New chronology for Ksâr 'Akil (Lebanon) supports Levantine route of modern human dispersal into Europe

Marjolein D. Bosch[a,1], Marcello A. Mannino[a], Amy L. Prendergast[b], Tamsin C. O'Connell[c], Beatrice Demarchi[d], Sheila M. Taylor[e], Laura Niven[a], Johannes van der Plicht[f,g], and Jean-Jacques Hublin[a]

[a]Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, D-04103 Leipzig, Germany; [b]Institute of Geosciences, Applied and Analytical Palaeontology, University of Mainz, D-55128 Mainz, Germany; [c]Department of Archaeology and Anthropology, University of Cambridge, Cambridge CB2 3DZ, United Kingdom; [d]BioArCh, Department of Archaeology, University of York, York YO10 5DD, United Kingdom; [e]Department of Chemistry, University of York, York YO10 5DD, United Kingdom; [f]Center for Isotope Research, Groningen University, 9747 AG Groningen, The Netherlands; and [g]Faculty of Archaeology, Leiden University, 2333 CC Leiden, The Netherlands

Edited by Gilbert Tostevin, University of Minnesota, Minneapolis, MN, and accepted by the Editorial Board April 30, 2015 (received for review January 23, 2015)

Modern human dispersal into Europe is thought to have occurred with the start of the Upper Paleolithic around 50,000–40,000 y ago. The Levantine corridor hypothesis suggests that modern humans from Africa spread into Europe via the Levant. Ksâr 'Akil (Lebanon), with its deeply stratified Initial (IUP) and Early (EUP) Upper Paleolithic sequence containing modern human remains, has played an important part in the debate. The latest chronology for the site, based on AMS radiocarbon dates of shell ornaments, suggests that the appearance of the Levantine IUP is later than the start of the first Upper Paleolithic in Europe, thus questioning the Levantine corridor hypothesis. Here we report a series of AMS radiocarbon dates on the marine gastropod *Phorcus turbinatus* associated with modern human remains and IUP and EUP stone tools from Ksâr 'Akil. Our results, supported by an evaluation of individual sample integrity, place the EUP layer containing the skeleton known as "Egbert" between 43,200 and 42,900 cal B.P. and the IUP-associated modern human maxilla known as "Ethelruda" before ∼45,900 cal B.P. This chronology is in line with those of other Levantine IUP and EUP sites and demonstrates that the presence of modern humans associated with Upper Paleolithic toolkits in the Levant predates all modern human fossils from Europe. The age of the IUP-associated Ethelruda fossil is significant for the spread of modern humans carrying the IUP into Europe and suggests a rapid initial colonization of Europe by our species.

modern human dispersal | Upper Paleolithic | Near East | chronology | zooarcheology

Fossil and genetic evidence suggest that anatomically modern humans (AMH) originated in Africa and colonized Europe between at least 50,000–40,000 calendar years ago (cal B.P.; i.e., calendar years relative to AD 1950) (1–6). The modern human fossil record for this time period is limited to only a few remains, including those found at Ksâr 'Akil (7) and Manot Cave (8) in the eastern Mediterranean region of southwestern Asia and Peştera cu Oase in Romania (2) (*SI Appendix*, Section 3). The interpretation of this scant record is affected by imprecise chronologies, and in some cases, by problematic stratigraphies or lack of contextual data (2, 8–10). The recently discovered fossil at Manot (Israel) places AMH in the Levant as early as 60,200–49,200 y ago (8). However, because the fossil was found on a natural shelf unconnected with the otherwise rich archeological deposits elsewhere in the cave, its affiliation to an archeological technocomplex is unclear. Based on the uranium–thorium dates, the authors suggest an attribution of the fossil to either a late Middle Paleolithic (MP) or Initial Upper Paleolithic (IUP) technocomplex. The lack of archeological association and contextual behavioral data limits our understanding of the fossil's relation to both the Levantine and the European record. Hence, there is very little information to study the dispersal trajectory of modern humans into Europe. However, bones of modern humans from the Levant (e.g., Üçağızlı I and Ksâr 'Akil) and Europe (e.g., Kostenki 1, 14, and 17) are found in archeological contexts and in association with Early UP (EUP) lithic technologies (7, 9, 11, 12). These lithic assemblages, therefore, can be used as a proxy for modern human dispersal (13) and links between several such Levantine and European technocomplexes have been documented (11, 12, 14–16). The archeological record suggests that modern human dispersal from Africa likely took place in several episodes rather than one large exodus (3, 6, 14, 17–19). This hypothesis is supported by genetic and fossil data (20).

AMH dispersal into Europe is broadly contemporaneous with the disappearance of Neanderthals and the beginning of the UP, as witnessed by changes in the archeological record including frequent use of red ochre, modified marine shells and perforated animal teeth as body ornaments, elaborate bone and antler technology, as well as changes in lithic technology (19). Most scholars (3, 6, 14, 19, 21, 22) advocate the importance of southwestern Asia, including the Levant, as a "gateway" to Eurasia for modern humans coming from Africa. This Levantine corridor hypothesis has recently been questioned, as it has been argued that the UP and modern behavior, evidenced by the presence of shell beads in the material culture, first appeared in Europe before their first occurrence in the Levant (23). This interpretation is based on a

Significance

Bayesian modeling of AMS radiocarbon dates on the marine mollusk *Phorcus turbinatus* from Ksâr 'Akil (Lebanon) indicates that the earliest presence of Upper Paleolithic (UP) modern humans in the Levant predates 45,900 cal B.P. Similarities in early UP lithic technology and material culture suggest population dispersals between the Levant and Europe around 50,000–40,000 cal B.P. Our data confirm the presence of modern humans carrying a UP toolkit in the Levant prior to any known European modern human fossils and allow rejection of recent claims that European UP modern humans predate those in the Levant. This result, in turn, suggests the Levant served as a corridor for the dispersal of modern humans out of Africa and into Eurasia.

Author contributions: M.D.B., M.A.M., and J.-J.H. designed research; M.D.B., M.A.M., A.L.P., B.D., S.M.T., L.N., and J.v.d.P. performed research; M.D.B., M.A.M., A.L.P., T.C.O., B.D., and J.v.d.P. analyzed data; and M.D.B., M.A.M., B.D., L.N., and J.-J.H. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. G.T. is a guest editor invited by the Editorial Board.

Freely available online through the PNAS open access option.

[1]To whom correspondence should be addressed. Email: marjolein_online@hotmail.com.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1501529112/-/DCSupplemental.

Downloaded by guest on December 5, 2021

combination of relatively old ages (around 39,900 cal B.P.) for Uluzzian ornamental shell in southern Italy (10) and strikingly young ages (around 36,300–37,400 cal B.P.) for shell ornaments from Üçağızlı I and Ksâr 'Akil in the Levant (23, 24). If the UP in Europe truly predates the Levantine evidence, as Douka et al. (24) suggest, it should be considered unlikely that its makers traveled from Africa through the Levant before arriving in Europe. Here, we provide a new chronology for Ksâr 'Akil and show that the earliest UP and its associated AMH remains predate any European evidence.

Ksâr 'Akil

Located on the Lebanese coast, Ksâr 'Akil is a key site for the region and is best known for its 23-m-long sequence, which includes rich IUP (Layers XXV–XXI) and EUP (Layers XX–XIV) deposits, both of which contain modern human remains (*SI Appendix*, Fig. S1.2). The site, about 10 km north of Beirut, lies about 3 km from the present day coast (*SI Appendix*, Section 1). Excavations conducted in the 1930s and 1940s (7, 25) exposed the entire sequence, whereas later investigations (26) did not reach the earliest UP deposits.

In Layer XXV, the lowermost part of the deposit attributed to the IUP, a maxillary fragment ("Ethelruda") was found accompanied by IUP lithics (7, 27). Ethelruda was initially interpreted as having "Neanderthaloid" features by the excavators (7), but reexamination of the fossil suggests that it falls within the range of modern human variation (28). In general, the IUP lithic assemblages are characterized by opposed platform blade cores with parallel edges and facetted platforms (29). Tool types include chamfered pieces, endscrapers, and burins (27, 29). *Dama mesopotamica* is the dominant vertebrate species throughout all IUP layers. Further, the IUP witnessed a shift in the vertebrate fauna, with a drop in the numbers of *Bos* sp. and *Sus scrofa* in favor of *Capra ibex*, *Capra aegagrus*, and *Capreolus capreolus*. Evidence for marine mollusk consumption is rare and first occurs in Layer XXII (*SI Appendix*, Section 1).

The EUP or Early Ahmarian is associated with the remains of an 8-y-old modern human ("Egbert") and possibly a second individual (25) in Layer XVII, both now lost. The classic Early Ahmarian (Layers XVIII–XVI) also features opposed platform cores with parallel edges, in this case with plain platforms and marginal flaking resulting in thinner blanks (29). Tool types include endscrapers, retouched blades, and bladelets including el-Wad points and *pointe à face plane*, whereas burins are virtually absent (29). *Dama mesopotamica* dominates the vertebrate fauna, but there is a shift to more evenly distributed numbers of *Cervus elaphus*, *Capra aegagrus*, *Capra ibex*, *Sus scrofa*, *Gazella* cf. *dorcas*, and *Testudo graeca* compared with the underlying IUP. In addition, marine intertidal gastropods increase in number and were a foodstuff consumed by the site's EUP occupants (*SI Appendix*, Section 1).

Results

The multidisciplinary approach adopted in this study included absolute dating (AMS radiocarbon), an attempt to attribute layers to climatic events (*SI Appendix*, Section 2) using oxygen isotope analysis as a paleotemperature proxy, the use of amino acid racemization (AAR) to verify the extent of intracrystalline protein diagenesis and thus to highlight potentially compromised samples, as well as in-depth zooarcheological and taphonomic analyses. A relatively large shell assemblage (n > 3,500) was recovered during the 1930s and 1940s excavations mainly from the UP layers (XXIV–I) (25, 30). The shells belong to marine, terrestrial, and freshwater species from a variety of habitats (*SI Appendix*, Table S1.2). Marine shells, collected empty from active beaches or fossil deposits, were used as tools (e.g., *Glycymeris* sp.) and ornaments (e.g., *Nassarius gibbosulus* and *Columbella rustica*) (30–32). Limpets (*Patella rustica*, *Patella caerulea*, and *Patella ulyssiponensis*) and topshells (*Phorcus turbinatus* and *Phorcus articulatus*) were live-collected for consumption and are the best-preserved taxa in the assemblage. Evidence for collection of live limpets and topshells includes the overall integrity of their shells, absence of bioerosion, and encrusting organisms on inner shell surfaces, as well as edge notches on limpet shells congruent with damage resulting from prying the animals off the rocks. Other subsistence-related anthropogenic modifications include the frequent intentional removal of the apices of *Phorcus turbinatus* to facilitate flesh extraction and occasional burning (*SI Appendix*, Section 1). By dating food remains, the "dated event" (i.e., incorporation of ^{14}C in the shell carbonate during growth) and "target event" (i.e., human foraging) directly follow each other (33). Therefore, dating *Phorcus turbinatus* shells captures a concise timeframe including mollusk collection and consumption and is thus a good proxy for site occupation. Individual shells of this species were selected based on their excellent preservation, by considering a combination of macroscopic and physicochemical characteristics (*SI Appendix*, Section 2).

Radiocarbon Dating. We obtained 16 AMS radiocarbon dates for the Ksâr 'Akil UP sequence (Layers XXII–V) (*SI Appendix*, Table S2.2). All age estimations are calibrated using the Marine13 curve (34) and are given at the 68.2% probability level (*SI Appendix*, Section 2). *Phorcus turbinatus* occurs in the IUP starting from Layer XXII, which is dated to 44,400–43,100 cal B.P. The 11 dates for the EUP (Layers XX–XVI) show a wide range of ages from 44,000–37,200 cal B.P., whereas the later UP (Layers XII, XI, and VI) dates to ∼40,700–31,700 cal B.P. The start of the Epipaleolithic or Proto-Kebaran (Layer V) can be placed at 30,400–29,500 cal B.P. Artifact associations made during the 1930s and 1940s were based on broad geological layers that potentially include several thinner archeological horizons (*SI Appendix*, Section 1). This limited detail in provenience could account for wide age ranges within a layer. The dates of samples XVII (1) and XVIII do not fit well in the overall sequence because they provided younger ages than overlying samples. These specimens could be intrusive from younger deposits or be subjected to contamination. In general, contamination of a sample of this age results in a younger estimate than the true age of the sample, because the effect of introducing modern carbon in highly ^{14}C-depleted samples is more pronounced than the effect of introducing radiocarbon-dead contaminants (35, 36). The fact that the dated material comes from an old excavation with inherent provenience limitations, and the problems of identifying and eliminating contaminants in shells, make it imperative to evaluate individual sample integrity. We have applied three independent methods to evaluate our chronological data and identify potential outliers: (*i*) modeling using Bayesian statistics (37), (*ii*) using AAR values as a proxy for diagenetic integrity of the shells, and (*iii*) analyzing the oxygen isotope composition of shell carbonates to evaluate whether all specimens from the same layer are likely to be contemporary and to compare paleotemperature estimates from these analyses with those documented for different climatic phases in the NGRIP curve (*SI Appendix*, Section 2).

Bayesian Modeling of the Radiocarbon Ages. Bayesian modeling (37) and outlier analysis resulted in a model with an agreement index (A_model) of 118.2% (Fig. 1; see *SI Appendix*, Section 2 for discussion of rejected alternative models). For six dates, high posterior outlier probabilities (indicative of outliers) were calculated at various stages of the modeling (*SI Appendix*, Table S2.4). The model identifies the older EUP dates as best reflecting the true ages. We used the OxCal "Date" function to calculate a probability distribution function (PDF) for the age of the human fossil-bearing archeological layers. The PDF for Egbert's layer results in an age of 43,200–42,900 cal B.P. Regarding the age of Ethelruda, a lack of datable material from its

Downloaded by guest on December 5, 2021

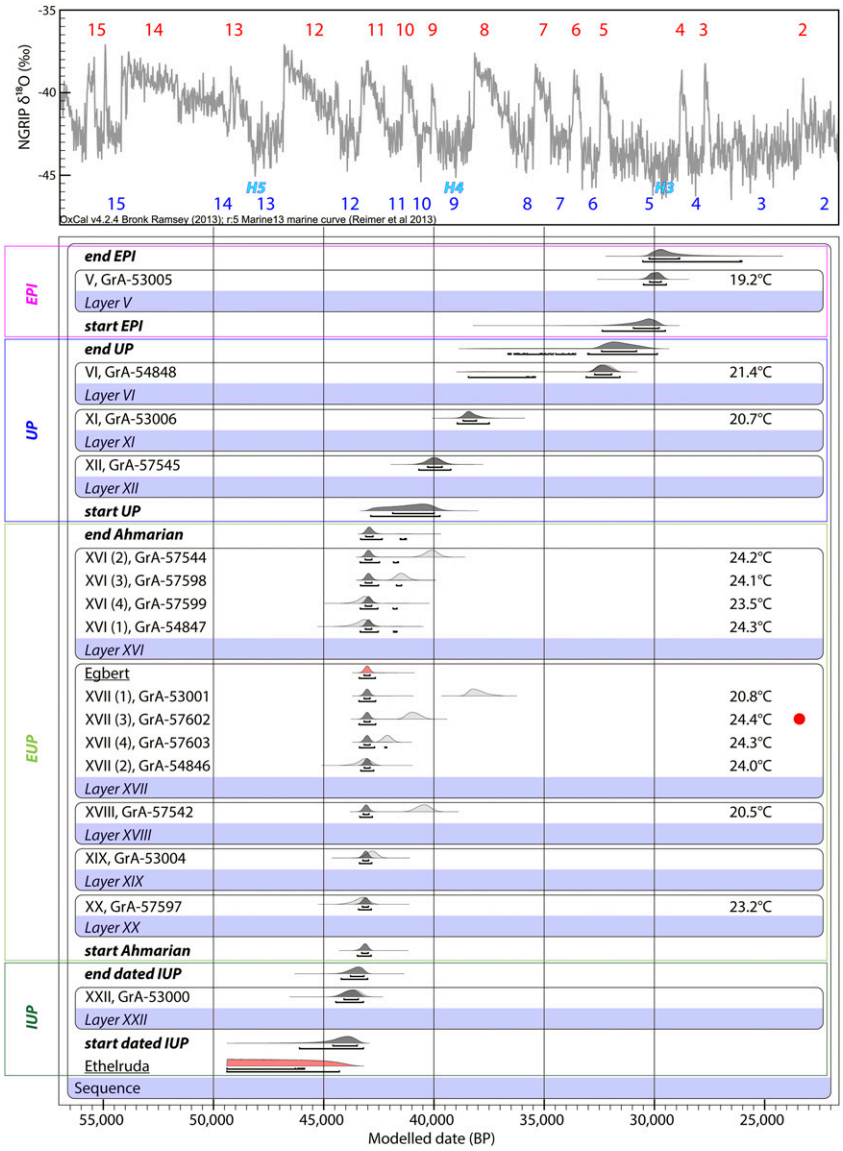

Fig. 1. Bayesian age model for the Ksâr 'Akil sequence produced using OxCal 4.2.4 (37). The radiocarbon dates are calibrated using the Marine13 dataset (34) ΔR value for the eastern Mediterranean (60). The individual radiocarbon likelihoods are shown in light gray, the posterior probability distributions are shown in dark gray, and PDFs for Ethelruda and Egbert's layers are shown in red. The modeled data are compared with the NGRIP $\delta^{18}O$ curve (gray), Greenland Interstadials (GIS; red) and Stadials (GS; blue), and Heinrich Events (H3-5; light blue). Mean annual SSTs are given in degrees Celsius (°C). A red dot marks date XVII (3), as AAR analyses of the intracrystalline proteins showed that this sample displays some indication of open-system behavior.

associated Layer XXV, as well as from the layers directly above and underneath, hampers precise age estimation. Nevertheless, the date of the overlying IUP Layer XXII and the modeled start of the dated part of the IUP sequence provide termini ante quem for Ethelruda (i.e., >44,100 cal B.P. and >44,600 cal B.P., respectively). The PDF for Ethelruda's layer extends beyond the range of the Marine13 calibration curve, and the upper limit of 45,900 cal B.P. can be used as a minimum age.

Amino Acid Racemization (AAR). The extent of racemization (D/L value) of 26 *Phorcus turbinatus* specimens, including 13 AMS dated samples, was evaluated. Both the total hydrolysable amino acids (THAA) and free amino acids (FAA) retained in an intracrystalline protein fraction (isolated by bleaching) of several amino acids were considered (*SI Appendix*, Section 2). Overall, intralayer variability of the D/L values was found to be comparable to the intrasite variability (*SI Appendix*, Fig. S2.7), and therefore D/Ls could not be used to resolve the relative chronology within the site. However, the covariance between FAA D/Ls and THAA D/Ls of different amino acids showed that the intracrystalline proteins in *Phorcus turbinatus* provide a robust fraction for AAR analyses (closed-system behavior). This result indicates that the shells had not been diagenetically compromised during their postdepositional history, supporting the results of the other geochemical methods and AMS dates (*SI Appendix*, Fig. S2.6). One exception is sample XVII (3), which shows some indication of open-system behavior, supporting the hypothesis that this date might be an outlier (Fig. 1).

Oxygen Isotope Analysis. $\delta^{18}O$ values of sequential carbonate samples from 13 specimens were converted to Sea Surface Temperatures (SST) and provided mean annual SST estimates (*SI Appendix*, Section 2). Observed fluctuations in mean annual SST, of 3–4 °C, are consistent with differences between warm Greenland Interstadials (GIS) and cooler Greenland Stadials (GS), including Heinrich events during Marine Isotope Stage 3 (MIS 3) (38). Oxygen isotope and SST data are consistent with the climatic phases inferred from tentative correlations of calibrated ages with the NGRIP data (Fig. 1). These tentative comparisons allow us to attribute samples with higher $\delta^{18}O_{shell}$ values [i.e., V, VI, XI, and XVII (1), and XVIII], corresponding to SST estimates between 19.2 °C and 21.4 °C, to cold events i.e., Heinrich 3, GS 5/6, GS 9, and GS 10, respectively. Samples with lower $\delta^{18}O_{shell}$ values, corresponding to temperatures ranging from 23.2 °C to 24.4 °C,

ANTHROPOLOGY

Downloaded by guest on December 5, 2021

could be attributed to GIS 11 [i.e., XVI (1), XVI (4), XVII (2), XVII (4), and XX] and GIS 10 [i.e., XVI (2, 3) and XVII (3)] (39). The colder annual SST estimate for sample XVII (1) is inconsistent with that of other Ahmarian samples, indicating that this specimen did not secrete its shell in the same temperature regime and is not contemporary with the others, which is also reflected by the younger AMS date. Provided the date is correct, this specimen is most likely intrusive from the later cold period GS 9.

Discussion

The chronological data reported above suggest that modern humans producing IUP and EUP assemblages were present at Ksâr 'Akil from before 45,900 cal B.P. and around 43,300–42,800 cal B.P., respectively. These age estimates have implications for (*i*) the chronology of the Levantine EUP and IUP, (*ii*) the age of UP modern human presence in the Levant, (*iii*) the spread of UP modern humans from the Levant into Eurasia, and (*iv*) the validity of the Levantine corridor hypothesis.

Ksâr 'Akil Chronology and Previous Dates. Our dates are in good agreement with conventional radiocarbon dates on charcoal (26, 40). They also overlap with the age estimates on shell by Douka et al. (24) for the upper part of the sequence, but are significantly older (3,000–4,000 y) for the IUP and EUP layers (*SI Appendix*, Section 2). The reasons behind the observed discrepancy are presently unresolved. Causes might include differences in (*i*) sample selection (i.e., shell preservation and its implications for time-averaging and diagenesis), (*ii*) sample pretreatment (e.g., potential incomplete elimination of contaminants by the CarDS method) (41), (*iii*) radiocarbon AMS laboratory (i.e., Groningen and Oxford), and (*iv*) the dated event based on taxa selection (i.e., collection of beached shells for ornaments or live mollusks for consumption; see *SI Appendix*, Section 2 for discussion).

Chronology in a Regional Context.

Levantine IUP chronology. The earliest IUP in the Levant is represented by Manot Cave and Boker Tachtit (both Israel), Üçağızlı I Cave (Turkey), and as inferred from Kebara Cave (Israel) (Fig. 2; *SI Appendix*, Section 3). For comparative purposes, radiocarbon dates were calibrated using IntCal/Marine13 (34) unless stated differently (*SI Appendix*, Section 3). A single AMS date from Unit 7 of Area C at Manot Cave of 48,700 ^{14}C B.P. is attributed to the IUP. It cannot be calibrated as it falls beyond the limits of the current calibration curve. The IUP lithics share features with Ksâr 'Akil IUP Layers XXV–XXI, but the unit also contains abundant EUP and scattered MP artifacts (8). Age calibration of conventional radiocarbon dates on charcoal suggests that the IUP at Boker Tachtit (Layers 1–4) dates to at least 50,000–40,000 cal B.P. (42), which should probably be considered a minimum estimate (43). The lithic assemblage of Layer 4 shows technological similarities with Ksâr 'Akil Layers XXII–XXI and is associated with a charcoal date of ~40,000 cal B.P., again a minimum age (42). The IUP at Üçağızlı I (Layers G–I) corresponds to Layer XXI of Ksâr 'Akil (31) and dates to 45,900–38,400 cal B.P. based on charcoal samples (9) and 40,800–37,800 cal B.P. based on shell ornaments (23). Kebara has a hiatus in the stratigraphy where the IUP would be expected to occur; based on age estimations for the Late Middle Paleolithic below and the EUP above, Rebollo et al. (44) assign a time window of 49,000–46,000 cal B.P. for the IUP. The estimated start of the IUP at Ksâr 'Akil, modeled to at least 45,900 cal B.P., is

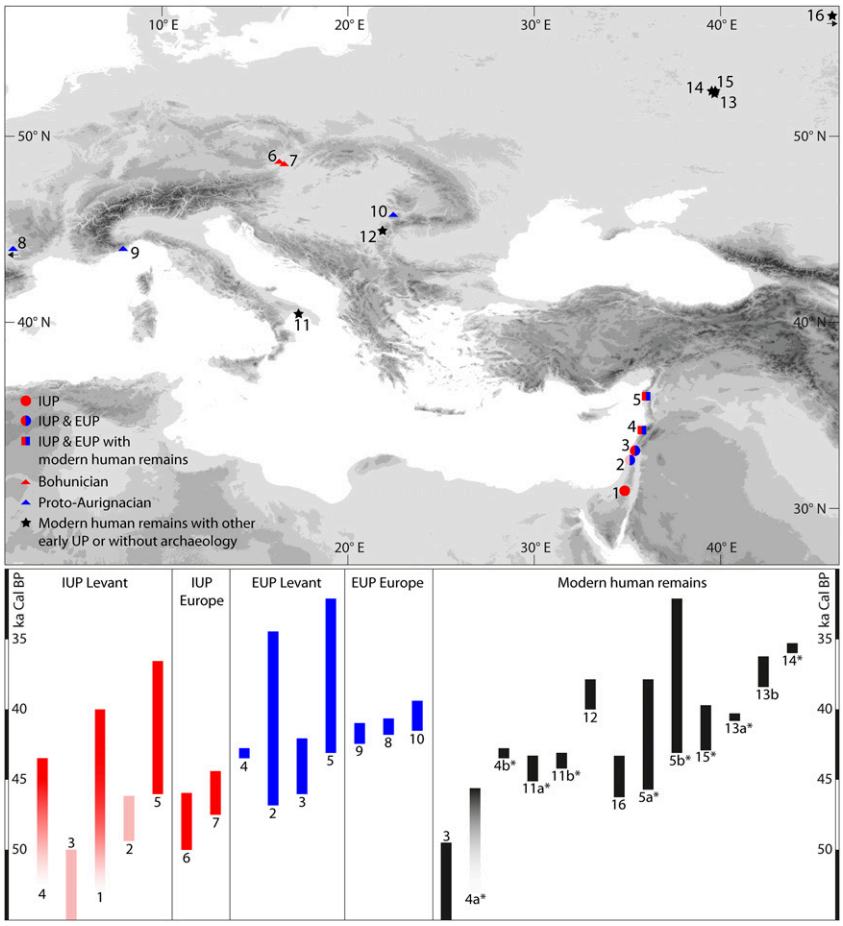

Fig. 2. Upper Paleolithic sites and human remains mentioned in the text (see also *SI Appendix*, Section 3). (*Upper*) Site location. (*Lower*) Age range (in 1,000 calendar ages before present) of sites and human remains (*: in association with UP). 1, Boker Tachtit; 2, Kebara Cave; 3, Manot Cave; 4, Ksâr 'Akil; 4a, Ethelruda; 4b, Egbert; 5, Üçağızlı I; 5a, Üçağızlı I IUP teeth; 5b, Üçağızlı I EUP teeth; 6, Brno-Bohunice 2002; 7, Brno-Kejbaly; 8, Isturitz; 9, Riparo Mochi; 10, Românești-Dumbrăviţa I; 11a Cavallo B; 11b, Cavallo C; 12, Peştera cu Oase; 13a, Kostenki 14 Layer IVb tooth; 13b, Kostenki 14 Burial; 14, Kostenki 1 Layer III; 15, Kostenki 17 Layer II; 16, Ust'-Ishim.

Downloaded by guest on December 5, 2021

congruent with technological and chronological data from all four sites, of which the Manot IUP might be the most ancient.

Levantine EUP chronology. Our dates agree with established chronologies for other Levantine EUP or Early Ahmarian sites including Kebara, Manot, and Üçağızlı I. The Early Ahmarian at Kebara (Units III and IV) is dated between 46,000 and 34,000 cal B.P. and corresponds archeologically to Ksâr 'Akil Layers XIX–XV (44, 45). The Early Ahmarian component of Unit 7 (Area C) at Manot has been dated to 46,000–42,000 cal B.P. (46) and corresponds to Layers XX–XVI. The EUP Layers B to B4 at Üçağızlı I, dated to 39,800–32,200 cal, are similar in lithic technology but younger than Ksâr 'Akil Layers XVI–XVII (9, 31). Age estimates for the entire EUP sequence (Layers B–E) range between 42,800 and 32,200 cal B.P. (9) and 40,800 and 36,400 cal B.P. based on shell ornaments (23). The EUP of the four sites overlaps, although its start at both Manot and Kebara predates that of Üçağızlı I and Ksâr 'Akil by several millennia.

Implications for UP Modern Human Dispersals into Europe and the Levantine Corridor Hypothesis.

AMH remains. Ksâr 'Akil is one of the few sites with AMH fossils that are associated with IUP and EUP assemblages in Europe and the Levant. Our age estimations, placing Egbert's layer between 43,200 and 42,900 cal B.P., predate directly dated AMH remains from Europe, including those from Peştera cu Oase and Kostenki 14 (Russia) (Fig. 2 and *SI Appendix*, Section 3) (2, 11, 47), and overlap at 1σ with the modeled age for Cavallo C (Italy) (10). Further, this age is consistent with those for the AMH teeth from the EUP layers of Üçağızlı I (42,800–32,200 cal B.P.) (9). Our data also provide a minimum age of at least 45,900 cal B.P. for the archeological layer bearing the remains of Ethelruda and the start of the IUP in Layer XXV, placing the fossil well before the oldest European AMH fossil (i.e., Cavallo B dated to 45,000–43,400 cal B.P., *SI Appendix*, Table S3.2) (10). In contrast to the Ust'-Ishim femur (46,200–43,700 cal B.P.) (22), the Manot 1 skull (60,200–49,200 y ago) (8) might predate the IUP at Ksâr 'Akil. However, the uranium–thorium age of the latter is rather imprecise and none of these specimens was found in direct archeological context. It is therefore unclear what toolkit these humans carried. Within the Levant, the Ksâr 'Akil data are in rather good agreement with the age estimations for Üçağızlı I, where AMH teeth from the IUP date between 45,900 and 37,100 cal B.P. (9). Compared with European modern human remains associated with UP toolkits, the Ksâr 'Akil data predate the human remains from early UP contexts at Kostenki 14 Layer IVb between 41,500 and 40,900 cal B.P. (11, 48) and at Kostenki 17 Layer II dated to 42,800–39,600 cal B.P. (12) (*SI Appendix*, Section 3).

Archeological record. Similarities between Levantine and European early UP technocomplexes have been interpreted as evidence of several dispersal episodes (3, 6, 14, 18, 19). The earliest connection concerns the Levantine IUP/Emirian and Central European Bohunician and similar assemblages in Eastern Europe and North Asia (11, 14, 15, 21, 49). Similarities have also been documented between the Levantine Early Ahmarian (EUP) and the European Proto-Aurignacian (3, 16, 19, 50, 51). Therefore, identifying the first occurrence of technologically similar lithic industries in the Levant and Europe holds potential information about dispersal trajectories. In the case of the Levantine IUP and European Bohunician connection, the latter is generally placed in GIS 12 (21, 52) with its onset around 46,860 ± 956 b2k (i.e., calendar years before A.D. 2000) (39), or in GS 13 (53). The estimated start of the IUP at Ksâr 'Akil falls within GIS 12, but could also predate it. The dates of Boker Tachtit and Manot predate GIS 12, and could be as early as GIS 13 and GIS 14, respectively. The start of the Levantine EUP at Ksâr 'Akil, Kebara, and Manot predates the appearance of the Proto-Aurignacian in Europe around 42,700–39,100 cal B.P., i.e., at Isturitz (54), Riparo Mochi (55) and Româneşti-Dumbrăviţa I (56), by several millennia (*SI Appendix*, Section 3).

Implications. On an interregional scale, similar UP lithic technocomplexes (e.g., IUP/Bohunician and Early Ahmarian/Proto-Aurignacian) first appear in the Levant. Our chronology for Ksâr 'Akil, corroborated by several lines of evidence, fits well with other early IUP and EUP Levantine sites. It is generally assumed that once there is a proven association between certain archeological assemblages and their makers, this could be extrapolated to the technocomplex as a whole (e.g., all Early Ahmarian is made by modern humans based on association of the Egbert fossil to the Ksâr 'Akil EUP). Although such extrapolations should be treated with caution especially when they are extended to other closely related assemblages over a large geographical area, the correlation of AMH associated technocomplexes with other closely related technocomplexes allows tracking of potential dispersal routes in the archeological record. Our data contribute to the debate on modern human dispersal patterns by providing age estimations for UP assemblages containing modern human fossils. Comparison of our age estimations with those of European AMH fossils place Eltheruda's layer before the first occurrence of modern humans in Europe. Similarly, Egbert's layer predates any known Aurignacian and other early UP modern humans in Europe. The antecedence of both UP lithic technocomplexes and modern human remains in the Levant, the latter also corroborated by Manot 1, indicates that modern humans carrying a UP toolkit were present in the Levant before arriving in Europe. This contradicts Douka et al.'s (24) hypothesis that shell beads, and by proxy UP modern humans, appeared first in Europe. Observed similarities in early UP lithic technology and other material culture of Levantine and European technocomplexes suggest a close interrelation that could well result from dispersal events. In turn, this implies that the Levant served as a corridor for modern humans dispersing out of Africa and into Europe rather than being a "cul-de-sac" where modern humans arrived after they dispersed into Europe.

That the first occurrence of the Levantine IUP and Bohunician takes place in a short time window suggests rapid dispersal events over large geographical areas (17), and the same is true for the first occurrence of the Proto-Aurignacian (13). The spread of modern humans and their material culture has implications for the replacement of Neanderthals by modern humans and acculturation debates, because current data suggest that at the time of these dispersals the former were still present in some parts of Europe (57–59). Changes in material culture of some of the last Neanderthals in Europe could therefore be related to contact and subsequent (stimulus) diffusion of modern human behaviors.

Materials and Methods

All analyses (AMS radiocarbon dating, AAR, and oxygen isotopes) have been conducted in conjunction on selected specimens to enable direct comparison and contextualization of the results of various datasets (*SI Appendix*, Section 2). We selected samples based on an evaluation of the shell preservation by using both macroscopic attributes and physicochemical characteristics (XRD, staining with Feigl and Mutvei solutions) (*SI Appendix*, Section 2). Radiocarbon dating at the Groningen radiocarbon laboratory consists of chemical cleaning of the outer surface using a 4% (wt/vol) HCl solution, followed by CO_2 development using concentrated H_3PO_4. All dates were calibrated using the Marine13 (34) calibration curve and the software OxCal 4.2.4 (37). Reservoir correction (R) was carried out taking into account a local ΔR of 53 ± 43 B.P. for the eastern Mediterranean (60). AAR was used as a test for diagenetic integrity after Demarchi et al. (61). Sampling for oxygen isotope analysis was adopted after Mannino et al. (62). Grossman and Ku's (63) equation with a correction for the conversion of VSMOW to VPDB (64) was used to calculate SST from $\delta^{18}O_{shell}$ values. Mean $\delta^{18}O_{water}$ is based on pore water estimations (65) and corrected for MIS 3 glacial conditions. For a full description of our sampling and analysis methods, see *SI Appendix*, Section 2.

ACKNOWLEDGMENTS. We thank Frank Wesselingh, Ronald Pouwer, Kirsty Penkman, James Rolfe, Shannon McPherron, Wil Roebroeks, Sahra Talamo,

ANTHROPOLOGY
Downloaded by guest on December 5, 2021

and especially Philip Nigst for helpful discussions and support. We also thank the three anonymous reviewers for their insightful and detailed comments. This study was funded by the Max Planck Society. A.L.P.'s oxygen isotope work was funded by The Rae and Edith Bennett Foundation, and B.D.'s AAR work was funded by EU FP7 Re(In)tegration Grant PERG07-GA-2010-268429 (Project: mAARiTIME).

1. Klein RG (2008) Out of Africa and the evolution of human behavior. *Evol Anthropol* 17(6):267–281.
2. Trinkaus E, et al. (2003) An early modern human from the Peştera cu Oase, Romania. *Proc Natl Acad Sci USA* 100(20):11231–11236.
3. Mellars P (2006) Archeology and the dispersal of modern humans in Europe: Deconstructing the "Aurignacian." *Evol Anthropol* 15(5):167–182.
4. Forster P (2004) Ice Ages and the mitochondrial DNA chronology of human dispersals: A review. *Philos Trans R Soc Lond B Biol Sci* 359(1422):255–264.
5. Stringer C (2002) Modern human origins: Progress and prospects. *Philos Trans R Soc Lond B Biol Sci* 357(1420):563–579.
6. Hublin J-J (2014) The modern human colonization of western Eurasia: When and where? *Quat Sci Rev*, 10.1016/j.quascirev.2014.08.011.
7. Ewing JF (1960) Human types and prehistoric cultures at Ksar'Akil. Lebanon. Men and Cultures: Selected Papers Fifth International Congress Anthropological Ethnological Science Philadelphia. 1956:535–539.
8. Hershkovitz I, et al. (2015) Levantine cranium from Manot Cave (Israel) foreshadows the first European modern humans. *Nature* 520:216–219.
9. Kuhn SL, et al. (2009) The early Upper Paleolithic occupations at Uçağizli Cave (Hatay, Turkey). *J Hum Evol* 56(2):87–113.
10. Benazzi S, et al. (2011) Early dispersal of modern humans in Europe and implications for Neanderthal behaviour. *Nature* 479(7374):525–528.
11. Sinitsyn AA (2003) The most ancient sites of Kostenki in the context of the Initial Upper Paleolithic of northern Eurasia. *The Chronology of the Aurignacian and of the Transitional Technocomplexes: Dating, Stratigraphies, Cultural Implications*, eds Zilhao J, d'Errico F (Instituto Português de Arqueologia, Lisboa), pp 89–107.
12. Hoffecker JF, et al. (2008) From the Bay of Naples to the River Don: The Campanian Ignimbrite eruption and the Middle to Upper Paleolithic transition in Eastern Europe. *J Hum Evol* 55(5):858–870.
13. Davies W (2001) A very model of a modern human industry: New perspectives on the origins and spread of the Aurignacian in Europe. *Proc Prehist Soc* 67:195–217.
14. Tostevin GB (2012) *Seeing Lithics: A Middle-Range Theory for Testing for Cultural Transmission in the Pleistocene* (Oxbow Books, Oxford).
15. Svoboda JA, Bar-Yosef O (2003) *Stránská skála. Origins of the Upper Paleolithic in the Brno Basin, Moravia, Czech Republic* (Peabody Museum of Archaeology and Ethnology, Harvard University, Cambridge, MA).
16. Tsanova T (2013) The beginning of the Upper Paleolithic in the Iranian Zagros. A taphonomic approach and techno-economic comparison of Early Baradostian assemblages from Warwasi and Yafteh (Iran). *J Hum Evol* 65(1):39–64.
17. Bar-Yosef O (2007) The dispersal of modern humans in Eurasia: A cultural interpretation. *Rethinking the Human Revolution: New Behavioural and Biological Perspectives on the Origin and Dispersal of Modern Humans*, eds Mellars P, Boyle K, Bar-Yosef O, Stringer C (McDonald Institute for Archaeological Research, University of Cambridge, Cambridge, U.K.), pp 207–217.
18. Goring-Morris NA, Belfer-Cohen A (2003) *More Than Meets the Eye: Studies on Upper Palaeolithic Diversity in the Near East* (Oxbow Books, Oxford).
19. Bar-Yosef O (2002) The Upper Paleolithic revolution. *Annu Rev Anthropol* 31:363–393.
20. Gunz P, et al. (2009) Early modern human diversity suggests subdivided population structure and a complex out-of-Africa scenario. *Proc Natl Acad Sci USA* 106(15):6094–6098.
21. Hoffecker JF (2009) Out of Africa: Modern human origins special feature: The spread of modern humans in Europe. *Proc Natl Acad Sci USA* 106(38):16040–16045.
22. Fu Q, et al. (2014) Genome sequence of a 45,000-year-old modern human from western Siberia. *Nature* 514(7523):445–449.
23. Douka K (2013) Exploring the great wilderness of prehistory: The chronology of the Middle to the Upper Paleolithic transition in the northern Levant. *Mitteilungen der Gesellschaft Urgeschichte* 22:11–40.
24. Douka K, Bergman CA, Hedges REM, Wesselingh FP, Higham TF (2013) Chronology of Ksar Akil (Lebanon) and implications for the colonization of Europe by anatomically modern humans. *PLoS ONE* 8(9):e72931.
25. Ewing FJ (1947) Preliminary note on the excavations at the Palaeolithic site of Ksâr 'Akil, Republic of Lebanon. *Antiquity* 21(84):186–196.
26. Mellars P, Tixier J (1989) Radiocarbon-accelerator dating of Ksar 'Aqil (Lebanon) and the chronology of the Upper Palaeolithic sequence in the Middle East. *Antiquity* 63: 761–768.
27. Azoury I (1986) *Ksar Akil, Lebanon: A Technological and Typological Analysis of the Transitional and Early Upper Palaeolithic Levels of Ksar Akil and Abu Halka* (BAR, Oxford).
28. Metni MC (1999) A re-examination of a proposed Neandertal maxilla from Ksar 'Akil rock shelter, Antelias, Lebanon. *Am J Phys Anthropol* S28:202.
29. Bergman CA (1988) Ksar Akil and the Upper Palaeolithic of the Levant. *Paléorient* 14(2):201–210.
30. van Regteren Altena CO (1962) Molluscs and echinoderms from Palaeolithic deposits in the rock shelter of Ksâr'Akil, Lebanon. *Zool Meded* 38(5):87–99.
31. Kuhn SL, Stiner MC, Reese DS, Güleç E (2001) Ornaments of the earliest Upper Paleolithic: New insights from the Levant. *Proc Natl Acad Sci USA* 98(13):7641–7646.
32. Douka K (2011) An Upper Palaeolithic shell scraper from Ksar Akil (Lebanon). *J Archaeol Sci* 38(2):429–437.
33. Dean JS (1978) Independent dating in archaeological analysis. *Adv Archaeol Method and Theory* 1:223–255.
34. Reimer PJ, et al. (2013) IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon* 55(4):1869–1887.
35. van der Plicht J (2012) Borderline radiocarbon. *Neth J Geosci* 91(1–2):257–261.
36. Higham T, et al. (2009) Problems with radiocarbon dating the Middle to Upper Palaeolithic transition in Italy. *Quat Sci Rev* 28(13–14):1257–1267.
37. Bronk Ramsey C (2009) Bayesian analysis of radiocarbon dates. *Radiocarbon* 51(1): 337–360.
38. Sánchez Goñi M, et al. (2002) Synchroneity between marine and terrestrial responses to millennial scale climatic variability during the last glacial period in the Mediterranean region. *Clim Dyn* 19(1):95–105.
39. Svensson A, et al. (2008) A 60 000 year Greenland stratigraphic ice core chronology. *Climate of the Past* 4(1):47–57.
40. Vogel JC, Waterbolk HT (1963) Groningen radiocarbon dates IV. *Radiocarbon* 5:163–202.
41. Douka K, Hedges RM, Higham TG (2010) Improved AMS ^{14}C dating of shell carbonates using high-precision X-ray diffraction and a novel density separation protocol (CarDS). *Radiocarbon* 52(2):735–751.
42. Marks AE (1983) The Middle to Upper Paleolithic transition in the Levant. *Advances in World Archaeology* 2:123–136.
43. Shea JJ (2003) The Middle Paleolithic of the east Mediterranean Levant. *J World Prehist* 17(4):313–394.
44. Rebollo NR, et al. (2011) New radiocarbon dating of the transition from the Middle to the Upper Paleolithic in Kebara Cave, Israel. *J Archaeol Sci* 38(9):2424–2433.
45. Bar-Yosef O, et al. (1996) The dating of the Upper Paleolithic layers in Kebara cave, Mt Carmel. *J Archaeol Sci* 23(2):297–306.
46. Barzilai O, Alex B, Boaretto E, Hershkovitz I, Marder O (2014) The Early Upper Palaeolithic at Manot Cave, Western Galilee, Israel. *PESHE* 3:34.
47. Marom A, McCullagh JSO, Higham TFG, Sinitsyn AA, Hedges REM (2012) Single amino acid radiocarbon dating of Upper Paleolithic modern humans. *Proc Natl Acad Sci USA* 109(18):6878–6881.
48. Haesaerts P, Damblon F, Sinitsyn A, van der Plicht J (2004) Kostienki 14 (Voronezh, Central Russia): New data on stratigraphy and radiocarbon chronology. Section 6: Le Paleolithique superieur / The Upper Palaeolithic: Sessions generals et posters / General sessions and posters, Acts of the XIVth UISPP Congress, University of Liege, Belgium, 2–8 September 2001, eds Dewez M, Noiret P, Teheux E (BAR Int Ser 1240), pp 169–180.
49. Kuhn SL, Zwyns N (2014) Rethinking the initial Upper Paleolithic. *Quat Int* 347:29–38.
50. Zilhão J (2006) Neandertals and moderns mixed, and it matters. *Evol Anthropol* 15(5): 183–195.
51. Le Brun-Ricalens F, Bordes J-G, Eizenberg L (2009) A crossed-glance between southern European and Middle-Near Eastern early Upper Palaeolithic lithic technocomplexes. existing models, new perspectives. *The Mediterranean from 50 000 to 25 000 BP: Turning Points and New Directions*, eds Camps M, Szmidt C (Oxbow Books, Oxford), pp 11–33.
52. Richter D, Tostevin G, Skrdla P, Davies W (2009) New radiometric ages for the Early Upper Palaeolithic type locality of Brno-Bohunice (Czech Republic): Comparison of OSL, IRSL, TL and ^{14}C dating results. *J Archaeol Sci* 36(3):708–720.
53. Nigst PR (2012) *The Early Upper Palaeolithic of the Middle Danube Region* (Leiden University Press, Leiden).
54. Szmidt CC, Normand C, Burr GS, Hodgins GW, LaMotta S (2010) AMS ^{14}C dating the Protoaurignacian/Early Aurignacian of Isturitz, France. Implications for Neanderthal-modern human interaction and the timing of technical and cultural innovations in Europe. *J Archaeol Sci* 37(4):758–768.
55. Douka K, Grimaldi S, Boschian G, del Lucchese A, Higham TF (2012) A new chronostratigraphic framework for the Upper Palaeolithic of Riparo Mochi (Italy). *J Hum Evol* 62(2):286–299.
56. Schmidt C, et al. (2013) First chronometric dates (TL and OSL) for the Aurignacian open-air site of Româneşti-Dumbrăviţa I, Romania. *J Archaeol Sci* 40(10):3740–3753.
57. Semal P, et al. (2009) New data on the late Neandertals: Direct dating of the Belgian Spy fossils. *Am J Phys Anthropol* 138(4):421–428.
58. Hublin J-J, et al. (2012) Radiocarbon dates from the Grotte du Renne and Saint-Césaire support a Neandertal origin for the Châtelperronian. *Proc Natl Acad Sci USA* 109(46):18743–18748.
59. Higham T, et al. (2014) The timing and spatiotemporal patterning of Neanderthal disappearance. *Nature* 512(7514):306–309.
60. Reimer PJ, McCormac FG (2002) Marine radiocarbon reservoir corrections for the Mediterranean and Aegean Seas. *Radiocarbon* 44(1):159–166.
61. Demarchi B, et al. (2013) Intra-crystalline protein diagenesis (IcPD) in *Patella vulgata*. Part I: Isolation and testing of the closed system. *Quat Geochronol* 16(100):144–157.
62. Mannino MA, Thomas KD, Leng MJ, Sloane HJ (2008) Shell growth and oxygen isotopes in the topshell *Osilinus turbinatus*: Resolving past inshore sea surface temperatures. *Geo-Mar Lett* 28(5–6):309–325.
63. Grossman EL, Ku T-L (1986) Oxygen and carbon isotope fractionation in biogenic aragonite: Temperature effects. *Chem Geol Isot Geosci Sect* 59:59–74.
64. Dettman DL, Reische AK, Lohmann KC (1999) Controls on the stable isotope composition of seasonal growth bands in aragonitic fresh-water bivalves (Unionidae). *Geochim Cosmochim Acta* 63(7):1049–1057.
65. Paul HA, Bernasconi SM, Schmid DW, McKenzie JA (2001) Oxygen isotopic composition of the Mediterranean Sea since the Last Glacial Maximum: Constraints from pore water analyses. *Earth Planet Sci Lett* 192(1):1–14.

Downloaded by guest on December 5, 2021