 years for *Denisova 11* (Supplementary Information 7).

The relative genetic ages of four Denisovans (*2, 3, 4* and *8*) and two Neanderthals (*5* and *15*), as well as *Denisova 11* (who carries a Neanderthal mitochondrial genome), were derived from a multiple sequence alignment of their mitochondrial genome sequences. We achieved this by counting the number of substitutions on the branches leading to each individual since the split from their most recent common ancestor with either the *Sima de los Huesos* individual[14], or with 19 Neanderthals from other archaeological sites and the *Hohlenstein-Stadel* Neanderthal (Extended Data Fig. 4). To convert these differences to time in years, we applied the mitochondrial mutation rate of 2.53×10^{-8}/nucleotide position/year (95% HPD: 1.76-3.23×10^{-8}) inferred for modern humans[15]. We caution that this conversion to time assumes that the mutation rate in archaic humans is the same as that in modern humans, and that the approach cannot detect back mutations and multiple substitutions occurring at the same position in the mitochondrial genome. The relative ages obtained were then included within the Bayesian model as relative constraints between the hominin remains. The split time estimates in the Denisovan and Neanderthal trees were treated as time differences assuming an Erlang distribution.

We tested four separate Bayesian models (Supplementary Information 9; Extended Data Figs 5-6). When the human remains are placed in their attributed stratigraphic positions (Model 1), low model agreement indices were obtained for *Denisova* 2 and *11*, suggesting that these two fossils must have moved post-depositionally. When we reassigned these to overlying layers (Models 2-4), significantly higher agreement indices were obtained. We tested the results of the models against ages derived using optical and genetic information only (Extended Data Fig. 7). The modelled age estimates for the human fossils we report here derived from probability distribution functions using Model 4 (Fig. 4; Extended Data Table 2; Supplementary Information 9).

Denisova 2, the oldest Denisovan fossil, yielded a modelled age estimate of 122,700**–**194,400 years. *Denisova 8*, found at the interface between layers 11.4 and 12 of the East Chamber, falls between 105,600–136,400 years. *Denisova 3*, the youngest Denisovan fossil from layer 11.2 in the East Chamber, yielded a modelled age of 51,600**–**76,200 years ago (at 95.4% probability). This is consistent with infinite radiocarbon ages of >48,600 (OxA-29857) and >50,100 BP (OxA-29858) obtained on two humanly-modified bones collected from the same square, sector and year of excavation as *Denisova 3*. The modelled age also overlaps with the age estimated based on branch shortening in the nuclear genome when calculated using transversion polymorphisms only and assuming a human/chimpanzee divergence time of 13 million years (60,000**–**84,000 years)[5](Supplementary Information 4). *Denisova 4* (layer 11.1, South Chamber) differs by only two mutations in its mtDNA compared to *Denisova 3,* and therefore has a similar age.

The three Neanderthals (*Denisova 5*, *9* and *15*) are derived from similar stratigraphic positions in the East Chamber. *Denisova 5* (layer 11.4) has a modelled age estimate of 90,900–130,000 years ago, which is consistent with the nuclear genome branch shortening age estimate (110,000–134,800 years)[5](Supplementary Information 4). *Denisova 15* (layer 11.4) differs by only a single mutation in its mtDNA compared to *Denisova 5*, and therefore yields an overlapping modelled age. No genetic information is available for *Denisova 9* (layer 12.3); its modelled age (119,100–147,300 years) is based on its stratigraphic position and is constrained only by the optical ages from layer 12.3.

Denisova 11, found in layer 12.3 in the East Chamber, pre-dates stratigraphically *Denisova 5*. If this position is maintained (e.g., Model 2), *Denisova 11* has an estimated age of 115,700–140,900 years, compared to the modelled age estimate of 92,800–132,000 years for *Denisova 5.* Genetic information, however, based on the differences in the number of mitochondrial substitutions and the sharing of nuclear substitutions with the high-coverage genome of *Denisova 5*, suggests strongly that *Denisova 11* is younger than *Denisova 5*. To further explore this, we placed *Denisova 11* above *Denisova 5* in Models 3 and 4. Both models yielded much higher agreement indices, supporting the notion that *Denisova 11,* discovered in the assemblage of unidentifiable bones from layer 12, is intrusive to it. This results in a final age estimate of 79,300–118,100 years for this specimen.

The age estimates for *Denisova 11* and all Neanderthal remains from the site largely overlap (Fig. 4). Slon et al.[8] found Neanderthal and Denisovan DNA in underlying sediments in the East Chamber (layers 14 and 15) and Neanderthal DNA in the Main Chamber (layers 14, 17 and 19) (Fig. 3) suggesting that both groups were present in the cave prior to the earliest human fossils currently recorded there. The modelled ages for Neanderthal fossils found in the East Chamber are consistent with optical ages for sediments containing Neanderthal DNA in the Main Chamber. The earliest sediments with Neanderthal DNA (layer 14 in the East Chamber) date to ~190,000 years ago[10]. This also overlaps with the optical age (layer 15, East Chamber)[10] from which Denisovan DNA was extracted[8], as well as with our modelled age for *Denisova 2*. The interstratification and temporal overlap of Denisovan and Neanderthal fossils and sedimentary DNA, as well as the direct genetic evidence[4], suggests that both groups lived in the region, met and, on occasion, interbred over the course of

150,000 years. The integration of all available data from Denisova highlights the very early appearance of Neanderthals in Siberia, as early as 190,000 years ago, during the late part of warm MIS 7, with the majority of the specimens thus far falling into the last Interglacial (MIS 5) (Fig. 4).

Denisovans appear to have survived later than Neanderthals. Our modelled age estimate for the most recent Denisovan fossil (*Denisova 3*: 51,600–76,200 years ago) is earlier than published estimates of the age of Denisovan admixture into modern humans (44,000–54,000[16] and 31,000–50,000 years ago[17]). If these admixture estimates are robust, then the Altai Denisovans may not have been the latest surviving population.

Our results also imply that all known Neanderthal and Denisovan fossils predate the appearance of the Initial Upper Palaeolithic (45,000–48,000 years ago) and the directly-dated personal ornaments and bone points. However, given that previous work on the lithic evidence from Denisova Cave indicated that the Initial Upper Palaeolithic may have developed through a local Middle Palaeolithic substrate[19], it is parsimonious to suggest at present that the makers of these artefacts may have been Denisovans. The presence of anatomically modern humans to the northwest of Denisova Cave as early as 45,000 cal BP at Ust'-Ishim, synchronous with the dated pendants and bone points (Fig. 2), also raises the possibility that modern humans may have been involved in the manufacture of these artefacts. Future discovery of fossils from this site and others, and determination of their ages and genomes, using a combination of methods will shed further light on the relationships between archaic and modern humans and their associated material cultures.

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

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Contributions: K.D., V.S., Z.J., B.L., D.C., L.K., T.D., S.B., B.V., and M.B. performed the laboratory work; K.D., T.H., C.B.R., D.C., T.D. obtained and analysed the radiocarbon data. V.S., F.M., J.K., M.M. and S.P. analysed the genetic data; C.B.R., K.D. and T.H. designed and tested the Bayesian models. S.B. and M.B. analysed the ZooMS samples. B.V. carried out morphological analyses of the fossils. Z.J., B.L. and R.G.R. analysed the optical dating data. L.K. and R.G. obtained and analysed the U-series data. A.P.D., M.V.S. and M.B.K. excavated the site and analysed all archaeological data. K.D., T.H. and Z.J. wrote the manuscript with input from all authors.

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Methods

Radiocarbon dating and Bayesian modeling

Bones for dating were sampled using an NSK Elector drill with cleaned tungsten carbide drill bits. The routine ORAU chemical pretreatment protocol was applied[20]. A small number of samples were tested using compound-specific methods in which underivatised amino acids were separated from hydrolysed bone collagen samples using preparative High Performance Liquid Chromatography (Prep-HPLC)[21]. Using this procedure, hydroxyproline (Hyp) was isolated and dated. This approach is the most efficient technique to remove contaminants including conservation materials. Samples of charcoal were prepared for dating using ABA (Acid-Base-Acid), ABOx-SC (Acid-Base-Oxidation/Stepped Combustion)[22] or a modified AOx-SC preparation. OxCal v4.3.2[11] and the IntCal13[12] calibration curve were used to calibrate the radiocarbon data and build Bayesian models incorporating chronometric, stratigraphic and genetic relative dating.

Code availability

CQL codes for Bayesian analyses are included in Supplementary Information, Section 9. These can be imported and used in the OxCal platform[11].

ZooMS collagen fingerprinting analysis for hominin identification

Because ~95% of the bone assemblage from Denisova Cave is unidentifiable to species/genus due to carnivore-derived fragmentation, allied with the fact that ancient DNA is well-preserved, we applied collagen peptide mass fingerprinting (ZooMS) to identify new human remains from the site. We analysed 2,212 non-diagnostic bone fragments using this technique, which we previously used to discover *Denisova 11*[4,13], bringing the total bones analysed from the site so far to 4,527 (Supplementary Information 8). Samples from bone fragments were cut and drilled at the University of Oxford and processed for ZooMS analysis at the University of Manchester, UK. This involved each bone sample being partially decalcified with 0.6 M HCl overnight (~18 h) and then 0.5 mL of solution from each sample being twice ultrafiltered (30 kDa molecular weight cut-off) into 50 mM ammonium bicarbonate. 100 μL was then digested with sequencing grade trypsin at 37ºC overnight (~18 h) and 1 μL samples were spotted with 10 mg/mL α-cyano hydroxycinnamic acid matrix on a plate, following Brown *et al.*[13], and allowed to air dry. Using a Brüker Ultraflex II Matrix Assisted Laser Desorption Ionization Time of Flight mass spectrometer, 2,000 laser acquisitions from random walking were acquired for each sample and the resulting spectra were screened for hominin collagen peptide markers published previously[13,23].

DNA sequencing and data processing

Bone powder was removed from the *Denisova 14* and the *Denisova 15* bone fragments using a disposable dentistry drill. The bone powder samples were treated with 0.5% sodium hypochlorite prior to DNA extraction[24,25]. 20% of each DNA extract (i.e., 10 µl) were converted into single-stranded DNA libraries[26] and indexed with two barcodes[27]. The DNA libraries were enriched for human mtDNA fragments using two rounds of an on-beads hybridization capture protocol[28]. The enriched DNA libraries were pooled with libraries generated as part of other projects and sequenced on a MiSeq platform (Illumina) in 76-cycle paired-end runs[27]. Basecalling was carried out using Bustard (Illumina) and demultiplexing was performed by requiring exact matches to the expected barcode combinations. Overlapping paired-end reads were merged using leeHom[29]. Sequences were mapped to a reference genome using BWA[30] with parameters adapted to ancient DNA. PCR duplicates were collapsed into a single sequence using bam-rmdup (https://github.com/mpieva/biohazard-tools/). Only sequences longer than 35 bases and with a mapping quality higher than 25 were retained.

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FIGURE LEGENDS

Figure 1 | New radiocarbon age determinations (in calibrated years before present) from the East and Main Chambers at Denisova cave. The radiocarbon determinations (n=40) are calibrated using OxCal 4.3 software[11] and the IntCal13 calibration curve[12] and are plotted in their respective stratigraphic sequences and chambers of origin. The finite probability distributions are in blue with error bars indicating 68.2 and 95.4% highest posterior density ranges. Orange denotes measured ages beyond the radiocarbon limit (50,000 BP). Raw data in Extended Data Table 1. a. East Chamber sequence and associated calibrated dates. b. Main Chamber sequence and associated calibrated dates. Number in stratigraphic columns refers to layer. An asterisk (*) next to the OxA- lab code indicates bone sample and a caret (^) charcoal. Images include the three directly dated human bone fragments (*Denisova 11*, *Denisova 14* and *Denisova 15;* labelled *11*, *14* and *15*, respectively), pendants (P) and bone points (B). Two significantly younger ages for layer 9.3 in the Main Chamber are not shown. *Artefacts and human bones not to scale*.

Figure 2 | Comparison of radiocarbon determinations obtained for the oldest bone points and tooth pendants from Denisova Cave with the two direct ages for the Ust'-Ishim modern human femur[14]. For each measurement, the lab code is indicated and, for the Denisova artefacts, the chamber and stratigraphic context are shown in brackets. Error bars below the probability distributions indicate 68.2 and 95.4% highest posterior density ranges. Marked ages (* and ^) were obtained on the same sample. *Artefacts and human bone not to scale.*

Figure 3 | Stratigraphic sequences for the southeast profiles exposed in the three chambers at Denisova Cave (a) and images of human fossil remains (b). The location of the human remains is denoted by circles and sediment-derived human DNA by a trowel silhouette. Red circle/trowel refers to Denisovans, blue to Neanderthals and grey to *Homo* sp. fossils for which no genetic data exist. Number in circle denotes the fossil number (for example, *Denisova 2*=2). Number in brackets refers to the layer that each of the fossils or human DNA was found. (Further information for each human fossil can be found in Extended Data Fig. 1 and Supplementary Information 3).

Figure 4 | Age estimates for the human fossils from Denisova Cave as determined from Bayesian Model 4, compared against the Marine Oxygen Isotope (MIS) curve from benthic $\delta^{18}O$ records[18] (Extended Data Fig. 6 *and* Supplementary Information 9). The probability distribution for *Denisova 14* is the calibrated radiocarbon age obtained directly for the fossil; it extends beyond the range of the calibration curve hence it is truncated at 50,000 BP. Error bars below the probability distributions indicate 68.2 and 95.4% highest posterior density ranges. Red probabilities: Denisovans; blue: Neanderthals; red-blue: *Denisova 11*, direct offspring of Denisovan and Neanderthal. No genetic data exist for *Denisova 6* and *Denisova 14*, these specimens are attributed only to *Homo* sp. and are shown in grey.

Data availability statement. Raw radiocarbon determinations and associated chemical data, calibrated age ranges, and CQL codes for the Bayesian models are included in Supplementary Information. All MALDI-ToF-MS raw data for the ZooMS analyses are available from the authors upon request. The mtDNA capture data for *Denisova 11*, *Denisova 14* and *Denisova 15* are available in the European Nucleotide Archive under accession PRJEB29061. The mtDNA sequence of *Denisova 15* can be downloaded from GenBank (accession MK033602). All other relevant data are available from the authors or are included in the manuscript (Supplementary Information).

EXTENDED DATA LEGENDS

Extended Data Figure 1 | Human remains from Denisova Cave. Red labels indicate Denisovans, blue Neanderthals, and grey *Homo* sp. bones unassigned to a group. *Denisova 11* is shown in red-blue. *Denisova 13*, mentioned in Supplementary Information 3, is unpublished and is not shown here. a, b: *Denisova 2* in occlusal (a) and lingual (b) views; c: *Denisova 3* in proximal view; d, e: *Denisova 4* in mesial (d) and occlusal (e) views; f, *Denisova 8* in occlusal view; g: *Denisova 9* in palmar view; h, i: µCT based renderings of *Denisova 5* in lateral (h) and plantar (i) views; j, k; *Denisova 15* and *Denisova 11*, l, m: *Denisova 14* and *Denisova 16*, n, o: *Denisova 6* in occlusal (n) and lingual (o) views.

Extended Data Figure 2 | Personal ornaments and bone points from Denisova Cave sampled for radiocarbon dating. N28 was discovered during section cleaning and is not assigned to a specific layer. N282 failed to produce enough collagen and was not dated. N3856/66 was dated twice. Direct dates are listed in Extended Data Table 1.

Extended Data Figure 3 | Proteomic and genetic data for hominin bones discovered using ZooMS. a-d: Collagen fingerprinting MALDI-ToF-MS spectra for *Denisova 11*, *14*, *15 and 16*; e-g: average coverage of the human mitochondrial reference genome for *Denisova 11*, *14*, and *15*. The average coverage of the mitochondrial genome is 2.0-fold for the sequences from *Denisova 14* and 62.7-fold for *Denisova 15*. Low collagen preservation indicated for *Denisova 14* based on its peptides fingerprint correlates well with poor aDNA recovery for the same specimen.

Extended Data Figure 4 | Inferred number of substitutions occurring on branches leading to the mtDNA genomes of Denisovan and Neanderthal individuals since their split from the common ancestor shared with other archaic individuals. DS and NS refer to Denisovan and Neanderthal split age estimates used in the Bayesian models to enable numerical calculation of the split times of the various points on this tree. Individuals from Denisova Cave are emphasized in bold. a: Denisovan mtDNA genomes; data taken from ref. 7. b; Neanderthal mtDNA genomes. Those used in this analysis are reported in Supplementary Table S6.

Extended Data Figure 5 | Bayesian age models (Models 1–2). Modelling details are given in Supplementary Information 9.

Extended Data Figure 6 | Bayesian age models (Models 3–4). Model 4 contains most prior information and yielded very high agreement index. We use this model to calculate and report the ages of the human fossils (Extended Data Table 2). Modelling details are given in Supplementary Information 9.

Extended Data Figure 7 | Comparison of hominin age estimates based on different types of data. Models 1-4 include stratigraphic information, mitochondrial mutation rates, radiocarbon dates and 11 optical ages, and are described in Supplementary Information 9. The green bars show hominin ages derived from an optical age-only model (not presented here) that included all data reported in ref.10. The red bars show schematic age ranges estimated using both mitochondrial and nuclear data. All ages are at 95.4% probability.

Extended Data Table 1 | New radiocarbon results from Denisova Cave. OxA- is the Oxford radiocarbon lab code, P-code denotes the pretreatment method and dated material (AG is gelatinised bone collagen without ultrafiltration; AF is ultrafiltered bone collagen; HYP is the single amino acid, hydroxyproline; ZR, XR and YR refer to ABA, ABOx-SC or AOx-SC methods, respectively, for charcoal samples). Samples highlighted in grey denote samples that produced more than one radiocarbon determination using different pretreatment methods.

Extended Data Table 2 | Comparison of modelled age estimates for human fossils obtained from Bayesian models 1–4, in thousand years ago (=kyr). The agreement index for each model is shown in the second row. All age ranges are at 95.4% probability. The ages listed for *Denisova 14* is the direct radiocarbon age and not a modelled estimate.