

Early modern human settlement of Europe north of the Alps occurred 43,500 years ago in a cold steppe-type environment

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The first settlement of Europe by modern humans is thought to have occurred between 50,000 and 40,000 calendar years ago (cal B.P.). In Europe, modern human remains of this time period are scarce and often are not associated with archaeology or originate from old excavations with no contextual information. Hence, the behavior of the first modern humans in Europe is still unknown. Aurignacian assemblages—demonstrably made by modern humans—are commonly used as proxies for the presence of fully behaviorally and anatomically modern humans. The site of Willendorf II (Austria) is well known for its Early Upper Paleolithic horizons, which are among the oldest in Europe. However, their age and attribution to the Aurignacian remain an issue of debate. Here, we show that archaeological horizon 3 (AH 3) consists of faunal remains and Early Aurignacian lithic artifacts. By using stratigraphic, paleoenvironmental, and chronological data, AH 3 is ascribed to the onset of Greenland Interstadial 11, around 43,500 cal B.P., and thus is older than any other Aurignacian assemblage. Furthermore, the AH 3 assemblage overlaps with the latest directly radiocarbon-dated Neanderthal remains, suggesting that Neanderthal and modern human presence overlapped in Europe for some millennia, possibly at rather close geographical range. Most importantly, for the first time to our knowledge, we have a high-resolution environmental context for an Early Aurignacian site in Central Europe, demonstrating an early appearance of behaviorally modern humans in a medium-cold steppe-type environment with some boreal trees along valleys around 43,500 cal B.P.

Modern humans dispersed out of Africa and into western Eurasia at least 50,000 calendar years ago (cal B.P.) and subsequently replaced all previous hominin species on our planet (1–4). Although the route and number of modern human dispersal(s) are an issue of ongoing debate (5), genetic studies strongly suggest that modern humans and older hominins (including Neanderthals in western Eurasia and Denisovans in Central Asia) met and mixed (6). For Europe, it is debated when and under which climatic conditions the first anatomically and behaviorally modern humans colonized the continent (2, 7–9).

Fully anatomically modern human fossils older than 35,000 cal B.P. outside Africa are scarce and often are not associated with any archaeology (4) or originate from old excavations with no (or highly biased) contextual information (10, 11). Therefore, their behavior remains unknown. The Aurignacian technocomplex is associated exclusively with modern human remains (12) and therefore can be used as a proxy for modern human presence in Europe (7, 13). Modern humans might have entered Europe earlier, because Bohunician stone tools in Central Europe are considered by some to be the material culture correlate of a modern human dispersal into Europe (14–17). Until now, however, no Bohunician assemblage in Europe has

been associated with modern human remains. Similarly, Uluzzian stone tools in Italy are claimed to be associated with modern human remains (18), although this association has been questioned (19). Therefore, the Aurignacian is used here as a proxy for anatomically modern human presence. Moreover, the Aurignacian is generally accepted as showing fully modern behavior, and thus it can be argued that when evaluating the Aurignacian, we are looking at anatomically and behaviorally modern humans.

Scenarios explaining Neanderthal demise and modern human dispersal are the focus of current discussions. Some argue that Neanderthals were replaced/outcompeted by modern humans because of inherent biological and behavioral differences between the two species (1–3). Others consider climatic change to be the major cause of Neanderthal extinction, as a consequence of either one particularly severe cold event (20, 21) or a number of cold events resulting in population attrition and finally a terminal decline during a severe cold event (22). Evaluating these scenarios of the Neanderthal–modern human replacement requires data on Neanderthal and modern human technology, subsistence, and settlement patterns but also high-resolution environmental data, chronostratigraphic background, and precise age estimations.

Significance

Modern humans dispersed into Europe and replaced Neanderthals at least 40,000 years ago. However, the precise timing and climatic context of this dispersal are heavily debated. Therefore, a new project combining paleoenvironmental and archaeological fieldwork has been undertaken at Willendorf II (Austria), a key site for this time period. This project has concluded that modern humans producing Aurignacian stone tools occupied Central Europe about 43,500 years ago in a medium-cold steppe environment with some boreal trees along valleys. This discovery represents the oldest well-documented occurrence of behaviorally modern humans in Europe and demonstrates contemporaneity with Neanderthals in other parts of Europe, showing that behaviorally modern humans and Neanderthals shared this region longer than previously thought.

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Here, we provide high-resolution environmental and chronological data for modern human occupation in the form of an Early Aurignacian archaeological horizon at Willendorf II, Austria. The site of Willendorf II (48° 19' 23.50" N, 15° 24' 15.20" E), an open-air locality in the Danube Valley, preserves a long loess–paleosol sequence with abundant archaeological remains (23, 24). The site has been excavated several times between 1908 and 1955 (*SI Appendix, SI Text*). Since 2006, new excavations have been undertaken (25). The chronological framework of the site rests on more than 50 radiocarbon dates produced on charcoal samples dated by the Groningen and Oxford radiocarbon laboratories, placing the sequence between 48,000 and 25,000 radiocarbon B.P. (~55,000–29,000 cal B.P.) (Fig. 1 and *SI Appendix, SI Text* and *Table S1*).

Key to current debates of early modern human settlement in Europe is archaeological horizon (AH) 3. In the past, AH 3 has

been attributed to the Early Aurignacian (17, 28–30) based on typical stone tool types (carinated endscraper, nosed endscraper, Aurignacian blade) and the blank production modes (disassociation of blade and bladelet production sequences) (*SI Appendix, Table S2*). This classification has been criticized, and the possibility that AH 3 represents a transitional assemblage has been raised (31). The old collection ($n = 48$) on which this previous discussion was based has been enlarged recently by the discovery of a box of lithic artifacts from the old excavations. This expanded old collection ($n = 490$) can be attributed securely to the Early Aurignacian (*SI Appendix, Tables S2 and S3*) (17, 29). Our new excavations have reopened the old excavations' trenches, correlated our new main section with the old western section (25), and produced a new lithic assemblage from AH 3. The location of AH 3 in our lithological layer C8-3 is in agreement with descriptions in the old excavations' reports. Importantly, the correlation of new and old collections is proven by several refits (Fig. 2 and *SI Appendix, SI Text*) of lithic artifacts from our new assemblage with specimens in the old collections. We also attribute the new collection to the Early Aurignacian based on its lithic technology, as described below.

Results

The Archaeological Collection. The AH 3 assemblage from the 2006–2011 excavations consists of 32 lithic artifacts and 23 faunal remains. The latter comprise fragments smaller than 20 mm, and most are burned. The bones are not identifiable to species, and their surface preservation hinders an assessment of anthropogenic modifications. It is unclear whether the burning is anthropogenic.

All lithic artifacts are made of different varieties of hornstones/cherts that occur in the local Danube gravels. Most of the lithic artifacts are flakes (*SI Appendix, Table S4*); there also are bladelets, chips, one core tablet, and shattered pieces. In total, five lithic artifacts show exposure to heat in the form of color change, craquelation, and/or irregular breakage surfaces. Unfortunately, these five heated specimens were too small for thermoluminescence dating. All lithic objects have fresh edges, i.e., they are unabraded, and show no traces of rounding or similar damage typical of postdepositionally reworked assemblages. Although 20 specimens show no edge damage, 12 exhibit unifacial damage probably deriving from use. Furthermore, the lithic artifacts vary in size and weight and include small and larger items, suggesting no redeposition reflected in typical differential movement of objects of different size (i.e., no size-sorting). These characteristics of the assemblage correspond well with the pedosedimentary data (*SI Appendix, SI Text*) showing that AH 3 was not affected by large-scale, postdepositional reworking.

The attribution of the new collection to the Early Aurignacian is based on the bladelet technology. Refitted artifacts between the new and old collection confirm this classification. These refitted artifacts directly connect our new small collection of 32 lithics with the larger collection from the 1908–1955 excavations ($n = 490$).

Bladelet technology. The bladelets from AH 3 demonstrate the presence of two bladelet production schemes, both suggesting a disassociation of blade and bladelet technology (for definitions see *SI Appendix, SI Text*). The bladelet WII-L20-2492 (Fig. 24 and *SI Appendix, SI Text*) is 8.60 mm long, 3.25 mm wide, and 1.16 mm thick and shows skewing to the right but no twisting. Such morphology is characteristic of a reduction sequence using carinated/nosed endscrapers as cores. This technique is well documented for the Early and Late Aurignacian in Western Europe (32). In this context it is interesting that the length of bladelet WII-L20-2492 is in the lower range of length of the last removals of carinated endscraper-cores from the old collection, indicating that WII-L20-2492 originated from a carinated endscraper-core similar in size to those represented in the

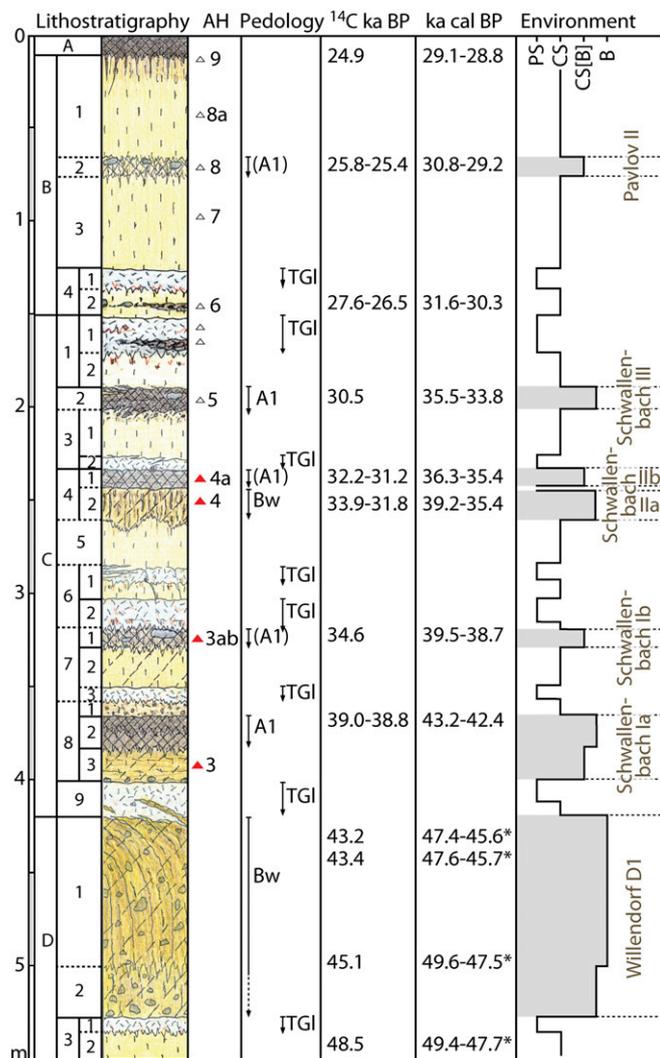


Fig. 1. Stratigraphic column of the Willendorf II sequence showing the position of AH 3–9 pedological features (A1, humic horizon; Bw, incipient B horizon; TGI, tundra gley), stratigraphic position of radiocarbon dates obtained on charcoal [shown in thousands of years (ka) B.P.; *SI Appendix, Table S1*], paleoenvironmental reconstruction (PS, periglacial steppe; CS, cold steppe; CS[B], medium-cold steppe with some boreal trees along valleys; B, boreal), and the interstadials (brown font) documented at Willendorf II. Radiocarbon ages were calibrated using the IntCal13 calibration curve (26) and OxCal 4.2.3 software (27). Asterisks (*) mark out-of-range dates. The key to the graphic symbols is given in *SI Appendix, Fig. S20*.

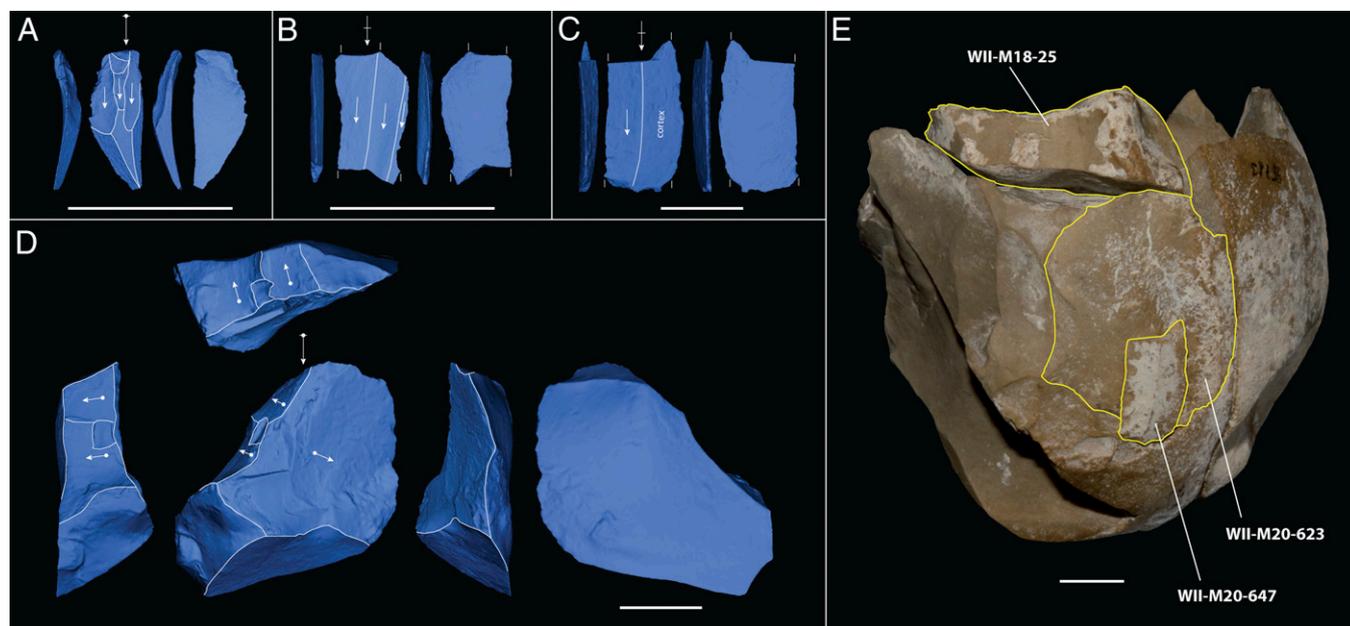


Fig. 2. Lithic artifacts of AH 3 at Willendorf II. (A) Bladelet WII-L20-2492. (B) Bladelet fragment WII-M20-640. (C) Bladelet fragment WII-M20-647. (D) Core tablet WII-M18-25. (E) Refitted lithic artifacts of the new collection (yellow outline; WII-M18-25, WII-M20-623, WII-M20-647) and the old collection (no outline). (Scale bars: 10.00 mm in all images.) Images A–D were created from 3D models of the lithics (SI Appendix, SI Text). The key to graphic symbols is given in SI Appendix, Fig. S21.

old collection. A second bladelet (WII-M20-640, Fig. 2B and SI Appendix, SI Text) is a medial fragment 8.12 mm long, 4.48 mm wide, and 0.89 mm thick. Its dorsal face demonstrates unidirectional core exploitation. The bladelet fragment shows no skewing or twisting and could have been produced using carinated/nosed endscraper-cores, but, because it is fragmented and hence lacking some diagnostic landmarks, it also could have been made using other bladelet production techniques. A third bladelet, WII-M20-647 (Fig. 2C and SI Appendix, SI Text), is a medial fragment that is 18.60 mm long, 9.80 mm wide, and 2.31 mm thick. The direction of the dorsal scar, the absence of twisting or skewing, and its rather wide width (9.80 mm) suggest that this bladelet was produced from a unidirectional, prismatic core. Moreover, systematic refitting studies conducted on the AH 3 lithic collection showed that WII-M20-647 could be refitted onto the flake WII-M20-623. This sequence refit shows that, in addition to WII-M20-647, at least one more bladelet of the same morphology was removed. These large, straight bladelets without torsion or skewing are obtained from a unidirectional, prismatic core. This type of bladelet production is described for early phases of the Aurignacian in Western Europe, the Proto-Aurignacian, and Early Aurignacian (32). Taken together, the co-occurrence of these two bladelet production schemes demonstrated by WII-L20-2492 and WII-M20-647 strongly suggests an Early Aurignacian attribution of the small new assemblage, and this classification is supported by the old collection that also shows the co-occurrence of these two bladelet production schemes (17).

Refitted artifacts. During systematic refitting studies, four lithic artifacts from the 2006–2011 collection and three from the 1908–1909 collection could be refitted (Fig. 2E and SI Appendix, SI Text). From the new collection, bladelet WII-M20-647, flakes WII-M20-623 and WII-M20-641, and core tablet WII-M18-25 (Fig. 2D and SI Appendix, SI Text) refit onto a core (WII-95782) and two pieces of shatter (WII-95783 and WII-95784) from the old collection. This refit group supports our classification of the 2006–2011 assemblage as Early Aurignacian for two reasons. First, it demonstrates that the above-mentioned special reduction

sequence for producing large bladelets (e.g., WII-M20-647) does not result from the reduction of a larger blade core and hence shows a disassociation of blade and bladelet production typical of Early Aurignacian (32). This conclusion is based on the size of the original nodule (estimated to be only ~80 mm) and the amount of cortex on the refitted artifacts, as well as the convexity of cortical areas. Second, this refit group directly connects our small collection of 32 lithics with the larger collection from the 1908–1955 excavations comprising 490 lithics, including typical stone tool types (carinated endscraper, nosed endscraper, Aurignacian blade), two specific bladelet production schemes (one using carinated/nosed endscraper-cores, the other using small prismatic cores), and a clear disassociation of the blade and bladelet production typical of the Early Aurignacian material culture tradition (17, 29). Material culture traditions, described by variation in the way tools are made, are learned behaviors that are passed on between generations (14). The Early Aurignacian material culture tradition as defined above differs significantly from that of the Proto-Aurignacian, which is characterized by a bladelet production from reduced larger blade cores resulting in larger bladelets than in the Early Aurignacian.

Age, Environmental Context, and Chronostratigraphic Position of the Archaeology. The age and chronostratigraphic position of AH 3's Early Aurignacian in lithological layer C8-3 is constrained by a combination of climatostratigraphy and radiocarbon dating. The upper 5 m of the sequence show evidence of seven interstadial paleosols separated from each other by loess deposits and tundra gley paleosols, indicative of stadial conditions. Here, we concentrate on the part of the sequence most important for the context of AH 3, units D3–C7 (Fig. 3 and SI Appendix, SI Text and Fig. S3). A first paleosol is recorded in D2–D1 resting on top of the D3 loess. It is developed in ~1 m of colluvial deposits with a strong polyhedral structure and biogenic activity (burrows) pointing to a brown boreal soil. This classification correlates with the boreal mollusk assemblages (SI Appendix, SI Text and Table S5) ascribed to the Willendorf D1 Interstadial

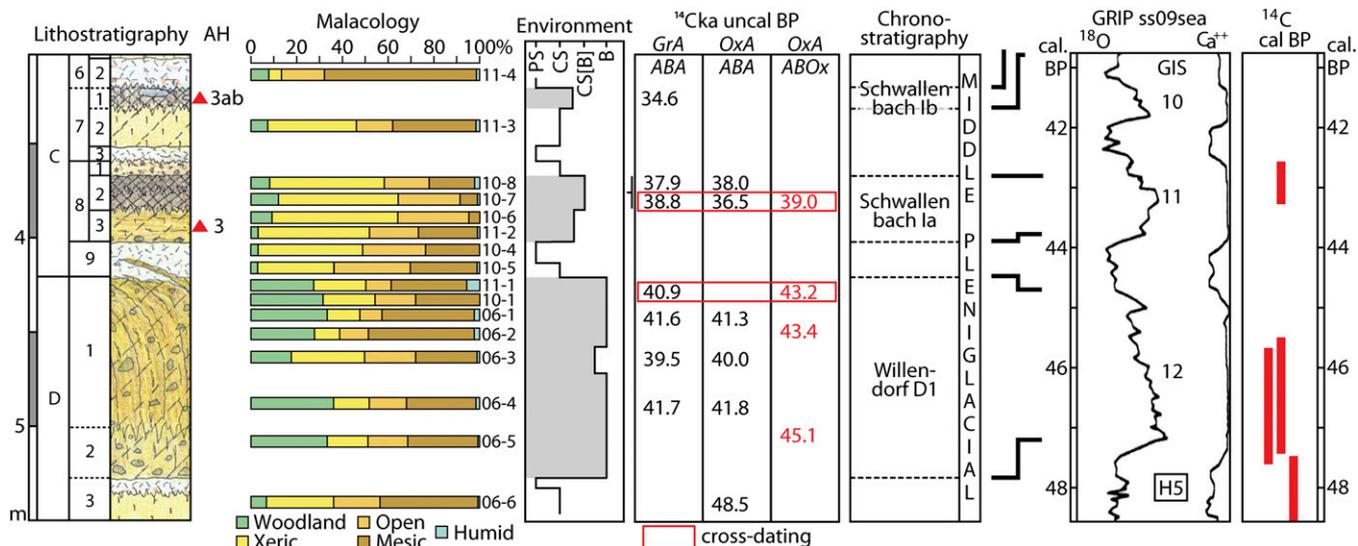


Fig. 3. Correlation of the lower part of the Willendorf II sequence and the Greenland ice-core climatic data showing the chronostratigraphic position of AH 3 at the onset of GIS 11. Shown are the lithostratigraphy, the position of AH 3 and AH 3ab, malacological data (numbers right of the bars are sample IDs in *SI Appendix, Tables S5 and S6*), paleoenvironment (PS, periglacial steppe; CS, cold steppe; CS[B], medium-cold steppe with some boreal trees along valleys; B, boreal), radiocarbon dates [in uncalibrated (uncal) ka B.P.; grouped by radiocarbon laboratory and sample pretreatment; GrA, Groningen radiocarbon laboratory; OxA, Oxford radiocarbon laboratory; cross-dating: radiocarbon dates on the same, homogenized sample (33)], interstadials defined at Willendorf II, correlation with the GRIP ss09sea data (H5, Heinrich event 5), and calibrated radiocarbon ages (in ka cal B.P.; *SI Appendix, Table S1*) for the samples with ABOx-SC pretreatment. Radiocarbon ages were calibrated using the IntCal13 calibration curve (26) and OxCal 4.2.3 software (27). The key to the graphic symbols is given in *SI Appendix, Fig. S20*.

(24). A major break occurs on top of D1; the overlying lithological complex C records conditions characterized as cold steppe to medium-cold steppe with some boreal trees. Unit C9 demonstrates aeolian input of sandy silt and development of a tundra gley soil suggesting deep frost or permafrost conditions (34), i.e., periglacial steppe conditions. Later, parts of C9 were eroded before the deposition of loamy sediment. C8-3 contains AH 3. C8-3's pedosedimentary and malacological data suggest a slight improvement in climatic conditions (Fig. 3 and *SI Appendix, SI Text and Table S5*). Immediately after the deposition of C8-3, a humic horizon of pararendzina type (C8-2) developed under a medium-cold steppe environment with boreal trees in river valleys. No evidence of aeolian sedimentary input (suggesting stadial conditions) or an erosional event (removing such input) was observed between C8-3 and C8-2. The absence of such evidence suggests that both units belong to the same interstadial (Schwallenbach Ia Interstadial). After localized erosion and solifluction, a new input of aeolian material (C7) preceded the development of a second weak humic horizon (C7-1), ascribed to the Schwallenbach Ib Interstadial (Figs. 1 and 2 and *SI Appendix, SI Text, Fig. S3, and Table S5*).

Maximum and minimum ages for AH 3 are provided by radiocarbon dates of charcoal from below and above C8-3; the horizon itself contains only scattered small charcoal fragments unsuitable for radiocarbon dating. The directly underlying unit C9 lacks any charcoal; therefore, AH 3's maximum age is provided by radiocarbon dates obtained on charcoal from D1, between 45,000 and 43,000 B.P. (~48,000–46,000 cal B.P.) (Fig. 3 and *SI Appendix, SI Text and Table S1*). AH 3's younger age limit is constrained by dating of *Picea/Larix* charcoal from the overlying C8-2 paleosol to ~39,000 B.P. (~43,000 cal B.P.). Based on environmental and radiometric data, the Willendorf D1 Interstadial in D2–D1 can be correlated with Greenland Interstadial (GIS) 12 (35) of the Greenland Ice Core Project (GRIP) ss09sea (36), which shows the best agreement with calibrated ages of radiocarbon dates obtained for D1 (Fig. 3 and *SI Appendix, SI Text and Table S1*). Similarly, we correlate the Schwallenbach Ia

Interstadial (C8-3 and C8-2) with GIS 11 (*SI Appendix, SI Text*), thus placing AH 3 at the onset of GIS 11 at ~43,500 cal B.P.

Discussion

The chronostratigraphic position of AH 3's lithic and faunal assemblages at the onset of GIS 11 (~43,500 cal B.P.), its cultural attribution to the Early Aurignacian, and its presence in a medium-cold steppe environment raise a number of discussion points.

Age and Chronostratigraphy. The chronostratigraphic position of AH 3 shows that modern humans were present in Central Europe at least slightly before 43,300 cal B.P., at the onset of the cool Schwallenbach Ia Interstadial. This age is in strong contrast to late appearance models (based on radiocarbon chronology) according to which the Early Aurignacian occurs within an extremely cold event synchronous with the North Atlantic Heinrich Event 4 (19, 37), dated ~40,200–38,300 cal B.P. (*SI Appendix, Fig. S16*). Similarly, models arguing for a first appearance of the Aurignacian after ~41,500 cal B.P. (31) must be questioned based on AH 3's age. Comparison with other Aurignacian sites in Central Europe shows that most other sites are younger and technologically different (e.g., Stránská skála, Stratzing, and Alberndorf), or chronostratigraphic information is not available because of their excavation decades ago (e.g., Krems-Hundssteig and Senftenberg) (17). Although significantly younger than AH 3, the Early Aurignacian assemblage of Geißenklösterle-AH III in Germany, modeled to between 42,940 and 39,910 cal B.P. (38), and the Aurignacian bone point of Peskő in Hungary, dated to between 41,730 and 40,265 cal B.P. (39) (*SI Appendix, Fig. S16 and Table S11*), also predate the North Atlantic Heinrich Event 4 and therefore support our early appearance model (17).

Environmental Conditions. The high paleoenvironmental resolution of the Willendorf II sequence, combined with high-quality radiocarbon dating, provides a unique opportunity to discuss the environmental context of the first anatomically and behaviorally modern humans in Central Europe. The mollusk and charcoal

records at Willendorf II indicate that the first evidence (to our knowledge) of modern human presence in AH 3 appears in a medium-cold steppe with some boreal trees along the Danube. In fact, attempts to compare our datasets with those of other sites point out the scarcity of high-resolution environmental datasets for the time period of modern human dispersal into Europe. The great majority of currently available information on the environmental or climatic context of this dispersal is inferred from calibrated radiocarbon dates and their correlation with the Greenland Ice records (10, 19, 38) rather than from independent environmental datasets. The problem with such an approach is that ages provided by radiocarbon dating, even when modeled (38), often overlap with more than one climatic event, i.e., at least one warm interstadial and one cold stadial. Therefore, such an approach can provide only very low-resolution environmental data. Additionally, the resulting environmental context provides information only about temperature ($\delta^{18}\text{O}$ data of the ice record). Key factors for changes in the environment include moisture and nutrient availability, not temperature alone (40). Moisture and nutrient availability are of crucial importance for animal abundance and diversity, especially for large herbivores (41). Similarly, one can argue that late Neanderthal and modern human settlement and survival were constrained by such factors (42).

Our environmental data indicating a medium-cold steppe with boreal trees are in contrast with the few other available studies. For Western and Central Europe, two conflicting scenarios have been proposed. One assumes that the Aurignacian first appeared under very cold conditions, i.e., the Heinrich 4 (H4) event (19, 37, 43). Such a scenario for Central Europe is quite unlikely based on both AH 3's chronostratigraphic position and the environmental data. The second scenario proposes that Aurignacian modern humans in Western Europe first appeared during a period of climatic warming, e.g., GIS 10 or 11 (2), under at least partially wooded conditions as opposed to colder, open tundra or steppe conditions (44). It also has been argued that these environmental conditions were similar to those of the warmer, more forested regions of southeastern Europe and, hence, that Early Aurignacian modern humans might have come from southeastern Europe, tracking these environments as they expanded further north and west (2, 45). This scenario is in stark contrast to our central European data showing modern human presence in a medium-cold steppe environment. If the pattern for Western and Southern Europe holds true, the evidence would suggest that the first modern humans in Europe were well-adapted to a variety of environments, i.e., both warm forest in Western and Southern Europe, and cold steppe in Central Europe. Their presence in such different environmental settings suggests flexibility and resilience rather than specialization or focus on a single type of environment.

Implications. The attribution of AH 3 to the Early Aurignacian and its chronostratigraphic position have implications for the taxonomic and chronological relationship of the two early phases of the Aurignacian (Proto-Aurignacian and Early Aurignacian). Until now, it has been argued the Proto-Aurignacian is older than the Early Aurignacian, i.e., that differences between the two phases are solely a factor of time (19, 30, 32). AH 3 shows that, at least for Central Europe, this argument is not valid. The AH 3 Early Aurignacian overlaps with the first Proto-Aurignacian assemblages (46, 47) elsewhere in Europe (*SI Appendix, Fig. S17*). This overlap suggests that the Proto- and Early Aurignacian might represent different developmental trajectories of modern humans foraging within Europe. A cultural interpretation of this distinction might be that the Proto-Aurignacian and Early Aurignacian represent the southern and northern dispersal routes, respectively, of modern humans within Europe (2). Alternatively, the differences between the Proto-

and Early Aurignacian could relate to the exploitation of specific foraging niches requiring different food-acquisition technologies. Future explanations of the differences between Proto- and Early Aurignacian should consider factors such as site function, occupation density, and adaptation to particular environments, e.g., seasonally different mobility of populations in the Mediterranean eco-zone and in the cold-steppe conditions at Willendorf II when explaining the differences between Proto- and Early Aurignacian (7, 13, 17, 46).

The ~43,500 cal B.P. age of AH 3 has significant implications for the appearance of behaviorally modern humans in Europe and their potential contact with Neanderthals. AH 3 predates the oldest directly dated modern human remains in Europe (*SI Appendix, Fig. S18*) and all other Early Aurignacian assemblages (*SI Appendix, Fig. S16*). Thus, it pushes back the presence of modern humans in Central Europe to at least ~43,500 cal B.P. Based on the correlation of the Bohunice soil in southern Moravia with GIS 12 (35, 48), the Bohunician of the Middle Danube region is interpreted as evidence of modern human presence there in GIS 12 (3, 14–16, 20) or predating GIS 12 (17). Until now, no modern human remains have been discovered in association with this industry. In addition, the Bohunician, in contrast to the Aurignacian, has not yet yielded clear evidence of a fully modern material culture including evidence of symbolic artifacts, although this absence may be related in part to taphonomic factors. Currently, behaviorally modern humans are first documented with the Central European Aurignacian and potentially with the Italian Uluzzian (18), although the association between the modern human teeth and Uluzzian artifacts has been questioned (19). However, the age of AH 3 overlaps or predates the latest directly dated Neanderthal remains (*SI Appendix, Fig. S19*) (49, 50) and thus suggests direct or indirect contact between the two species on a European scale, potentially leading to interbreeding and acculturation. The evidence presented here shows that behaviorally modern humans occupied Central Europe in an environment characterized as medium-cold steppe with some boreal trees. To our knowledge, this conclusion offers the first, high-resolution environmental record for early modern human settlement of Europe and, together with other available data, suggests that modern humans occupying Europe ~43,500 cal B.P. were well adapted to a variety of environmental conditions.

Methods

The fieldwork methodology at Willendorf II involved excavation of loessic deposits and the recording of the stratigraphic context as well as the 3D position of all objects ≥ 5 mm. Charcoal for dating was sampled according to a special protocol, including sampling from freshly cleaned vertical sections to control the microstratigraphic position of each sample precisely. A full description of our fieldwork and sampling methodology is provided in *SI Appendix*.

For the analysis of lithic artifacts, attribute analysis was applied, and reduction sequences were reconstructed. Faunal analysis included specimen identification, examination of bone surfaces for anthropogenic and natural modifications, and classification of burning stages. Charcoal was dried, cleaned, and identified; only *Pinus cembra*-type, *Picea*, *Picea/Larix*, or *Larix*-type charcoal was used for radiocarbon dating with acid-base-acid (ABA) pretreatment and acid-base-wet oxidation chemical pretreatment, followed by stepped combustion (ABOx-SC) in the Groningen and Oxford Accelerator Mass Spectrometry laboratories. Site-formation processes were assessed by a combination of geological, geoarchaeological (including micromorphology), and microstratigraphic analyses. GIS analysis of 3D recorded objects and fabric analysis on archaeological objects were carried out. Paleoenvironmental reconstruction is based on the pedosedimentary signature of the deposits and the rich charcoal material and mollusk fauna. Our approach to chronostratigraphy combines litho- and climatostratigraphic work with a robust chronological framework based on reliable radiocarbon dates. A detailed explanation of our laboratory methodology is provided in *SI Appendix*.

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- Klein RG (2008) Out of Africa and the evolution of human behavior. *Evol Anthropol* 17(6):267–281.
- Mellars P (2006) Archeology and the dispersal of modern humans in Europe: Deconstructing the "Aurignacian". *Evol Anthropol* 15(5):167–182.
- Hublin JJ (2012) The earliest modern human colonization of Europe. *Proc Natl Acad Sci USA* 109(34):13471–13472.
- Trinkaus E, et al. (2003) An early modern human from the Peștera cu Oase, Romania. *Proc Natl Acad Sci USA* 100(20):11231–11236.
- Reyes-Centeno H, et al. (2014) Genomic and cranial phenotype data support multiple modern human dispersals from Africa and a southern route into Asia. *Proc Natl Acad Sci USA* 111(20):7248–7253.
- Prüfer K, et al. (2014) The complete genome sequence of a Neanderthal from the Altai Mountains. *Nature* 505(7481):43–49.
- Davies W (2001) A very model of a modern human industry: New perspectives on the origins and spread of the Aurignacian in Europe. *Proceedings of the Prehistoric Society* 67:195–217.
- Zilhão J, d'Errico F (2003) *The Chronology of the Aurignacian and of the Transitional Technocomplexes: Dating, Stratigraphies, Cultural Implications* (Instituto Português de Arqueologia, Lisbon).
- Conard NJ (2006) *When Neanderthals and Modern Humans Met* (Kerns, Tübingen, Germany).
- Higham T, et al. (2011) The earliest evidence for anatomically modern humans in northwestern Europe. *Nature* 479(7374):521–524.
- White M, Pettitt P (2012) Ancient digs and modern myths: The age and context of the Kent's Cavern 4 maxilla and the earliest Homo sapiens specimens in Europe. *Eur J Archaeol* 15(3):392–420.
- Hublin JJ, The modern human colonization of western Eurasia: When and where? *Quaternary Science Reviews*, in press.
- Davies W (2007) Re-evaluating the Aurignacian as an expression of modern human mobility and dispersal. *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, UK), pp 263–274.
- Tostevin GB (2012) *Seeing Lithics: A Middle-Range Theory for Testing for Cultural Transmission in the Pleistocene* (Oxbow Books, Oxford, UK).
- Bar-Yosef O (2006) Neanderthals and modern humans: A different interpretation. *When Neanderthals and Modern Humans Met*, ed Conard NJ (Kerns, Tübingen, Germany), pp 467–482.
- 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.
- Nigst PR (2012) *The Early Upper Palaeolithic of the Middle Danube Region* (Leiden Univ Press, Leiden, The Netherlands).
- Benazzi S, et al. (2011) Early dispersal of modern humans in Europe and implications for Neanderthal behaviour. *Nature* 479(7374):525–528.
- Banks WE, d'Errico F, Zilhão J (2013) Human-climate interaction during the Early Upper Paleolithic: Testing the hypothesis of an adaptive shift between the Proto-Aurignacian and the Early Aurignacian. *J Hum Evol* 64(1):39–55.
- Müller UC, et al. (2011) The role of climate in the spread of modern humans into Europe. *Quat Sci Rev* 30(3-4):273–279.
- Zilhão J (2006) Genes, fossils, and culture. An overview of the evidence for Neanderthal-modern human interaction and admixture. *Proceedings of the Prehistoric Society* 72:1–20.
- Tzedakis PC, Hughen KA, Cacho I, Harvati K (2007) Placing late Neanderthals in a climatic context. *Nature* 449(7159):206–208.
- Felgenhauer F (1959) *Willendorf in der Wachau. Monographie der Paläolith-Fundstellen I–VII* (Rohrer, Vienna).
- Haesaerts P, Dambon F, Bachner M, Trnka G (1996) Revised stratigraphy and chronology of the Willendorf II sequence, Lower Austria. *Archaeologia Austriaca* 80: 25–42.
- Nigst PR, et al. (2008) New research on the Aurignacian of Central Europe: A first note on the 2006 fieldwork at Willendorf II. *Quartär* 55:9–15.
- Reimer P, et al. (2013) IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon* 55(4):1869–1887.
- Bronk Ramsey C (2009) Bayesian analysis of radiocarbon dates. *Radiocarbon* 51(1): 337–360.
- Hahn J (1977) *Aurignacien: Das ältere Jungpaläolithikum in Mittel- und Osteuropa* (Böhlau, Cologne, Germany).
- Nigst PR (2006) *The first modern humans in the Middle Danube Area? New Evidence from Willendorf II (Eastern Austria). When Neanderthals and Modern Humans Met*, ed Conard NJ (Kerns, Tübingen, Germany), pp 269–304.
- Teyssandier N (2007) *En route vers l'Ouest: Les Débuts de l'Aurignacien en Europe* (John and Erica Hedges Ltd., Oxford, UK).
- Zilhão J, d'Errico F (1999) The chronology and taphonomy of the Earliest Aurignacian and its implications for the understanding of Neanderthal extinction. *J World Prehist* 13(1):1–68.
- Le Brun-Ricalens F, Bordes JG, Bon F (2005) Productions Lamellaires Attribuées à l'Aurignacien: Chaînes Opératoires et Perspectives Technoculturelles (Musée National D'histoire Et D'art, Luxembourg).
- Haesaerts P, Dambon F, Nigst P, Hublin JJ (2013) ABA and ABOx radiocarbon cross-dating on charcoal from Middle Pleniglacial loess deposits in Austria, Moravia, and Western Ukraine. *Radiocarbon* 55(3-4):641–647.
- Haesaerts P (1983) Stratigraphic distribution of periglacial features indicative of permafrost in the Upper Pleistocene loesses of Belgium. *Permafrost. Proceedings of the Fourth International Conference* (National Academy, Washington D.C.), pp 421–426.
- Haesaerts P, et al. (2009) Climatic signature and radiocarbon chronology of Middle and Late Pleniglacial loess from Eurasia: Comparison with the marine and Greenland records. *Radiocarbon* 51(1):301–318.
- Johnsen SJ, et al. (2001) Oxygen isotope and palaeotemperature records from six Greenland ice-core stations: Camp Century, Dye-3, GRIP, GISP2, Renland and North-GRIP. *J Quaternary Sci* 16(4):299–307.
- 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(5):782–802.
- Higham T, et al. (2012) Testing models for the beginnings of the Aurignacian and the advent of figurative art and music: The radiocarbon chronology of Geißenklösterle. *J Hum Evol* 62(6):664–676.
- Davies W, Hedges R (2008) Dating a type site: Fitting Szeleta cave into its regional chronometric context. *Praehistoria* 9–10:35–45.
- Guthrie RD, Kolfschoten TV (2000) Neither warm and moist, nor cold and arid: The ecology of the Mid Upper Palaeolithic. *Hunters of the Golden Age. The Mid Upper Palaeolithic of Eurasia 30,000 – 20,000 BP*, eds Roebroeks W, Mussi M, Svoboda J, Fennema K (Leiden University, Leiden), pp 13–20.
- Olff H, Ritchie ME, Prins HHT (2002) Global environmental controls of diversity in large herbivores. *Nature* 415(6874):901–904.
- Verpoorte A (2009) Limiting factors on early modern human dispersals: The human biogeography of late Pleniglacial Europe. *Quat Int* 201(1-2):77–85.
- Conard NJ, Bolus M, Goldberg P, Münzel SC (2006) The Last Neanderthals and First Modern Humans in the Swabian Jura. *When Neanderthals and Modern Humans Met*, ed Conard NJ (Kerns, Tübingen, Germany), pp 305–341.
- van Andel TH, Davies W (2003) Neanderthals and modern humans in the European landscape during the last glaciation: Archaeological results of the Stage 3 Project (McDonald Institute for Archaeological Research, University of Cambridge, Cambridge, UK).
- Mellars P (1998) The impact of climatic changes on the demography of late Neanderthal and early anatomically modern populations in Europe. *Neanderthals and Modern Humans in Western Asia*, eds Akazawa T, Aoki K, Bar-Yosef O (Plenum, New York), pp 493–507.
- Szmidt CC, Normand C, Burr GS, Hodgins GW, LaMotta S (2010) AMS 14C 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.
- 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.
- Valoch K (2008) Brno-Bohunice, eponymous Bohunician site: New data, new ideas. *Man - Millennia - Environment. Studies in Honour of Romuald Schild*, eds Sulgowski Z, Tomaszewski J (Polish Academy of Sciences, Warsaw), pp 225–236.
- Semal P, et al. (2009) New data on the late Neanderthals: Direct dating of the Belgian Spy fossils. *Am J Phys Anthropol* 138(4):421–428.
- Hublin JJ, et al. (2012) Radiocarbon dates from the Grotte du Renne and Saint-Césaire support a Neanderthal origin for the Châtelperronian. *Proc Natl Acad Sci USA* 109(46): 18743–18748.