Direct radiocarbon dates for Vindija G_1 and Velika Pećina Late Pleistocene hominid remains

Fred H. Smith*[†], Erik Trinkaus[‡§], Paul B. Pettitt[¶‖], Ivor Karavanić**, and Maja Paunović[††]

*Department of Anthropology, Northern Illinois University, DeKalb, IL 60115; [‡]Department of Anthropology, Campus Box 1114, Washington University, St. Louis, MO 63130; [§]Unite Mixte de Recherche 5809 du Centre National de la Recherche Scientifique, Laboratoire d'Anthropologie, Université de Bordeaux I, 33405 Talence, France; [¶]Radiocarbon Accelerator Unit, Research Laboratory for Archaeology and the History of Art, University of Oxford, 6 Keble Road, Oxford OX1 3QJ, United Kingdom; [‖]Keble College, University of Oxford, Oxford OX1 3PG, United Kingdom; **Arheološki Zavod, Filozofskog Fakulteta Sveučilišta u Zagrebu, I. Lučića 3, HR-10000 Zagreb, Croatia; and [††]Zavod za Paleontologiju i Geologiju Kvartara Hrvatske Akademije Znanosti i Umjetnosti, Ulica A. Kovačića 5/II, HR-10000 Zagreb, Croatia

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New accelerator mass spectrometry radiocarbon dates taken directly on human remains from the Late Pleistocene sites of Vindija and Velika Pećina in the Hrvatsko Zagorje of Croatia are presented. Hominid specimens from both sites have played critical roles in the development of current perspectives on modern human evolutionary emergence in Europe. Dates of ≈28 thousand years (ka) before the present (B.P.) and ≈29 ka B.P. for two specimens from Vindija G_1 establish them as the most recent dated Neandertals in the Eurasian range of these archaic humans. The human frontal bone from Velika Pećina, generally considered one of the earliest representatives of modern humans in Europe, dated to ≈5 ka B.P., rendering it no longer pertinent to discussions of modern human origins. Apart from invalidating the only radiometrically based example of temporal overlap between late Neandertal and early modern human fossil remains from within any region of Europe, these dates raise the question of when early modern humans first dispersed into Europe and have implications for the nature and geographic patterning of biological and cultural interactions between these populations and the Neandertals.

Neandertals | early modern humans | Croatia | Europe

The nature of the biological relationship between Neandertals and early modern humans remains highly contentious in paleoanthropology (1). The fundamental questions have changed little since the debates surrounding the initial Neandertal discoveries during the last half of the 19th century (2–4); they focus on the taxonomy, phylogenetic position, and "humanness" of these archaic people. Although these questions have not changed, the complexity and diversity of the data, methodologies, and models used to approach them have increased significantly. In addition to the accumulation of pertinent fossil remains and traditional morphological and morphometric analyses of both fossil and recent human skeletal series, studies of genetic variability in recent and ancient humans are seen frequently as having revolutionized scientific perspectives on Late Pleistocene human evolution. Although not as widely acknowledged, changes to the chronological framework of the Late Pleistocene hominid remains and archeological complexes that have resulted from the application of several chronometric methods have also fundamentally impacted perspectives on the Neandertals and their role in modern human origins.

Analyses of morphology and morphometrics have constituted the core of the debates on fossil human systematics, and continue to drive current perspectives on the Neandertals. For example, several recent morphological studies have rekindled the search for anatomical features or/and complexes that represent uniquely derived (autapomorphic) characters for Neandertals (5–8). These studies normally also advocate that such features establish Neandertals as a species distinct from *Homo sapiens* and that the Neandertals had, at best, marginal biological input into early modern human populations in Eurasia. Alternatively, analyses of specific aspects of morphology have been argued to demonstrate varying degrees of regional continuity in Eurasia, linking the Neandertals in western Eurasia to early modern humans (9–12). Such studies frequently place the Neandertals within *Homo sapiens* and promote some degree of ancestral status for the Neandertals. Still other studies, although not necessarily taking positions on issues of systematics, have challenged the validity of many of the proposed autapomorphies that were used to distinguish the Neandertals from other late Pleistocene groups (13–16).

Partially because of the differing interpretations of morphological patterns, genetic studies have exerted an important influence on current interpretations of Neandertal evolutionary history. Data on the mtDNA structure of a single Neandertal individual (17, 18) and the patterns of variation of mtDNA and other genetic systems in recent human samples (19–21) have been presented as refuting any Neandertal contribution to western Eurasian early modern human gene pools. It is often implied that there is unanimity among geneticists in support of these interpretations; but several researchers have questioned these conclusions, arguing that the genetic data are also commensurate with models of Late Pleistocene human phylogeny, involving varying degrees of regional continuity (22–25).

A reasoned consideration of these debates and of the human paleontological and molecular arguments finds that the analyses of both sets of data have serious limitations. Both data sets are restricted in terms of sample size, completeness, and distributions in time and space, and the associated analyses contain layered *a priori* assumptions, some of which can be refuted, and many of which are currently untestable. Increasing recognition of these ambiguities has led to a softening of positions regarding modern human origins and the fate of the Neandertals.

Chronology and Perspectives on Neandertal Phylogeny

Morphological and genetic studies appear to be the driving forces molding current interpretations of Late Pleistocene human evolution in general and the fate of the Neandertals in particular. It is important to realize that changes in the chronological framework in which the fossil evidence is interpreted have been equally critical, although often less overtly so, to the current state of scientific perspectives on these issues (26). This impact is best documented by the fact that, up through the mid-1980s, it was not possible to demonstrate conclusively either a differential temporal pattern for the appearance of modern human morphology across the Old World or a temporal overlap of early modern and archaic humans in any specific region (27, 28). Beginning in the last half of the 1980s, the application of thermoluminescence (TL), ESR, uranium series, and accelerator mass spectrometry (AMS) radiocarbon dating to pertinent sites

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Abbreviations: AMS, accelerator mass spectrometry; ka, thousand years; TL, thermoluminescence.

[†]To whom reprint requests should be addressed. E-mail: fsmith@niu.edu.

Table 1. Non-Croatian European sites

Site (Country)	Specimens present	Cultural association	Dating technique	Date (ref.)
Neandertal				
St. Césaire (France)	Adult partial skeleton	Châtelperronian	TL*	36.3 ± 2.7 ka (48)
Arcy-sur-Cure (France)	Teeth, subadult temporal	Châtelperronian	AMS*	33.82 ± 0.72 ka (37)
Probable Neandertal				
Bacho Kiro (Bulgaria)	Fragmentary pieces of maxilla and mandible, teeth	Bachokirian	^{14}C*	>43 ka (44, 45)
Early Modern Human				
Vogelherd (Germany)	Two adult calvaria, humerus, mandible, vertebrae	Aurignacian	^{14}C*	31.9 ± 1.1 ka (47, 49)
Kent's Cavern (England)	Maxilla	British Upper Paleolithic	AMS†	30.9 ± 0.9 ka (50)
Hahnöfersand (Germany)	Adult frontal	None	^{14}C, AAR†	36.3 ± 0.6 ka, 36.0 ka (51)
Kelsterbach (Germany)	Adult calvarium	None	^{14}C, AAR†	31.2 ± 0.6 ka, 32.0 ka (52)
Probable Early Modern Human				
Istállóskö (Hungary)	Molar germ	Aurignacian	^{14}C	30.9 ± 0.6 ka (53)

Non-Croatian European sites (≥ 30 ka B.P.) with either direct chronometrically-dated human skeletal remains (†) or with associations between human skeletal remains and chronometrically-dated Upper Paleolithic contexts (*). TL, Thermoluminescence; ^{14}C, conventional radiocarbon; AMS, accelerator mass spectrometry radiocarbon; AAR, amino acid racemization.

and specimens resulted in significant changes to this chronological framework.

In 1988, early modern humans in western Asia were dated to ≈90 thousand years (ka) B.P. at the site of Qafzeh, based on their association with TL determinations on burned flint (29). This date provided the first conclusive evidence for the existence of an early modern human morphological pattern in excess of ∼40 ka B.P. anywhere in the world. In the previous year, a date of ≈60 ka B.P. was obtained for the Kebara 2 Neandertal skeleton, also on the basis of TL analysis of associated burned flints (30). Both of these dates were later supported by ESR determinations on associated fauna (31).

These dates suggested that Neandertals existed in the Near East more recently than some populations of early modern humans, thus demonstrating temporal overlap of these human groups. However, it is not possible to demonstrate that these populations were actually present in the Levant during the same temporal span (32, 33). This early occurrence of modern humans and late survival of Neandertals (to as recently as ≈42 ka B.P.) were confirmed subsequently by chronometric dating of other pertinent sites (31, 34).

In Europe, radiometric dates on organic samples apparently associated with fossil human remains demonstrate that Neandertals continued to exist until ≈34 ka B.P. in France (35) and ≈33 ka B.P. on the Iberian Peninsula (36). Dates on levels containing Mousterian cultural remains, but no human fossil remains at Zafarraya, Spain (36), Caldeirão, Figueira Brava, and Foz de Enxarrique in Portugal (37), and Gorhams Cave in Gibraltar (38) suggest that Neandertals may have existed in the latter region until ≈30 ka B.P. In addition, level G_1 at Vindija Cave in northern Croatia yielded fragmentary, but clearly Neandertal, human remains that were dated to this same time span (see below).

Early dates for modern human remains have not been forthcoming in Europe as they have in western Asia. It has been argued that AMS radiocarbon dates on nonhuman materials from Spain place the beginnings of the Aurignacian cultural complex at ≈40 ka B.P. (39, 40), but re-evaluation of the stratigraphic contexts and the archeological associations of the dated materials (41, 42) have shown that these dates cannot support such an early date for the Aurignacian in western Europe. The Aurignacian Upper Paleolithic complex is always associated with early modern human remains when there are diagnostic fossils securely associated with the archeological remains (41, 43), but so far the earliest phases of the Aurignacian have failed to yield diagnostic human remains.

In central and eastern Europe, human remains have been recovered in association with early Upper Paleolithic assemblages at Bacho Kiro (Bulgaria), dated to >43 ka B.P. by conventional radiocarbon analysis, and at Velika Pećina (Croatia), where a hominid frontal bone has been considered to be >34 ka B.P. (44, 45). The human remains from Bacho Kiro are fragmentary and not diagnostic (46). The Velika Pećina specimen is fully modern in morphology (47). Only a few other early modern human skeletal specimens are associated with dates >30 ka B.P. (see Table 1), and many of these, especially those older than ≈32 ka B.P., are problematic. In particular, the Hahnöfersand and Kelsterbach remains have no secure stratigraphic associations and are dated only by amino acid racemization and conventional radiocarbon (47). The human remains from the other European site (El Castillo), yielding early modern humans and radiocarbon dates are lost and cannot be stratigraphically related to the dated levels from the site.

This relatively late appearance of modern humans in Europe compared with that in western Asia, coupled with the late survival of Neandertals in portions of Europe and indications of contemporaneity between Neandertals and early moderns in specific regions (35, 45), is one of the strongest underpinnings supporting an essentially total replacement of Neandertals by modern humans dispersing into Europe. Although this temporal pattern has appeared to be clearest in western Europe, the nature of the pattern in central Europe seemed, for many years, to be different. Early modern humans appeared to be earlier there than in western Europe, and Neandertals did not seem to survive as late (11, 47). The region of central Europe that has figured most prominently in this assessment is the Hrvatsko Zagorje of Croatia.

Late Pleistocene Humans of the Hrvatsko Zagorje

The Hrvatsko Zagorje is a region of rolling, sometimes rugged terrain, located between the flat plains of the Pannonian Basin and mountainous areas to the west and northwest. Several

Table 2. Human skeletal remains from Vindija G_1

Specimen	Description	Salient features
Vi 207	Right mandibular ramus with edentulous posterior corpus	Retromolar space* Horizontal-oval mandibular foramen*† Medial pterygoid tubercle*†
Vi 208	Anterior, superior fragment of left parietal	Breschet's sulcus well developed*†
Vi 287	Right upper canine	——
Vi 290	Right upper central incisor	Strongly shovel-shaped*† Large size*†
Vi 307	Left zygomatic bone	Columnar frontal process*† Multiple zygomaticofacial foramina*
Vi 308	Left frontal fragment with medial supraorbital torus	True supraorbital torus† Large frontal sinus, restricted to torus†

*Features occurring in high frequencies among the Neandertals but may be present in other later Pleistocene *Homo* groups.

†Features tending to distinguish Neandertals from European early modern humans.

important cave and rock shelter sites have been discovered there, yielding archeological remains of both the Mousterian and early Upper Paleolithic and human skeletal remains of Neandertals and early modern humans (11, 45, 47, 54, 55). The most famous of these sites, the Krapina rockshelter, yielded only Mousterian tools and Neandertal skeletal remains (56). The other most significant sites, Vindija and Velika Pećina, contained both Mousterian and early Upper Paleolithic cultural assemblages and the remains of Neandertals (at Vindija) and modern humans (at both) (11, 45, 47).

Excavations at Velika Pećina produced a partial human frontal bone from level J, in association with a single stone tool attributed to the "proto-Aurignacian" (57). The level immediately above level J yielded a distinctly early Upper Paleolithic assemblage, and this stratum (level I), was dated to 33,850 ± 520 B.P. (GrN-4979) by conventional radiocarbon on nonhuman material (58). The human frontal, although exhibiting marked superciliary arches for its size, has a fully modern morphology (47).

Vindija is a large cave with a long stratigraphic sequence. The upper portion of the G complex (levels G_1–G_3) produced a lithic assemblage that combines Mousterian and Upper Paleolithic elements, including bone tools characteristic of the Aurignacian in the upper-most G_1 level (45). The human remains from level G_3 exhibit a Neandertal morphological pattern, albeit with certain features that approach modern human morphology to a greater extent than most other Neandertals (11, 54, 59, 60). Level G_1 yielded six human cranial fragments (Table 2). Fortunately, these specimens preserve informative anatomical regions and characteristics (59, 60), which are outlined in Table 2. Although most of these characteristics are unique to the Neandertals (14–16), their presence as a complex on the G_1 specimens, in addition to the absence of uniquely derived modern human features, warrants the assignment of these specimens to the Neandertals (45).

A 1995 AMS radiocarbon date of 33,000 ± 400 yr B.P. (ETH-12714), derived from a fragment of *Ursus spelaeus* (cave bear) bone from level G_1 (55), indicated that Neandertals from this level at Vindija were among the most recent in Europe, comparable to the dates noted earlier from France and Iberia. This date, along with the apparent date of more than ≈34 ka B.P. for the modern Velika Pećina frontal, provided the best example from either the Near East or Europe for contemporaneity in the same well-defined region of Neandertals and early modern humans (45). This circumstance is rendered more intriguing by the nature of the archaeological assemblage from Vindija G_1, which combines Middle and Upper Paleolithic lithic elements with clear Upper Paleolithic bone/antler points, including an Aurignacian-like, split-based point (45, 55).

It has been argued that the archaeological complex and Neandertal remains from Vindija G_1 represent an artificially mixed assemblage, due at least in part to the action of cryoturbation and *U. spelaeus* denning in the cave (41, 61). Additional support for the admixture argument could be drawn from γ-ray spectrometry dates taken directly on the Vindija 207 mandible and the single split-based bone point from level G_1. This technique yielded dates of 51.0 ± 8.0 ka B.P. and 46.0 ± 7.0 ka B.P. (U-Th and U-Pa, respectively) for the Neandertal mandible (62). Results on the split-based bone point were less consistent, providing 45.0 ± 6.0 ka B.P. by U-Th, but only 30.0 ± 5.0 ka B.P. by U-Pa (62). Although the dating of the bone point is inconclusive, the γ-ray spectrometry dates for the mandible raise two possibilities. Either the Neandertal mandible and the cave bear bone (dated to ≈33 ka) were postdepositionally mixed in this stratum, or one of the determinations (γ-ray or AMS radiocarbon) is wrong.

Direct AMS Dating of the Vindija G_1 and Velika Pećina Hominid Remains

In light of the pivotal position of the Vindija G_1 and Velika Pećina hominid remains as the currently best case for the chronological overlap of late Neandertals and early modern humans within a geographically restricted area of Europe, we undertook to assess directly the geological ages of the human remains from these sites by using AMS radiocarbon dating. Because the question of the contemporaneity of the bone tools with the Neandertals at Vindija also has important implications, we took samples of several of these specimens. Samples of between 200 mg and 600 mg of bone were drilled from a total of nine pieces, five human bones and four bone or antler points (including the pivotal split-based bone point from level G_1).

Each of these samples received the standard Oxford pretreatment for bone and antler. This pretreatment is aimed at extracting and purifying collagen, the carbon from which the date determination is made. Each sample was decalcified in acid and given an alkaline rinse to remove humic acids before being

Table 3. AMS radiocarbon dating of the Velika Pećina (VP) and Vindija G_1 (Vi) human remains

	Velika Pećina VP-1 frontal	Vindija Vi-207 mandible	Vindija Vi-208 parietal
Sample mass, mg	236	229	233
Collagen yield, mg	5.7	9.7	15.2
Burnt weight, mg	2.8	3.8	8.2
Carbon mass, mg	1.1	1.4	3.0
C/N ratio	3.16	3.60	3.21
δ^{13}C	−21.3	−20.5	−19.5
δ^{15}N	8.04	10.77	10.09
Laboratory sample no.	OxA-8294	OxA-8296	OxA-8295
Date (yr B.P.)	5,045 ± 40	29,080 ± 400	28,020 ± 360

gelatinized by heating in a weak acid. Each sample was then freeze-dried for combustion. Chemical pretreatment, target preparation, and AMS measurement follow the protocols described in detail elsewhere (63, 64). The now-abandoned ion-exchange procedure was not used.

Unfortunately, six of the nine samples failed. These failures resulted either from the presence of too little collagen from which to extract a sufficient amount of carbon, or from the presence of contamination, probably a preservative, which could not be removed. The failed samples are: (*i*) VP (Velika Pećina)-133, bone/antler point (insufficient collagen); (*ii*) Vi (Vindija)-228, Neandertal humerus from level G_3 (low collagen and contamination); (*iii*) Vi-253, Neandertal humerus from the G complex (insufficient collagen); (*iv*) Vi-3450, bone/antler point from level Fd/d (insufficient collagen); (*v*) Vi-3437, bone/antler point from level G_1 (low collagen and contamination); and (*vi*) Vi-3439, bone/antler point from level G_1 (insufficient collagen).

The most disappointing of these failures is the Vi-3437 split-based point purportedly associated with the Neandertal human remains from Vindija G_1 (45). Given the failure, it was not possible to test this association. It should also be noted that one of the Neandertal humeri samples (Vi 253) is of unknown provenience within the G complex at Vindija, whereas the other (Vi 228) is from the earlier G_3 level (59); they may both derive from the older G_3 level and thus have reduced collagen preservation.

Three human samples from these sites contained enough collagen and, ultimately, enough carbon to allow dating with confidence (Table 3). These dates are uncalibrated and given in radiocarbon years B.P. (before AD 1950) using the half life of 5,568 years. Isotopic fractionation has been corrected by using the measured δ^{13}C values quoted (to ± 0.3 per thousand, relative to Vienna PeeDee belemnite). Sample weights, yields, and measurement chemistry are shown in Table 3. The C/N and δ^{13}C ratios and the nitrogen amounts fall within expected ranges for human omnivores. These data (and the fact that there were obvious, chemistry-related reasons for the failure of the other six samples cited above) provide confidence in the reliability of these three results.

At two standard deviations, the ages found for the Vindija Neandertal specimens vary between 28,740 and 27,300 yr B.P. (Vi-208) and between 29,880 and 28,280 yr B.P. (Vi-207). These results require two comments. First, at two standard deviations, the values are statistically the same, indicating an antiquity of ≈29.8 to ≈27.3 ka B.P. Therefore, one cannot rule out the possibility that the two samples were deposited at the same time. Second, although these dates are much closer to the date on the *U. spelaeus* bone than to the γ-ray dates, both are still statistically different ages from the cave-bear bone date, and indicate that level G_1 at Vindija yielded samples spanning a minimum of ≈3 ka of radiocarbon time.

Implications of the Revised Hrvatsko Zagorje Dates

Several conclusions can be inferred from the AMS dating of the Hrvatsko Zagorje sites; some relate primarily to the prehistory of the Hrvatsko Zagorje, but all are relevant to the broader issues of European Late Pleistocene human evolution.

First, the Holocene age estimate, derived directly from the Velika Pećina frontal bone, removes this specimen from the list of chronometrically dated early modern humans in Europe (Table 1). The standard radiocarbon age for level I may be correct for the archeological assemblage, but the human frontal must be intrusive into this level. Holocene age human skeletal remains were recovered from the site and may represent the source for the intrusive frontal bone. Furthermore, in light of recent indications that several presumed Late Pleistocene remains represent more recent intrusions into Paleolithic contexts in several English caves (65–69), the case of Velika Pećina amplifies the advisability of direct dating for any human specimen of questionable early Upper Paleolithic association (see below).

The Holocene date for the Velika Pećina frontal bone removes from consideration one of the strongest cases for the presence of modern humans in Europe before ≈32 ka B.P. As previously noted, many chronometrically dated, purportedly early modern human remains from Europe are undiagnostic because of incompleteness (e.g., Istállóskö, Bacho Kiro) or because they were not described (e.g., the Castillo remains, now lost). Other important early Upper Paleolithic specimens (e.g., Cro-Magnon, La Crouzade, Mladeč, Zlatý Kůň) have not been radiometrically dated (43, 70). Omitting the Neandertals associated with the Châtelperronian (Table 1), the Kent's Cavern, Vogelherd, and Kelsterbach specimens are left as the only modern human remains associated with radiometric dates ≈32 ka B.P., and the Hahnöfersand frontal bone is the only one with an older (≈36 ka B.P.) apparent age. All are basically modern in morphology, although Vogelherd and Hahnöfersand have features that may be reminiscent of Neandertals (9, 47, 51, 71). The Vogelherd remains are associated with an early Aurignacian component that dates to ≈32 ka B.P. (49); the Kent's Cavern maxilla derives from an Aurignacian-like level; but the other two specimens have no archeological context. The Hahnöfersand frontal is now the only pertinent skeletal specimen dated to >32 ka B.P. in Europe, and redating by direct AMS radiocarbon is warranted. Thus, the first definitive evidence of modern human morphology in Europe may well be close to 32 ka B.P., somewhat younger that has been traditionally thought.

Second, the AMS ages of ≈28 ka B.P. and ≈29 ka B.P. for the Vindija 208 parietal and the 207 mandible establish the Vindija G_1 remains as the youngest chronometrically dated Neandertals.

Thus, Neandertals were late survivors not only in the cul-de-sac of Atlantic Europe (35–38), but also in central Europe. This fact indicates that the disappearance of Neandertals in Europe did not follow a simple geographic pattern from east to west, which in turn implies that the dynamics involved in the disappearance of Neandertals were more complicated than a gradual retreat of Neandertal populations into peripheral refugia.

These radiocarbon ages for the Vindija G_1 human remains are broadly consistent with, albeit not statistically identical to, the previous date of $\approx$33 ka B.P., based on *U. spelaeus* bone from level G_1 (55). Although this suggests that the human and ursid occupations of Vindija Cave during the deposition of level G_1 may not have been contemporaneous, the AMS dates contrast strongly with the γ-ray spectrometry determinations for Vindija G_1 human remains. Given the large standard errors and/or inconsistent results associated with the Vindija γ-ray spectrometry determinations, the AMS radiocarbon dates presented here should be given priority in assessing the ages of these human fossils.

Third, the Holocene age for the Velika Pećina frontal removes the only radiometrically based example of overlap between Neandertal and early modern human skeletal remains from a single well-defined geographic region of Europe (45). Age estimates for modern human fossils from one region may overlap with those for Neandertals from a different region. For example, the ages for the Vogelherd early modern human specimens from Germany (Table 1) are earlier than the Vindija G_1 Neandertals, but these regions are separated by several hundred kilometers. There have been arguments for chronological overlap within regions, based on the presumed interstratification of Aurignacian and Châtelperronian components and the overlapping of mean radiometric dates from France and northern Spain (72), but careful consideration of these sites and the associated radiometric dates makes such inferences of archeological contemporaneity within these regions tenuous (42). More importantly, none of these regions have radiometrically dated and chronologically overlapping diagnostic human skeletal remains.

Finally, the survival of Neandertal populations after $\approx$32 ka B.P., and probably after $\approx$30 ka B.P., at least in Croatia and across much of Iberia, combined with the presence of early modern humans elsewhere in Europe by 32 ka B.P. and the spread of the Aurignacian culture across Europe by 36 ka B.P., raises several issues.

To what extent did the contemporaneity of these two human groups in Europe lead to gene flow between them? Was there significant admixture between Neandertals and early modern humans in central Europe, as has been previously proposed (11), or was the Neandertal–early modern human admixture indicated by Lagar Velho 1 in Iberia (12) an isolated and peripheral case? In other words, is the appearance of modern human morphology in Europe largely the result of changes in the degree and pattern of Late Pleistocene gene flow between archaic and more modern populations in western Eurasia (73)?

If the Aurignacian assemblage represents a significant cultural (technological and organizational) departure from the initial Upper Paleolithic industries (e.g., Châtelperronian, Uluzzian, Szeletian, and Bohunician) (41, 42, 74), does the current chronological reassortment of diagnostic human remains between $\approx$28 and $\approx$36 ka B.P. bring into question who was responsible for which archeological complexes?

And ultimately, what implications do these dates, the evidence for independent Neandertal development of Upper Paleolithic cultural elements (41) and the indications of Neandertal–early modern human admixture in Iberia (12) have for the possibility of biological interactions between Neandertal and early modern human populations across Europe?

Whatever answers emerge to these questions, it is apparent that the chronological, cultural and biological nature of the emergence of modern humans and of the Upper Paleolithic in Europe was temporally and spatially varied and complex. Across the entire Old World, this Late Pleistocene transition can only have been more varied, making simple models of the process increasingly improbable.

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