The spread of modern humans in Europe

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The earliest credible evidence of *Homo sapiens* in Europe is an archaeological proxy in the form of several artifact assemblages (Bohunician) found in South-Central and possibly Eastern Europe, dating to ≤48,000 calibrated radiocarbon years before present (cal BP). They are similar to assemblages probably made by modern humans in the Levant (Emiran) at an earlier date and apparently represent a population movement into the Balkans during a warm climate interval [Greenland Interstadial 12 (GI 12)]. A second population movement may be represented by a diverse set of artifact assemblages (sometimes termed Proto-Aurignacian) found in the Balkans, parts of Southwest Europe, and probably in Eastern Europe, and dating to several brief interstadials (GI 11–GI 9) that preceded the beginning of cold Heinrich Event 4 (HE4) (≈40,000 cal BP). They are similar to contemporaneous assemblages made by modern humans in the Levant (Ahmarian). The earliest known human skeletal remains in Europe that may be unequivocally assigned to *H. sapiens* (Peçstera cu Oase, Romania) date to this time period (≈42,000 cal BP) but are not associated with artifacts. After the Campanian Ignimbrite volcanic eruption (40,000 cal BP) and the beginning of HE4, artifact assemblages assigned to the classic Aurignacian, an industry associated with modern human skeletal remains that seems to have developed in Europe, spread throughout the continent.

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The spread of modern humans in Europe is a controversial topic in paleoanthropology. There is consensus that at the beginning of the interstadial period corresponding to Marine Isotope Stage 3 (MIS 3) at ≈60,000 years ago Europe was exclusively occupied by *Homo neanderthalensis*, who produced stone artifacts classified by archaeologists as Middle Paleolithic, and that by the end of MIS 3 [≈30,000 calibrated radiocarbon years before present (cal BP)], the continent was occupied by anatomically modern humans (*Homo sapiens*), who produced a variety of artifacts assigned to the Upper Paleolithic. There is considerable disagreement, however, about how this transition occurred.

Some paleoanthropologists have argued that the transition represents a relatively straightforward replacement of one congeneric hominin taxon by another. According to this view, Neanderthals made no significant genetic or cultural contribution to the human population that inhabited Europe at 30,000 cal BP. The lack of interaction between the two taxa is assumed to reflect genetic distance and/or profound biobehavioral differences (1, 2). The latter may be important to explaining how a replacement could have occurred: how a colonizing species from outside Europe could successfully compete with an established local species. Superior cognitive and communicative abilities (''behavioral modernity'') could have conferred a competitive advantage on modern humans despite their external origin.

An alternative model postulates substantial genic exchange and cultural influence between Neanderthals and modern humans. Advocates of the ''assimilation model'' emphasize human fossils that appear to exhibit a combination of Neanderthal and modern human anatomical traits and archaeological assemblages that contain a mixture of types both in Middle and Upper Paleolithic industries (3, 4). They conclude that Neanderthals made a significant genetic and/or cultural contribution to the modern human population of Europe.

The interpretation of the genetics of living human populations, supplemented with the analysis of fossil DNA extracted from Neanderthal and early modern human specimens, favors the replacement model. The limited number of mtDNA lineages among living non-African populations is consistent with a model of rapid dispersal, initially eastward out of Africa and subsequently northward into the Eurasian interior (5). Results to date from ongoing reconstruction of the Neanderthal genome indicate a distinctive pattern that cannot be found among living humans and suggests minimal genic exchange between the two taxa (6). Advocates of the assimilation model argue, however, that the existing molecular evidence does not preclude Neanderthal contributions to the early modern human European genome (7).

There are factors other than the anatomical and behavioral traits of the Neanderthals and modern humans that probably played a role in the transition. One of these is the changing climates of the MIS 3 interval and their impact on European biota. The most widely used stratigraphic framework for MIS 3 Europe is the climate proxy record of the North Atlantic and Greenland. According to this record, the period between 60,000 and 30,000 cal BP was characterized by a sequence of generally brief, but often relatively pronounced, oscillations in climate. Oxygen-isotope data from the Greenland Ice Sheet Project 2 (GISP2) ice core indicate no less than 13 warm intervals [or Greenland Interstadials (GI)] and 14 cold intervals [or Greenland Stadials (GS)] during this period (8). The most severe cold intervals correspond to Heinrich Events (HEs), and there are 3 such events during MIS 3 (HE5–HE3).

A more specific climate-related factor is the Campanian Ignimbrite (CI) volcanic eruption, dated at ≈40,000 cal BP, which apparently had devastating effects on plant and animal life across large areas of Southern and Eastern Europe and is linked to a cold interval. The CI eruption is identified in GISP2 in the form of a sulfate peak above an interstadial (GI 9) and below HE4 (9).

Problems with the Human Fossil and Archaeological Record

There are several reasons paleoanthropologists have found it difficult to reconstruct events related to the spread of modern humans in Europe. One is a scarcity of human fossils dating to the period of the transition, a problem exacerbated in recent years by the redating of a number of human fossils formerly assigned to this interval to a younger age (7). In some cases, human fossil remains are present, but they represent small portions of the skeleton (e.g., isolated teeth) difficult to assign to a specific taxon (10).

Because of the gaps and ambiguities of the human fossil record for this period, the transition from Neanderthals to modern humans in Europe has been reconstructed primarily on the basis of archaeological remains. The latter also contain ambiguities,

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however, and many artifact assemblages dating to this period cannot be firmly attributed to one taxon or the other. These include assemblages that are not associated with diagnostic human fossils and contain a combination of artifact types traditionally assigned to Middle and Upper Paleolithic. They are often interpreted as manifestations of cultural influence between Neanderthals and modern humans (11), but there are other reasons typical Middle and Upper Paleolithic artifact forms might be found together in the same occupation (12). Although stone blade technology is traditionally associated with Upper Paleolithic industries, it became apparent many years ago that Middle Paleolithic industries in various parts of Eurasia yield evidence of blade production. Blade manufacture is well documented in the Middle Paleolithic of Europe and the Near East (13, 14).

If Neanderthals produced at least some of the stone artifact forms found in Upper Paleolithic assemblages, anatomically modern humans continued to manufacture and use many typical Middle Paleolithic forms long after the transition. Production of side-scrapers, points, small bifaces, and other such forms continued into the Upper Paleolithic and post-Paleolithic industries. In North America, such artifacts are common in Paleoindian sites, where they are often associated with the killing and butchering of large mammals (e.g., refs. 15 and 16). In Europe, Middle Paleolithic tool types also are present in Upper Paleolithic assemblages, but usually in low percentages in the natural shelters of Western Europe. In the open-air sites (and some natural shelters) of Central and Eastern Europe, they are more common and often abundant (17).

At both open-air localities and natural shelters where Upper Paleolithic occupations directly overlie those of the Middle Paleolithic, the mixing of artifacts from different levels represents another potential source of assemblages containing typical forms from both industries. In addition to potential deposition of Neanderthal and modern human artifacts on the same surface, postdepositional mixing of surface and buried artifacts caused by trampling or frost action is possible (18).

Another problem is the dating of sites and occupation levels inhabited during the transition period. Much of MIS 3 lies beyond the effective range of radiocarbon and many dates (especially on bone) likely have been contaminated by younger carbon. Even dates that appear to be valid must be calibrated to account for the effects of past fluctuations in atmospheric radiocarbon, especially elevated during the cosmogenic nuclide peak at ≈40,000 cal BP. In this article, radiocarbon measurements have been calibrated with the CalPal-2007 curve (19). The application of other dating techniques, including optical-stimulated luminescence and electron spin resonance, has improved chronological control, and several widespread chronostratigraphic markers, such as the CI volcanic tephra and the Laschamp paleomagnetic excursion, have provided additional control in some places (9).

Modern Humans as a Colonizing Species

Modern humans entered Europe as a colonizing species and probably were characterized by comparatively low population density as they expanded into previously unoccupied territory and adapted to new environmental conditions (20). Low density might be expressed in terms of smaller residential group size and/or larger home ranges and higher mobility requirements. The initial phase of modern human settlement in Europe therefore could be represented by a relatively small number of archaeological sites and human skeletal remains per unit area. Their visibility probably would be even lower in landscapes where natural shelters are scarce or absent.

However, there is reason to believe that modern humans had acquired some unique abilities to colonize new environments. Behavioral modernity is often identified with the use of symbols (21), which is most clearly manifest in syntactical language. Language and other uses of symbols are, however, part of a broader capacity to create complex, hierarchically organized structures (sometimes labeled recursion) in a variety of media both symbolic and nonsymbolic (22). The latter include technology, which exhibits a pattern of accelerating innovation and expanding complexity during the Upper Paleolithic (23). The use of symbols also may have conferred some unique organizational abilities on modern humans (24), and the creation of novel technologies and organizational structures may have played a significant role in the dispersal of modern humans and their seemingly rapid colonization of a variety of habitats and climate zones.

Another factor is the presence of competitor species. Both Neanderthals and hyenas represent likely competitors for modern humans in Europe, especially with respect to large mammal prey. With this in mind, it should be noted that comparative analysis of stable isotope values for Neanderthal and hyena bone from a cave in France (late MIS 3) suggests that emphasis on superherbivores (mammoth and rhinoceros) by the former reduced resource competition with hyenas (25). As for modern humans, there is evidence for exploitation of smaller vertebrates, which might have reduced niche overlap with both competitors (26).

South-Central Europe

The earliest credible evidence for modern humans in Europe is a group of artifact assemblages found in South-Central Europe, assigned to the Bohunician industry, that are similar to assemblages of comparable age in the Near East associated indirectly with skeletal remains of modern humans. They are found at the type site of Brno-Bohunice and Stránská skála (Moravia), Bacho Kiro and Temnata Cave (Bulgaria), Dzierzyslaw (Poland), and others (27, 28). They contain Levallois cores used to produce flakes and blades with hard-hammer percussion and retouched pieces including a variety of side-scrapers, points, end-scrapers, and simple burins; some assemblages also contain bifacial leaf-shaped points (29). An associated human mandible fragment recovered from layer 11 at Bach Kiro is of uncertain taxonomic affiliation (10).

Although a case for local Middle Paleolithic origin has been made (30), many archaeologists perceive stronger similarities between the Bohunician and contemporaneous assemblages in the Near East, specifically at Bocher Tachtit, layers 1–3 (Israel), Ksar Akil, layers XXV-XXI (Lebanon), and Üçağizli Cave, layers F-H (Turkey), and little evidence of continuity with late Middle Paleolithic industries of Central Europe (31, 32). The Near Eastern assemblages, which are assigned to the Emiran industry [or simply Initial Upper Paleolithic (IUP)], lack associated human skeletal remains. They appear, however, to represent part of a local developmental continuum that subsequently yielded a related industry (Ahmarian) associated with modern human remains in layer XVII at Ksar Akil (33). Moreover, the Emiran reflects broader trends in technology observed in North Africa at older sites like Taramsa 1 (Nile Valley), which contains modern human remains dated to ≈75,000 years ago (34).

Assemblages assigned to the Bohunician in South-Central Europe are dated by radiocarbon and luminescence to ≈48,000–40,000 cal BP (35). They are associated with two buried soils that date to the MIS 3 interval and correlate with GI 12–GI 9 in the Greenland ice core record. The Bohunician appears at the beginning of a major warm interval (GI 12) and terminates before a major cold period (HE4). The apparent link between the Bohunician and GI 12 may be significant, because one of the striking characteristics of this industry, given its postulated status as a proxy for the initial movement of modern humans into Europe, is the scarcity of evidence for innovative technology. With the exception of a perforator from layer 11 of Bacho Kiro (36), Bohunician sites lack bone implements and other evidence

(e.g., large numbers of small mammal remains) that might reflect innovations to help modern humans cope with new environmental conditions.

The scarcity of such evidence could be partly because most Bohunician sites are open-air localities and some of them appear to have been workshop sites. Isolated bone and antler implements have been recovered from Emiran (or IUP) levels at Ksar Akil and Üçağizli Cave (33, 37). Moreover, evidence for possible organizational adaptations in the form of personal ornaments is present in layer 11 at Bacho Kiro and in the Emiran sites (33, 36, 37), and nonstone implements, personal ornaments, and signs of an expanding economy are associated with anatomically modern humans in an earlier African context (38).

There are also sites in Central Europe broadly contemporaneous with the Bohunician that yield bone artifacts. Many of them are classified as Szeletian, an industry that is most closely associated with a group of caves in the Bükk Mountains of Hungary, but is represented at sites in Moravia and southern Poland as well (39). The assemblages contain leaf-shaped stone points, bone points, side-scrapers, and others. Associated human remains include isolated teeth from layer 4 at Upper Remete Cave (Hungary) and a tooth germ from Dzeravá skála (Slovakia), which are ambiguous in terms of taxonomic affiliation (10).

Despite the ambiguity of the skeletal remains and the presence of bone points, the Szeletian is widely assumed to be the product of local Neanderthals (11, 12). The assumption is based on the fact that typical Middle Paleolithic artifacts are found in the assemblages and the pattern appears to be analogous to that of the Chatelperronian, a group of assemblages from the Franco-Cantabrian region that contain a mixture of Middle and Upper Paleolithic artifacts and are associated with Neanderthal remains (40). Many Szeletian sites contain small functionally specialized assemblages that are more parsimoniously explained as tool kits related to large mammal hunting and carcass processing (41).

A new set of artifact assemblages appear in South-Central (and Southwestern) Europe as early as 45,000 cal BP often referred to as Proto-Aurignacian. They vary widely in composition and the term Proto-Aurignacian may be more useful with respect to archaeological chrono-stratigraphy than industrial/cultural classification. In Bulgaria, they are represented at Temnata Cave (unit 4, levels C-A) by occupations containing end-scrapers (including some carinate forms), Font-Yves points, and others buried below the CI tephra and dating to one or more interstadials (GI 11–GI 9?) (42). The Proto-Aurignacian is better known in Italy and other parts of Southwest Europe (described below), where it is represented by assemblages containing high percentages (up to 85%) of retouched bladelets. Some Italian Proto-Aurignacian assemblages contain higher percentages of more typical Aurignacian artifacts, and many yield bone and antler artifacts and perforated marine shells (43).

The Proto-Aurignacian seems to have close ties with the Ahmarian industry of the Near East in much the same way that the Bohunician is tied to the preceding Emiran. As already noted, the Ahmarian is associated with modern human remains (33), and for this reason, and the scarcity of Middle Paleolithic artifact types in the assemblages, there is a consensus that the Proto-Aurignacian is a proxy for modern humans, despite the absence of unambiguous skeletal material (1, 30). If the Bohunician represents the earliest credible evidence for modern humans in Europe, the Proto-Aurignacian would seem to represent a second population movement from the Near East.

The earliest modern human skeletal remains in Europe date to the same time period and are plausibly linked to the Proto-Aurignacian, despite the lack of associated artifacts. At the Peçstera cu Oase in Romania, a nearly complete mandible (containing 5 molars) and nearly complete cranium, are dated to ≈42,000 cal BP and GI 11 (3, 44). They are assigned to anatomically modern humans but exhibit at least one feature that is common among *H. neanderthalensis* (bridging of mandibular foramen); younger specimens from two other Romanian caves (Cioclovina, Muierii) also are said to exhibit some typical Neanderthal characteristics (3, 44).

Unlike the Bohunician and Proto-Aurignacian, the classic Aurignacian has no obvious antecedent in the Near East. Some believe that it emerges in South-Central Europe and subsequently spreads to other parts of western Eurasia (45). The roots of the Aurignacian would seem to lie in the sequence of assemblages in Bulgarian caves described above, and possibly other sites/regions (e.g., Willendorf in Austria), that antedate 40,000 cal BP (27). The wider spread of the classic Aurignacian apparently took place in the aftermath of the CI eruption and beginning of the HE4 cold interval. In Moravia, an Aurignacian assemblage at Stránská skála (layer 4) is radiocarbon-dated to ≈37,000 cal BP (29). Modern human remains (cranium, maxilla, and other skeletal parts) associated with bone points and a few stone artifacts assigned to the Aurignacian from the cave of Mladeč yielded slightly younger dates (46).

Eastern Europe

At least two of the major archaeological entities linked to the spread of modern humans in South-Central Europe (i.e., Bohunician and Aurignacian) are present in Eastern Europe. The third (Proto-Aurignacian) has not been widely recognized but may be present on the central plain. As in South-Central Europe, only the youngest of these entities (Aurignacian) is associated with skeletal remains that may be assigned unequivocally to anatomically modern humans. The other two are archaeological proxies for modern humans, and the oldest of these (Bohunician) is problematic as such.

A Bohunician artifact assemblage has been identified in the lowest layer at Kulychivka in western Ukraine (47). It comprises Levallois blade cores and typical Upper Paleolithic subprismatic cores used to generate crested blades; Upper Paleolithic tool types predominate (48). The lower layer at Kulychivka underlies a buried soil that correlates with the end of MIS 3 and yielded a problematic ^{14}C date of ≈35,000 cal BP; it is generally thought to be younger than the Bohunician of South-Central Europe. An older Bohunician industry may be represented on a Don River tributary at Shlyakh. The artifacts are similar to Emiran assemblages in the Levant and have been labeled "transitional" from the Middle to the Upper Paleolithic. They are associated with the Laschamp paleomagnetic excursion and appear to date to ≈44,000 cal BP (49).

Kostenki on the Middle Don River (Russia) contains a lengthy sequence of early Upper Paleolithic (EUP) occupations, including some that underlie the CI tephra and date to >40,000 cal BP (17, 50). Kostenki contains a unique EUP landscape of various types of sites, distributed along several side-valley ravines incised into the west bank of the main valley. Active springs in the ravines probably attracted large mammals to the area, and some of the sites represent kill-butchery locations. The earliest assemblages appear to be related to the Proto-Aurignacian movement into South-Central Europe or something comparable.

Artifacts recovered from within the CI tephra at Kostenki 14 comprise backed bladelets, retouched blades, and personal ornaments (decorated bone and perforated shell and fox teeth) (17, 51). This assemblage is similar to those from Italy and adjoining areas of the Mediterranean coast that are classified as Proto-Aurignacian and tied to the Ahmarian of the Near East. The Proto-Aurignacian sites are buried below the CI tephra and date to the brief interstadials that preceded HE4 (GI 11–GI 9) (50).

Both Kostenki 14 and 17 also contain assemblages buried below the CI tephra that appear to represent one or more local industries currently unknown in other parts of Europe (17, 50). They contain prismatic blade cores, burins, some end-scrapers, personal ornaments (perforated fox teeth and fossils), and

nonstone implements (e.g., bone awls and points). Each yielded an isolated tooth tentatively assigned to modern humans (52). Although not especially similar to the Proto-Aurignacian sites of South-Central Europe, these assemblages do share some elements with them (e.g., retouched bladelets, thick end-scrapers) and they represent a similar phenomenon dating to GI 11–GI 9 (≈44,000–40,000 cal BP).

Also buried below the CI tephra at Kostenki are some artifact assemblages that are sometimes compared with the Szeletian (e.g., Kostenki 12, layer III), because they contain a high percentage of Middle Paleolithic types (e.g., side-scrapers, bifacial points) along with end-scrapers; nonstone implements and ornaments are absent. Although traditionally considered a separate industry (17, 47), their consistent association with traces of large-mammal butchery suggests that they may simply represent tool kits similar to those found in Paleoindian kill-butchery sites in North America.

Like the Proto-Aurignacian sites in South-Central Europe, the occupations of comparable age on the central East European Plain contain evidence of technological innovations that may have played a role in modern human colonization of the region. The lowest levels at Kostenki 14 yielded large concentrations of small and medium mammal remains (hare, fox) that probably reflect development of some new devices (e.g., nets, snares) for harvesting small game (23). This represents an expansion of the ecological niche relative to the Neanderthals. The lowest level contained antler mattocks, apparently for digging, whereas the ornaments at Kostenki 17 were perforated with a hand-operated rotary drill (50).

Further evidence of an expanding economy is provided by traces of settlement at high latitudes during this period. The site of Mamontovaya Kurya, located on the Arctic Circle in northern Russia and dating to >40,000 cal BP, contains artifacts similar to those of Kostenki 12, layer III (53). It may also represent a short-term occupation related to large mammal procurement (and only seasonal use of high latitude areas?).

An assemblage often compared with the classic Aurignacian sites of Western and Central Europe overlies the CI tephra at Kostenki 1 (layer III). Although the diagnostic split-base or lozenge-shaped bone/antler points are lacking, many typical Aurignacian elements are present, such as carinate end-scrapers, large blades with scalar retouch, and backed bladelets (17). Some nonstone implements and personal ornaments are present as well. Associated skeletal remains, comprising fragments of a tibia, pelvis, and isolated tooth, are assigned to modern humans (52). The artifacts and human remains are buried within and below a paleosol correlated with the end of MIS 3 and apparently represent an extended interval of time from the beginning of HE4 through GI 6 (40,000–30,000 cal BP?) (50).

Other assemblages in the same stratigraphic context at Kostenki contain some elements found in the Aurignacian such as thick end-scrapers, a rich inventory of nonstone implements (including eyed needles), and many Middle Paleolithic types (e.g., side-scrapers, points). They have been assigned to a local industry (17, 47), but a more parsimonious interpretation is that, like some of the older sites described above, the Middle Paleolithic types represent artifacts related to the killing and dismembering of large mammals. Most yield evidence of kill-butchery events (primarily horse), in this case associated with habitation areas, which also reflects a pattern found among Paleoindian sites in North America [i.e., camps near large-mammal kill/butchery locations (15, 16)]. Modern human skeletal remains have been recovered from several of them, including Kostenki 12, layer I and Kostenki 15 (52), although the skeleton recovered from Kostenki 14, layer II recently has yielded some mid-Holocene radiocarbon dates (54).

Most of the assemblages at Kostenki dating to 40,000–30,000 cal BP may be assigned to an industry produced by modern humans that is broadly similar to the Aurignacian of Western and Central Europe. Assemblages dating to the same interval from other parts of the East European Plain, including Mira (Dnepr Basin) and Molodova 5, layer X (Dnestr Valley) follow the same pattern. The often high proportion of typical Middle Paleolithic forms reflects a wider range of open-air site types than found among the rock shelters of Southwest Europe. The nonstone implements also exhibit differences with those of Western and Central Europe. Most significant is the presence of eyed needles, which do not show up in Western Europe until MIS 2 and probably reflect colder winter climates in Eastern Europe.

Southwest Europe

To date, there is no evidence of the Bohunician in Southwest Europe. The westernmost occurrence of this industry appears to be Hradsko in north-central Bohemia or possibly Willendorf II (layer 2) in Austria (29). If the Bohunician assemblages are proxies for colonizing groups of modern humans entering Europe at ≈48,000 cal BP, then it appears that such groups did not spread into Western Europe at this time (GI 12). The reasons for this are unclear, but seem likely to be related to the local Neanderthal population, which continued to occupy the region at least until the time of the CI eruption and beginning of HE4 (40,000 cal BP).

In Italy, nevertheless, there is a group of occupations that are broadly contemporaneous with the Bohunician. In sites such as Grotta del Cavallo and Castelcivita Cave, artifacts assigned to the Uluzzian industry are stratified below the CI tephra (and sometimes the Proto-Aurignacian) and correlated with GI 12 and younger interstadials (48,000–40,000 cal BP) (9). The Uluzzian occupations contain a mixture of typical Middle and Upper Paleolithic forms, such as side-scrapers, end-scrapers, backed pieces, and occasional bone implements (awls and points) (43, 55, 56). Cavallo yielded several perforated marine shell ornaments and two human teeth of uncertain taxonomic status (10). As in the case of the Szeletian, Uluzzian assemblages are often regarded as manifestations of local Neanderthal acculturation (30, 57). In the absence of firmly assigned skeletal remains, however, the Uluzzian seems equally likely to represent traces of modern humans.

Assemblages assigned to the Proto-Aurignacian represent the earliest widely accepted proxy for modern humans in Southwest Europe (57). As noted earlier, these assemblages are found in Italy and other parts of Mediterranean Europe. Proto-Aurignacian occupations at L'Abreda and El Castillo in northeastern Spain are dated to ≈44,000–42,000 cal BP (58). In Italy, they are stratified below the CI tephra, correlating with GI 11–GI 9 and dating to ≈44,000–40,000 cal BP (9). The composition of the assemblages, often dominated by retouched bladelets, and their similarities to the Ahmarian industry of the Near East are described above. As in South-Central and Eastern Europe, the Proto-Aurignacian is striking in its evidence for novel technological and organizational adaptations (43, 59).

The classic Aurignacian industry, which may have developed in the Balkans (27, 28, 45), seems to have spread across Southwest Europe in the aftermath of the CI eruption with the onset of the HE4 cold interval (1). The direct effects of the CI ash plume fell primarily on other parts of the continent (9), but the impact of HE4 climates was significant in Southwest Europe. The effects are evident in the frost disturbance to cave deposits and the heavy use of bone fuel in Aurignacian hearths (60).

Early Aurignacian occupations in southern Germany are dated by radiocarbon and luminescence to ≈40,000–38,000 cal BP (HE4), although the wide range of radiocarbon dates underscores the problems of the method in this time range (61). Middle and Upper Paleolithic assemblages are not interstratified in southern Germany and the Aurignacian overlies the former. These sites are thought to reflect a westward route of modern

human dispersal along the Danube corridor, although it should be noted that formerly associated human skeletal remains have been redated to younger time periods (7). Teeth associated with an early Aurigancian assemblage at Brassempouy (France) are now assigned to modern humans (62).

Evidence for assimilation or acculturation is reported from the Franco-Cantabrian region in the form of assemblages (Chatelperronian) comprising Middle and Upper Paleolithic tool types, along with personal ornaments in at least one site (40). Unlike the Szeletian and Uluzzian sites described above, these artifacts are associated with human skeletal remains that may be firmly classified as Neanderthal at two sites. Their stratigraphic position in relation to the Aurignacian has been disputed, however. Some believe that they are contemporaneous and interstratified with early Aurignacian assemblages (1), whereas others suggest that they significantly antedate the latter and represent an independent development on the part of the local Neanderthals before the appearance of modern humans (30). Yet another view of the Chatelperronian is that the assemblages represent a mixture (perhaps caused in part by cryoturbation during HE4) of the latest Middle and earliest Upper Paleolithic occupations (12, 63).

Summary and Conclusions

The earliest evidence of anatomically modern humans in Europe is currently dated to ≈48,000 cal BP and the beginning of the GI 12 warm interval. It is based on artifact assemblages (Bohunician) that are similar to an earlier industry in the Near East (Emiran) probably produced by modern humans. Bohunician sites are present in South-Central Europe (27, 29, 32) and possibly Eastern Europe as well, during this interval. Many paleoanthropologists will want to see this conclusion supported by discovery of modern human skeletal remains in these sites or at least in a context that may be dated to the same period.

A possible second movement of modern humans into Europe may be represented by another group of artifact assemblages that date to as early as 45,000–44,000 cal BP and GS 11/GI 11. They vary significantly in composition and are sometimes referred to as Proto-Aurignacian (27, 43, 50, 64). Many are similar to a contemporaneous industry in the Near East (Ahmarian) manufactured by modern humans (1, 33). Proto-Aurignacian assemblages are found in Southwest and South-Central Europe and seem to be present in Eastern Europe at this time (50). Although the oldest known modern human skeletal remains in Europe date to this interval, they are not associated with artifacts (44). Nevertheless, the Proto-Aurignacian is widely attributed to *H. sapiens* on the basis of its apparent link to the Ahmarian and the artifacts, which include small backed bladelets and points, personal ornaments, and bone/antler implements (30, 57).

Both the Bohunician and Proto-Aurignacian sites probably represent modern human population movements from the Near East into Europe via the Balkans. This conclusion is based on the proximity of South-Central Europe to the most probable source of the two sets of assemblages (i.e., the Levant). Central Asia is considered another possible source of modern human populations in Europe, especially for adjoining Eastern Europe (65). The Iberian Peninsula and the Caucasus seem less likely routes, because local Neanderthal populations were present in both areas until relatively late (66, 67). After the onset of cold HE4 at ≈40,000 cal BP, a new industry (Aurignacian) possibly developed in South-Central Europe spread rapidly throughout the continent. Aurignacian assemblages are associated with the remains of modern humans in Western, Central, and Eastern Europe (1, 7, 10, 46, 52, 62).

Although the Bohunician sites yield little direct or indirect evidence of technological innovation, this may be caused in part by the functional and preservation biases of open-air lithic workshops. If the caves containing bone points traditionally assigned to the Szeletian industry (11) are considered part of the same phenomenon [and added to an isolated bone implement in layer 11 at Bacho Kiro (36)], nonstone implements in these sites are comparable to those in the related Emiran or IUP industry of the Levant (37). Indirect evidence for organizational adaptations in the form of personal ornaments also is present in Bacho Kiro and in the related Emiran or IUP sites of the Levant (10, 36, 24). The pattern indicates that although modern humans seem to have initially entered Europe during a warm climate interval (GI 12), both technological and organizational innovations, reflecting behavioral modernity, may have facilitated their colonization of new environments.

The extent to which modern humans and Neanderthals in Europe exchanged genetic and/or cultural traits remains unclear. Significant niche overlap between the two species would seem to preclude sustained coexistence in the same region without substantial interbreeding. Evidence for interstratifications of Neanderthal and modern human occupations is limited and problematic, and in most places, modern human occupation debris either directly overlies traces of Neanderthal occupation or there is a hiatus between the two (57, 61). Genic exchange is inferred from the presence of anatomical traits in modern human skeletal remains that are common among Neanderthals and perhaps most parsimoniously explained by interbreeding. These traits could have evolved among modern humans, however, in the absence of genic exchange with Neanderthals. Cultural influences are inferred from the co-occurrence of artifacts typically made by both taxa, or in the case of the Chatelperronian, the reported co-occurrence of artifacts typically made by one taxon with the skeletal remains of the other. There are alternative explanations of these co-occurrences, however, and the evidence is not conclusive (63).

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