

Revised age of late Neanderthal occupation and the end of the Middle Paleolithic in the northern Caucasus

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Advances in direct radiocarbon dating of Neanderthal and anatomically modern human (AMH) fossils and the development of archaeostratigraphic chronologies now allow refined regional models for Neanderthal–AMH coexistence. In addition, they allow us to explore the issue of late Neanderthal survival in regions of Western Eurasia located within early routes of AMH expansion such as the Caucasus. Here we report the direct radiocarbon (¹⁴C) dating of a late Neanderthal specimen from a Late Middle Paleolithic (LMP) layer in Mezmaiskaya Cave, northern Caucasus. Additionally, we provide a more accurate chronology for the timing of Neanderthal extinction in the region through a robust series of 16 ultrafiltered bone collagen radiocarbon dates from LMP layers and using Bayesian modeling to produce a boundary probability distribution function corresponding to the end of the LMP at Mezmaiskaya. The direct date of the fossil (39,700 ± 1,100 ¹⁴C BP) is in good agreement with the probability distribution function, indicating at a high level of probability that Neanderthals did not survive at Mezmaiskaya Cave after 39 ka cal BP ("calendrical" age in kiloannum before present, based on IntCal09 calibration curve). This challenges previous claims for late Neanderthal survival in the northern Caucasus. We see striking and largely synchronous chronometric similarities between the Bayesian age modeling for the end of the LMP at Mezmaiskaya and chronometric data from Ortvale Klde for the end of the LMP in the southern Caucasus. Our results confirm the lack of reliably dated Neanderthal fossils younger than ~40 ka cal BP in any other region of Western Eurasia, including the Caucasus.

ultrafiltration | admixture

Recent paleogenetic studies have contributed enormously to our growing understanding of the Neanderthals and have extended our knowledge regarding this hominin's eastern geographic range (1). They have also provided clear indications that the split between anatomically modern humans (AMHs) and Neanderthals occurred ~500,000 y ago (2), and shown no sign of introgression of modern genes into the Neanderthal sequence (3). Analysis of the first Neanderthal draft genome further suggests that Neanderthals made a detectable but limited genetic contribution (1–4%) to the ancestry of modern humans and that this contribution likely occurred outside Africa, in the Middle East, before AMH expansions into Europe and Asia (4). These intriguing results highlight the acute need for revised regional chronologies of late Neanderthal survival and extinction across Eurasia that is based on the direct dating of hominin fossils as a means to assess the nature and timing of major demographic dispersals, Neanderthal extinctions, and admixture across Western Eurasia. They also stress the need to focus on the chronology of the latest Neanderthal survival and extinction events in regions located within early routes of AMH expansion, such as the Caucasus.

In the last decade, archaeological research has focused on the development of high-resolution Late Middle Paleolithic (LMP) and Initial/Early Upper Paleolithic (IUP/EUP) chronologies for regions of Western Eurasia (e.g., 5) in which the late Neanderthals and early AMHs may have coexisted. However, the archaeological and fossil records indicate that the relationship between material

culture and biology is more complex than traditionally assumed. Revised, improved, and corrected regional LMP and EUP chronologies are required to assess any possible associations between Neanderthal extinctions, AMH dispersals, and climatic events (6). Before bone pretreatment by ultrafiltration (7) and charcoal pretreatment by acid–base oxidation/stepped combustion (8), radiocarbon (¹⁴C) ages appear to have systematically underestimated the true age of LMP and EUP deposits, artifacts, and fossils by up to several thousand years (5, 9). This resulted in a "coexistence effect" (10) that gave the impression of a significant temporal overlap between late Neanderthals and AMHs in certain regions that is not supported by lithostratigraphic data.

Direct ¹⁴C dating of Neanderthals and AMH fossils (5, 11–17) is of vital importance to the study of the Middle to Upper Paleolithic (MP–UP) transition/replacement events in Eurasia. Such dating projects can clarify and often reject presumed associations between specific hominin fossils and LMP and EUP archaeological contexts, provide reliable chronological frameworks for the calibration of molecular clocks and phylogenetic simulations, and allow the derivation of more accurate estimates of the timing and duration of Neanderthal extinction and AMH establishment in Eurasia. There are, at present, direct ¹⁴C dates of Neanderthal fossils from seven Eurasian sites (from east to west): Okladnikov (Russia), Mezmaiskaya (Russia), Vindija (Croatia), Kleine Feldhofer (Germany), Spy (Belgium), Les Rochers-de-Villeneuve (France), and El Sidrón (Spain). Of these, two dates from Okladnikov, four dates from Mezmaiskaya, seven dates from Vindija, and six dates from Spy are younger than 36 ka ¹⁴C BP and hence suggest the possibility of late Neanderthal survival (5). However, only the extraction protocols of two of the Vindija dates (OxA-X-2089-06 and OxA-X-2094-10) (12), two of the Okladnikov dates, and three of the Spy dates (13), involved the ultrafiltration or similarly rigorous pretreatment step (see below). The redating of fossils using improved chronometric methods has drastically altered current interpretations regarding late Neanderthal survival/extinction and their possible interactions with AMHs. This paper reports chronometric data from Mezmaiskaya Cave of well-provenanced LMP faunal and human fossil material in an attempt to provide high-resolution temporal data on the termination of Middle Paleolithic occupation and Neanderthal extinction and the establishment of AMH populations in the Caucasus.

Mezmaiskaya Cave is located 1,310 m above sea level in the Azish-Tau karst ridge in the northwestern Caucasus (18, 19). Since 1987, about 80 m² have been carefully excavated to a maximum depth of 5 m, yielding thousands of lithic and organic artifacts and a rich faunal assemblage. Currently, the stratigraphic

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sequence of the cave consists of 3 Holocene and 20 Pleistocene strata. The Holocene layers, 1-1, 1-2, and 1-2A, are underlain by eight stratified Upper Paleolithic layers (from top to bottom): 1-3, 1-4, 1A-1, 1A-2, 1A-3, 1B-1, 1B-2, and 1C, beneath which is found stratum 1D, lying at the MP-UP transition and containing no archaeological finds or bones. The Middle Paleolithic sequence consists of seven layers (from top to bottom): 2, 2A, 2B-1, 2B-2, 2B-3, 2B-4, and 3. The lowest Pleistocene layers (4–7) contain no archaeological material. The Pleistocene strata are most completely preserved toward the interior of the cave. Near the cave entrance, heterogeneous erosive processes have destroyed Upper Paleolithic strata, and the Holocene layers unconformably overlie the Middle Paleolithic deposits.

Previous accelerator mass spectrometry (AMS) radiometric data from Mezmaiskaya Cave estimated the onset of the EUP in layer 1C and the end of the LMP in layer 2 at ~33 ka ¹⁴C BP (6). There is some chronological overlap among previously published AMS dates for layers 1C and 2, and a comparison of radiocarbon and electron spin resonance (ESR) dates (20) from levels 2B-4 and 2 shows that there is agreement between the two methods once calibrated against the same timescale. At present, the only comparable chronometric and archaeological sequence in the Caucasus is found at Ortvale Klde (Georgian Republic), in the southern Caucasus (21). The MP-UP chronology in Mezmaiskaya combining AMS dates (for EUP layers) and ESR dates (for Middle Paleolithic layers) is in broad agreement with the MP-UP chronology (combined from thermoluminescence and AMS estimates) in Ortvale Klde in the southern Caucasus. In this paper, we report the direct radiocarbon (¹⁴C) dating of the Mez 2 Neanderthal specimen from Mezmaiskaya Cave, the stratigraphically youngest known Neanderthal fossil from the Caucasus. Additionally, we provide a more accurate chronology of the timing of Neanderthal extinction in the region revealed by a robust series of ultrafiltration radiocarbon dates and analyzed using a modeled Bayesian sequence focusing on the latest Middle Paleolithic layers. This was generated with the IntCal09 (22) calibration dataset and OxCal 4.1 software (23).

Two Neanderthal fossil specimens were discovered at Mezmaiskaya during excavations: The skeleton of a Neanderthal neonate (Mez 1) was recovered in anatomical position in the lowermost 3–5 cm of layer 3, the oldest Middle Paleolithic layer,

and 24 cranial fragments of an infant (Mez 2, 1–2 y of age) were recovered from a pit that originates in layer 2, the youngest Middle Paleolithic layer, and penetrates into Middle Paleolithic layers 2A, 2B-1, and 2B-2 (4, 19, 24). A rib fragment of Mez 1 was directly ¹⁴C-dated to 29,195 ± 965 ¹⁴C BP (Ua-14512) (25). Whereas some scholars (26, 27) have accepted this sole estimate as proof of late Neanderthal survival in the Caucasus, additional research has shown that the ¹⁴C age estimate of Mez 1 is not in agreement with a robust series of independent ¹⁴C and ESR chronometric dates of associated archaeological materials and stratigraphic sequence at the site (6, 20, 24). Because the Mez 2 cranial fragments (layer 2) are stratigraphically overlying the Mez 1 infant (layer 3), Mez 2 can be significantly younger than Mez 1, perhaps in line with the age ~40 ka BP suggested for layer 2 on the basis of ESR dating (28). Without the direct dating of the Mez 2 specimen, this claim cannot be assessed objectively.

Results

The direct dating of the stratigraphically youngest Neanderthal specimen in the Caucasus (Mez 2 infant, top of the Middle Paleolithic sequence, layer 2) produced a result on ultrafiltered collagen extracted from the bone of 39,700 ± 1,100 ¹⁴C BP (Table 1), which we calibrated to 42,960–44,600 cal BP (68.2%) and 42,300–45,600 cal BP (95.4%) (Table S1). The Mez 2 specimen was very well preserved, and yielded 14.6% collagen by weight (in modern unadulterated bone, ~20% by weight is collagen) and the C:N atomic ratio was 3.2 (in modern bone, this should be 3.21). Therefore, there is no reason to doubt the accuracy of this result given the preservation state of the specimen, and the direct date of Mez 2 confirms that the younger date for the Mez 1 specimen (layer 3) is a significant underestimate.

A total of 26 AMS determinations dated at the Oxford Radiocarbon Accelerator Unit (ORAU) were obtained from humanly modified cut-marked bones from Middle Paleolithic and Upper Paleolithic layers of the cave, and were combined with previous radiometric determinations into a Bayesian model. The radiocarbon ages we obtained from the Upper Paleolithic levels at Mezmaiskaya (Table S2) are more variable than the previous AMS estimates for Upper Paleolithic layers, and two of our results (OxA-21818 and OxA-21819) are significantly younger compared with all other dates and the site stratigraphy.

Table 1. AMS determinations from Mezmaiskaya measured at the ORAU

Layer	OxA	Date	±	Material	Weight used	Yield	%yield	%C	δ ¹³ C (‰)	C:N
2	21836	36,200	750	Bone, unidentified	920	29.04	3.2	41.8	-19.0	3.3
2	21826*	38,200	900	Bone, unidentified	710	37.85	5.3	44.6	-19.2	3.2
2	21827*	38,200	1,000	Bone, unidentified	810	51.62	6.4	41.1	-19.1	3.2
2	21839	39,700	1,100	Mez 2 infant	740	108.3	14.6	44.1	-17.4	3.2
2	21824	40,200	1,200	Bone, unidentified	700	17.48	2.5	42.9	-19.0	3.4
2	21825	44,500	2,000	Bone, unidentified	640	25.91	4	41.2	-19.4	3.2
2	21823	47,200	2,800	Bone, unidentified	650	33.94	5.2	41.3	-19.6	3.2
2	21822	>46,200	—	Bone, unidentified	596	6.2	1	40.4	-19.6	3.2
2A	21829	41,500	1,400	Bone, unidentified	556	6.4	1.2	41.7	-19.6	3.2
2A	21828	>46,100	—	Bone, unidentified	547	16.54	3	42.4	-19.3	3.3
2B-2	21830	>44,400	—	Bone, unidentified	534	8.96	1.7	40.8	-18.7	3.2
2B-3	21831	48,400	3,200	Bone, unidentified	655	34.23	5.2	41.4	-19.1	3.2
2B-3	21832	>44,700	—	Bone, unidentified	532	9.48	1.8	41.4	-19.1	3.2
2B-4	21833	>46,500	—	Bone, unidentified	541	6.29	1.2	40.2	-19.9	3.2
3	21834	>45,200	—	Bone, unidentified	618.4	17.93	2.9	40.3	-20.0	3.2
3	21835	>46,100	—	Bone, unidentified	527.1	5.98	1.1	40.3	-19.8	3.2

All are ultrafiltered gelatin samples. Stable isotope ratios are expressed in ‰ relative to Vienna Pee-Dee Belemnite. Mass spectrometric precision is ±0.2‰ for carbon. Weight used is the amount of bone pretreated, and the yield represents the weight of gelatin or ultrafiltered gelatin in milligrams. %yield is the wt% collagen, which should not be <1 wt% at the ORAU. This is the amount of collagen extracted as a percentage of the starting weight. %C is the carbon present in the combusted gelatin. For ultrafiltered gelatin this averages 41.0 ± 2%. C:N is the atomic ratio of carbon to nitrogen. At the ORAU this is acceptable if it ranges between 2.9 and 3.5.

*Duplicate samples.

Further work is required to investigate the variations in the ages, and we therefore limit our present analyses to the modeling of the Middle Paleolithic layers to examine the age of the latest Middle Paleolithic occupation. A note of caution is required regarding the calibration and Bayesian modeling of dates close to the maximum range of radiocarbon dating (and the limit of the IntCal09 curve) or extending out of the range. The majority of our ^{14}C results for the lower Middle Paleolithic levels in Mezmaiskaya are “greater-than” ages and therefore are consistent with the ESR chronology for these levels (28), which suggests ages in the range from 57 ± 4 y modeled to 68 ± 5 y modeled. This is beyond the radiocarbon limit, and is reflected in the predominance of greater-than or near-background limit ages for the lower Middle Paleolithic layers 2B-3, 2B-4, and 3.

There is variability in the sequence of ^{14}C determinations throughout the site; for example, in layer 3, the determination Ua-14512 ($29,195 \pm 965$ BP) co-occurs with two determinations of >45.2 and >46.1 ka BP. One explanation could be that the difference is due to contamination for the former and improved pretreatment chemistry for the latter measurements (7, 29). Material dated from several sites shows that ultrafiltration is a more effective method for removing low-level contaminants than other methods, such as the Longin collagen (gelatinization) method, and therefore we place more weight on these determinations.

It is possible to quantify anomalous or outlying data with respect to stratigraphy using a probabilistic Bayesian modeling approach. The Bayesian approach allows archaeological information to be included within an age model alongside the ^{14}C likelihood data (e.g., 30, 31). The so-called prior archaeological information, when incorporated mathematically with the ^{14}C likelihoods (or calibrated probability distributions) and analyzed using Markov chain Monte Carlo simulation techniques, results in a new probability distribution termed the *posterior*. The fit of individual ^{14}C likelihoods within the models was tested using an outlier detection approach (32). This was applied to enable an objective assessment of the probability associated with individual measurements being demonstrable outliers. We used a *t*-type outlier model and a probability of $P < 0.05$ for each value in the first iterations of the model. This type of model is suitable where a proportion of the samples might be expected to be out of context given possible cryoturbation/depositional influences (32).

Different models were tested to assess the sensitivity of the posterior results to both the priors and likelihood information. ESR determinations from layer 2, as well as radiocarbon determinations from the same horizon, were included within initial models. Due to wide variations in the Upper Paleolithic layers, as mentioned above, and the greater-than ages of much of the material from the lower levels, only layer 2 itself was modeled finally, as a single phase of activity. First, we modeled only the Oxford determinations from layer 2 (termed model 1). Second, we modeled the Oxford results along with ESR [early uptake (EU) and linear uptake (LU)] determinations from layer 2 published by Skinner et al. (20) (model 2). We tested models with both EU and LU determinations included; there was virtually no difference between them. According to Skinner et al. (20), the ages do not depend significantly on which uptake model is adopted, and they produce closely similar results within measurement errors. Finally, we modeled all of the available AMS and conventional radiocarbon ages along with the ESR LU determination (model 3) (Fig. S1). The results show that there are no measurable outliers in any of the models except LE-4735 in model 3, which produced a posterior outlier probability of 58%, suggesting it is too young. The results also showed that the probability distribution function (PDF) for the end of layer 2, which is the PDF for the end of the Middle Paleolithic at Mezmaiskaya, varies with respect to the model and the likelihoods’ input to it. For model 1, the PDF is 42,040–39,640 BP (at 68.3% probability) and 42,730–36,530 BP (at 95.3% probability). For the

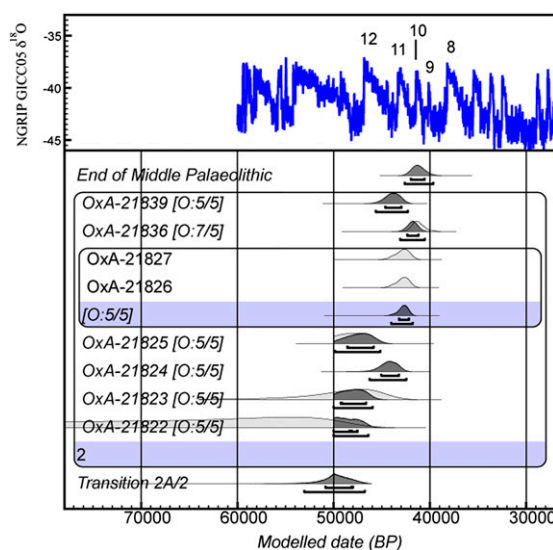


Fig. 1. Bayesian model for the ^{14}C dates from layer 2, the penultimate Middle Paleolithic context, at Mezmaiskaya. The model is based on the assumption that the determinations derive from a single phase of occupation, with the only constraint being the fact that determinations from layer 1C (not shown) are later than this phase. This model was generated using OxCal 4.1 and the new IntCal09 calibration curve (22). Lighter-shaded distributions are calibrated ^{14}C likelihoods, and the darker-outline distributions are posterior probabilities after Bayesian modeling. Outlier posterior and prior probabilities are given in brackets next to the OxA numbers. The data are compared against the North Greenland Ice core Project (NGRIP) $\delta^{18}\text{O}$ ice-core record of Svensson et al. (41) and Andersen et al. (42). See *SI Methods* for a fuller discussion of sensitivity testing of this model.

second model, the result is 41,790–38,730 BP (68.3%) and 42,430–35,580 BP (95.4%), and for the third the result is 38,020–34,920 BP (68.1%) and 39,160–31,810 BP (95.4%) (Fig. S2). The first model, based only on the Oxford determinations, therefore produces markedly older results for this boundary.

The sensitivity of the models to the inclusion of determinations that are close to, or beyond, the radiocarbon calibration limit was tested by setting the prior outlier probability of OxA-21822 and OxA-21823 to 1.00, meaning they are 100% likely to be outliers and therefore not included a posteriori. The results

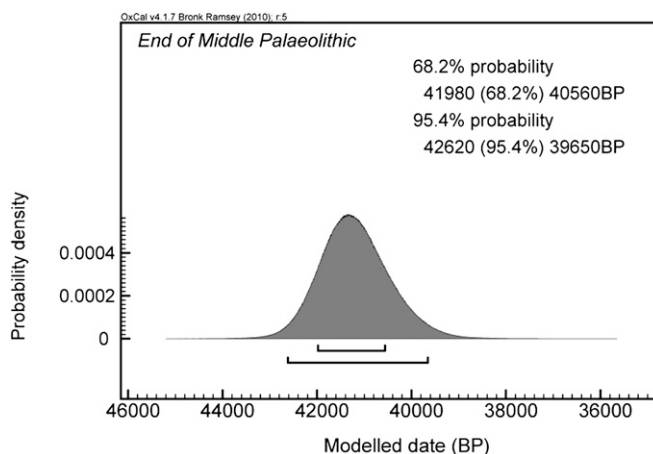


Fig. 2. Probability distribution (calibrated) for the end boundary of layer 2 at Mezmaiskaya. This distribution represents the end of the Middle Paleolithic at the site and suggests that Neanderthals were not present after $\sim 39,500$ cal BP at the site.

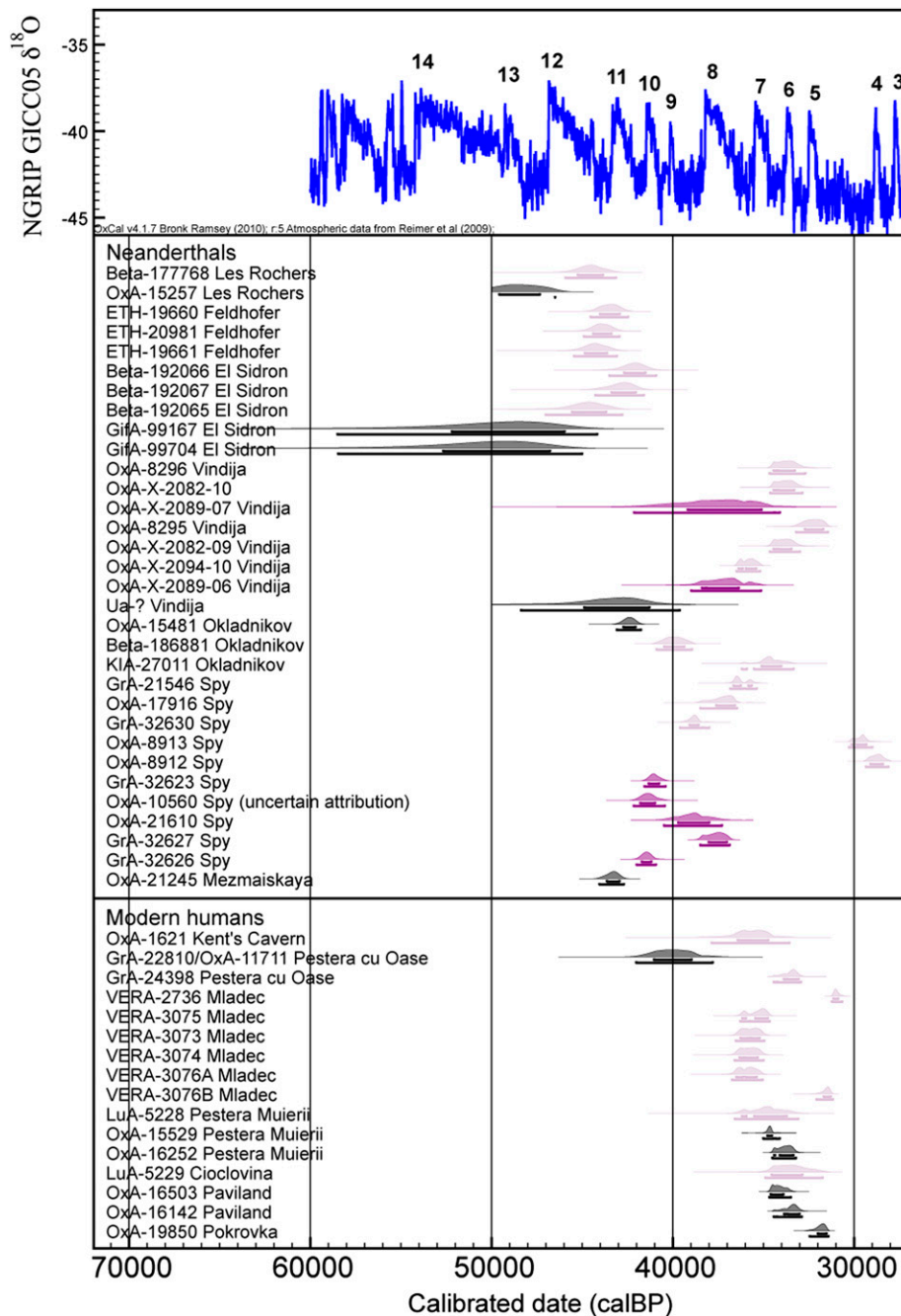


Fig. 3. Direct ^{14}C dates of AMH and Neanderthal fossils. The data are plotted against the new IntCal09 calibration curve (22) and compared with the NGRIP $\delta^{18}\text{O}$ ice-core record of Svensson et al. (41) and Andersen et al. (42). Numbers indicate Greenland interstadials. Calibrated probability distributions shown in light mauve are considered problematic. These include determinations now known to be underestimates of the “true” age [e.g., Kent’s Cavern (38)], those which have been remeasured using improved preparative techniques shown to be more reliable (12), or those that are repeat dates of the same bone which are unrealistically young (7) (see also ref. 5 for further discussion). Results in dark purple are considered likely minimum ages. All others are in black and considered acceptable. The Kent’s Cavern specimen originally identified as AMH is now being reanalyzed, but for the time being we include it in the AMH group. Its likely age is between 35 and 37 ka BP (38).

showed that the models are not sensitive to their inclusion: The PDFs for the end of the Middle Paleolithic were the same regardless. Constraints were also added to the models by including the radiocarbon likelihoods from layer 1C in the form of a succeeding unordered phase. This reduced the wide variation in the critical Middle Paleolithic boundary PDF between the models run, due to the influence of the constraints provided by this later modeled phase. Under these constraints, model 1 (only the Oxford determinations) provided a PDF for the final Middle Paleolithic

boundary of 41,980–40,560 BP (68.2%) and 42,620–39,650 BP (95.4%). Model 2 (Oxford determinations along with the ESR LU determination) gave 41,790–40,340 BP (68.2%) and 42,410–39,440 BP (95.4%), and finally model 3 (all radiocarbon determinations and the ESR LU determination) yielded 41,140–39,330 BP (68.2%) and 41,890–38,240 BP (95.4%). These three PDFs are plotted in Fig. S1. We favor model 1 of the three, followed by model 2, because the radiocarbon determinations for model 1 were obtained using the more rigorous ultrafiltration preparative

technique, whereas model 3 contains determinations produced using less-refined methods. Models 1 and 2 produce virtually identical posterior results, and their PDFs overlap significantly.

The results enable a boundary PDF corresponding to the end of the LMP at Mezmaiskaya to be determined. For our favored model (model 1), this distribution ranges from 41,980 to 40,560 BP (68.2%) and 42,620 to 39,650 BP (95.4%) (Figs. 1 and 2). This implies a very high probability that Neanderthals did not survive at Mezmaiskaya after 39 ka cal BP ("calendrical" age in kiloyears before present, based on IntCal09 calibration curve) and allows us to reject claims for their late survival at this site (25) and in the wider northern Caucasus.

Discussion

Although Neanderthal fossils from the southern Caucasus have yet to be dated directly, the chronometric data from Ortvale Klde have suggested that the demise of the last Neanderthals and the establishment of modern human populations in the region took place ~38–34 ka ¹⁴C BP [42–39 ka cal BP_{Hulu} (calibration curve based on the Chinese Hulu Cave speleothem records)] (21). We interpret the striking similarities between the EUP lithic and organic technologies at both Mezmaiskaya Cave and Ortvale Klde (6, 18, 33), and the chronometric similarities between the two sites (21, 34), as compelling evidence for the regional demographic demise of the Neanderthals, followed closely in time (given the precision of AMS) by the range expansion of AMHs into the Caucasus. Although it is not currently possible to determine how or whether these two demographic processes are linked, our research highlights the need to carefully reassess existing AMS records based on modern pretreatment techniques and directly dated hominin specimens from secure stratigraphic and archaeological contexts, and consider the importance of regional chronologies when building demographic models for geographically widespread hominin species.

The critical reanalysis of directly dated Neanderthal and AMH fossils from across Eurasia, taking into consideration pretreatment histories and redating results (5), supports our findings in the Caucasus and highlights the lack of reliably dated Neanderthal fossils younger than ~40 ka cal BP (Fig. 3). Contrary to traditional arguments for up to 10,000 y of coexistence, these data suggest that Neanderthal extinction across Western Eurasia, including the Caucasus, was probably a rapid process, and that coexistence with AMHs, when it occurred, may have been of limited duration. The recent draft sequence of the Neanderthal genome (4) indicates only a minor genetic contribution (between 1 and 4%) of Neanderthals to the genetic structure of modern Eurasian populations, and that this contribution occurred before the divergence of modern Europeans, East Asians, and Papuans, possibly in the Middle East, before AMH expansion into Europe.

Our data are in agreement with the genetic results, as they cast doubts about the possibility of any long-term interactions and coexistence between Neanderthals and AMHs for any region of Western Eurasia, including the Caucasus.

Methods

Radiocarbon dating was undertaken at the ORAU, University of Oxford, using AMS. Collagen was extracted using the methods outlined by Bronk Ramsey et al. (35), Higham et al. (7), and Brock et al. (36). All collagen was obtained using a final ultrafiltration step after Brown et al. (37). This method has been shown to improve the reliability of the ages obtained by more effectively removing low-molecular weight contaminants (7, 37, 38). Radiocarbon ages are given as conventional ages BP after Stuiver and Polach (39). The ¹⁴C ages have been corrected for laboratory pretreatment background using a bone-specific background correction (40). Bones that were analyzed range from very well preserved (a maximum of 14.9 wt% collagen) to poorly preserved (a minimum of 1.0 wt% collagen). The C:N atomic ratios ranged from 3.2 to 3.4, a range entirely consistent with that accepted at the ORAU (2.9–3.5) and consistent with modern collagen ratios. All other analytical parameters measured were within accepted ranges. One sample was dated twice as a check on reproducibility. Two subsamples were treated from the start of the chemical preparative sequence, and disclosed acceptable agreement (OxA-21826 and OxA-21827) (Table 1). This provides further evidence for the good reproducibility of these series of ages.

A note of caution is required regarding the calibration of ages close to the maximum dating limit of the measuring laboratory, the limit of the IntCal09 curve, and similarly to the curve itself, which is unlikely to be the final iteration. At its older end, the current curve is based on marine records rather than being terrestrially based, and this therefore embraces a degree of uncertainty. We use this curve in the interim, recognizing that updated records may require us to undertake further modeling work.

The ORAU maximum age (T_{max}) for the dating of extracted bone collagen was recalculated in early 2010 to 49,900 BP, or 0.002 fM (fraction modern). Several determinations we obtained reach or exceed this limit (Table 1). When the measured sample activity ($F^{14}C$) after correction for AMS, combustion, and graphitization blanks is less than twice its SD, or produces ranges including negative fM values, the ages are conventionally reported as greater-than ages (39).

When $F^{14}C < 2\sigma(F^{14}C)$, we recalculate the age such that $F^{14}C = F^{14}C + 2\sigma(F^{14}C)$ using $T > -8033 \ln F^{14}C$ (where T is the measured greater-than age in years BP). This is given in the form >45,000 or >48,000 BP (see Table 1). This means that the actual age is at least this old, and could well be much older.

When the ages determined for levels 2B-3, 2B-4, and 3 are considered, the majority are either greater-than ages or very close to the effective measurement limit. This fits well with ESR determinations published from the site by Skinner et al. (20), who showed that layer 3 dated to ~64–68 ka BP, whereas 2B-3 and 2B-4 were dated to ~55–70 ka BP, depending on whether LU or EU models were adopted in the age calculation. This attests that the age of these levels is greater than ~50 ka BP.

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- Krause J, et al. (2007) Neanderthals in central Asia and Siberia. *Nature* 449:902–904.
- Green RE, et al. (2006) Analysis of one million base pairs of Neanderthal DNA. *Nature* 444:330–336.
- Pennisi E (2009) Neanderthal genomics. Tales of a prehistoric human genome. *Science* 323:866–871.
- Green RE, et al. (2010) A draft sequence of the Neanderthal genome. *Science* 328:710–722.
- Jöris O, Street M (2008) At the end of the ¹⁴C time scale—The Middle to Upper Paleolithic record of Western Eurasia. *J Hum Evol* 55:782–802.
- Golovanova LV, et al. (2010) Significance of ecological factors in the Middle to Upper Paleolithic transition. *Curr Anthropol* 51:655–691.
- Higham TFG, Jacobi RM, Bronk Ramsey C (2006) AMS radiocarbon dating of ancient bone using ultrafiltration. *Radiocarbon* 48:179–195.
- Bird MI, et al. (1999) Radiocarbon dating of 'old' charcoal using a wet oxidation-stepped combustion procedure. *Radiocarbon* 41:127–140.
- Higham T, et al. (2009) Problems with radiocarbon dating the Middle to Upper Palaeolithic transition in Italy. *Quat Sci Rev* 28:1257–1267.
- Conard NJ, Bolus M (2003) Radiocarbon dating the appearance of modern humans and timing of cultural innovations in Europe: New results and new challenges. *J Hum Evol* 44:331–371.
- Conard NJ, Grootes PM, Smith FH (2004) Unexpectedly recent dates for human remains from Vogelherd. *Nature* 430:198–201.
- Higham T, Ramsey CB, Karavanić I, Smith FH, Trinkaus E (2006) Revised direct radiocarbon dating of the Vindija G1 Upper Paleolithic Neanderthals. *Proc Natl Acad Sci USA* 103:553–557.
- Semal P, et al. (2009) New data on the late Neanderthals: Direct dating of the Belgian Spy fossils. *Am J Phys Anthropol* 138:421–428.
- Svoboda JJ, Van der Plicht J, Kuželka V (2002) Upper Palaeolithic and Mesolithic human fossils from Moravia and Bohemia (Czech Republic): Some new C14 dates. *Antiquity* 76:957–962.
- Svoboda JJ, Van der Plicht J, Kuželka V, Vlček E (2004) New radiocarbon datings of human fossils from caves and rockshelters in Bohemia (Czech Republic). *Anthropologie (Brno)* 42:161–166.
- Tillier AM, Mester Z, Bocherens H, Henry-Gambier D, Pap I (2009) Direct dating of the "Gravettian" Balla child's skeleton from Bükk Mountains (Hungary): Unexpected results. *J Hum Evol* 56:209–212.
- Wild EM, et al. (2005) Direct dating of Early Upper Palaeolithic human remains from Mladec. *Nature* 435:332–335.
- Golovanova LV, et al. (2006) The Early Upper Paleolithic in the Northern Caucasus (new data from Mezmaiskaya Cave, 1997). *Eurasian Prehistory* 4:43–78.
- Golovanova LV, Hoffercker JF, Kharitonov VM, Romanova GP (1999) Mezmaiskaya Cave: Neanderthal occupation in the northern Caucasus. *Curr Anthropol* 40:77–86.
- Skinner AR, et al. (2005) ESR dating at Mezmaiskaya Cave, Russia. *Appl Radiat Isot* 62: 219–224.

21. Adler DS, et al. (2008) Dating the demise: Neanderthal extinction and the establishment of modern humans in the southern Caucasus. *J Hum Evol* 55:817–833.
22. Reimer PJ, et al. (2009) IntCal09 and Marine09 radiocarbon age calibration curves, 0–50,000 years cal BP. *Radiocarbon* 51:1111–1150.
23. Bronk Ramsay C (2009) Bayesian analysis of radiocarbon dates. *Radiocarbon* 51:337–360.
24. Ponce de León MS, et al. (2008) Neanderthal brain size at birth provides insights into the evolution of human life history. *Proc Natl Acad Sci USA* 105:13764–13768.
25. Ovchinnikov IV, et al. (2000) Molecular analysis of Neanderthal DNA from the northern Caucasus. *Nature* 404:490–493.
26. Delson E, Harvati K (2006) Palaeoanthropology: Return of the last Neanderthal. *Nature* 443:762–763.
27. Finlayson C, et al. (2006) Late survival of Neanderthals at the southernmost extreme of Europe. *Nature* 443:850–853.
28. Blackwell BAB, et al. (2009) ESR dating at hominid and archaeological sites during the Pleistocene. *Sourcebook of Paleolithic Transitions*, eds Camps M, Chauhan P (Springer, New York), pp 93–119.
29. Higham TFG (2011) European Middle and Upper Palaeolithic radiocarbon dates are often older than they look: Problems with previous dates and some remedies. *Antiquity* 85:235–249.
30. Buck CE, Cavanagh WG, Litton CD (1996) *Bayesian Approach to Interpreting Archaeological Data* (Wiley, Chichester, UK).
31. Bronk Ramsay C (1998) Probability and dating. *Radiocarbon* 40:461–474.
32. Bronk Ramsay C (2009) Dealing with outliers and offsets in radiocarbon dating. *Radiocarbon* 51:1023–1045.
33. Bar-Yosef O, Belfer-Cohen A, Adler DS (2006) The implications of the Middle-Upper Paleolithic chronological boundary in the Caucasus to Eurasian prehistory. *Anthropologie (Brno)* 44:81–92.
34. Golovanova LV, Doronichev VB, Cleghorn NE (2010) The emergence of bone-working and ornamental art in the Caucasian Upper Palaeolithic. *Antiquity* 84:299–320.
35. Bronk Ramsey C, Higham TFG, Bowles A, Hedges REM (2004) Improvements to the pretreatment of bone at Oxford. *Radiocarbon* 46:155–163.
36. Brock F, Ramsey CB, Higham T (2007) Quality assurance of ultrafiltered bone dating. *Radiocarbon* 49:187–192.
37. Brown TA, Nelson DE, Vogel JS, Southon JR (1988) Improved collagen extraction by modified Longin method. *Radiocarbon* 30:171–177.
38. Jacobi RM, Higham TFG, Bronk Ramsey C (2006) AMS radiocarbon dating of Middle and Upper Palaeolithic bone in the British Isles: Improved reliability using ultrafiltration. *J Quarter Sci* 21:557–573.
39. Stuiver M, Polach H (1977) Discussion: Reporting of ^{14}C data. *Radiocarbon* 19:355–363.
40. Wood RE, Bronk Ramsey C, Higham TFG (2010) Refining the ultrafiltration bone pretreatment background for radiocarbon dating at ORAU. *Radiocarbon* 52:600–611.
41. Svensson A, et al. (2006) The Greenland ice core chronology 2005, 15–42 ka. Part 2: Comparison to other records. *Quat Sci Rev* 25:3258–3267.
42. Andersen KK, et al. (2006) The Greenland ice core chronology 2005, 15–42 ka. Part 1: Constructing the time scale. *Quat Sci Rev* 25:3246–3257.