ARTICLES

Neandertals and Moderns Mixed, and It Matters

JOÃO ZILHÃO

Twenty-five years ago, the Middle-to-Upper Paleolithic transition in Europe could be represented as a straightforward process subsuming both the emergence of symbolic behavior and the replacement of Neandertals by modern humans. The Aurignacian was a proxy for the latter, during which enhanced cognitive capabilities explained ornaments and art. The few instances of Neandertal symbolism were deemed to long postdate contact and dismissed as "imitation without understanding," if not geological contamination. Such views were strengthened by the recent finding that, in southern Africa, several features of the European Upper Paleolithic, including bone tools, ornaments, and microliths, emerged much earlier. Coupled with genetic suggestions of a recent African origin for extant humans, fossil discoveries bridging the transition between "archaics" and "moderns" in the realm of anatomy (Omo-Kibish, Herto) seemingly closed the case. Over the last decade, however, taphonomic critiques of the archeology of the transition have made it clear that, in Europe, fully symbolic *sapiens* behavior predates both the Aurignacian and moderns. And, in line with evidence from the nuclear genome rejecting strict replacement models based on mtDNA alone, the small number of early modern specimens that passed the test of direct dating present archaic features unknown in the African lineage, suggesting admixture at the time of contact.

In the realm of culture, the archeological evidence also supports a Neandertal contribution to Europe's earliest modern human societies, which feature personal ornaments completely unknown before immigration and are characteristic of such Neandertal-associated archeological entities as the Châtelperronian and the Uluzzian. The chronometric data suggest that, north of the Ebro divide, the entire interaction process may have been resolved within the millennium centered around 42,000 calendar years ago. Such a rapid absorption of the Neandertals is consistent with the size imbalance between the two gene reservoirs and further supports significant levels of admixture.

This review uses a calibrated time scale. Suggestions that spikes in ^{14}C production rendered calibration impossible in the period of the Middle-to-Upper Paleolithic transition in Europe[1,2] are now superseded, and the different calibration tools available for this time range produce comparable results.[3] Here, calibration uses the CalPal software with the SFCP age model for the GISP2 ice core;[4–6] uncalibrated results are in years or kiloyears (kyr) "^{14}Cbp" and calendar ages are noted "calBP."

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Key words: Neandertals, modern humans, ornaments, Châtelperronian, Aurignacian

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GENES AND FOSSILS

The notion that the patterns of variability in extant humans' mtDNA indicate a recent African ancestry has been central to complete replacement models of modern human origins.[7,8] The history of a particular gene system, however, does not represent the full history of a population, much less that of an entire species and, when the nuclear genome is considered, the picture changes.[9,10] For instance, a unique pattern of nucleotide polymorphism is now known that roots in East Asia and has an estimated time of coalescence of ca. 2 Myr.[11] If such ancient, non-African parts of the human genome are still extant, the implication is that the early Upper Pleistocene expansion of modern humans involved some level of admixture with contemporary archaic groups.

Based on a standard phylogeographic technique, the multilocus nested-clade analysis, the most recent review of the evidence from 25 nonrecombining parts of the human genome[9,10] concludes that ever since the first Out-of-Africa event ca. 1.5 Myr ago, human evolution has been characterized by gene flow with isolation by distance, and that the complete replacement model is rejected with a P-value of $<10^{-17}$. This study, however, does not exclude the possibility that total replacement occurred in restricted areas; conceivably, the Neandertals, in particular, could well have become extinct without descent even if, at a global scale, the general pattern was one of admixture or hybridization. The fact that the mtDNA extracted from many Neandertal fossils over the last decade has revealed polymorphisms unknown among today's humans and undetected in early modern Europeans[12–14] has been used to support precisely such notions of the Neandertals' fundamental separateness from the human tree.

However, because of several unresolved technical and methodological problems, such aDNA studies must be taken with great caution. For instance, DNA degrades with time, a process that can generate mutational artifacts. The production of such artifacts in the extraction chain has also been observed in controlled experiments; some loci in particular seem to

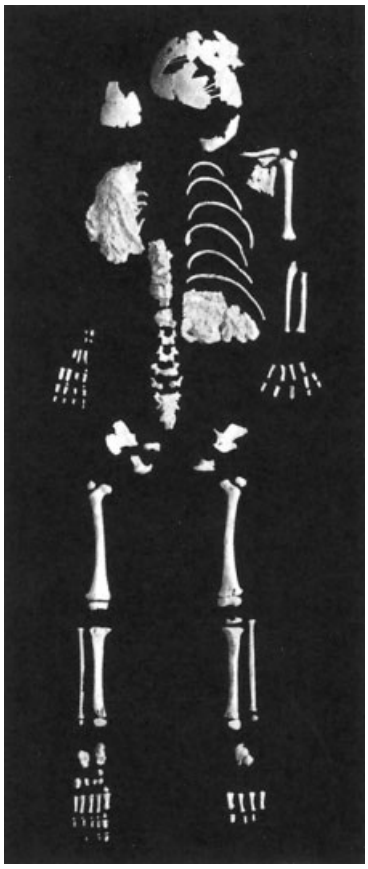


Figure 1. The Lagar Velho child skeleton (photo: José Paulo Ruas).

be repeatedly, nonrandomly affected, and among them are those where Neandertal divergence has been observed.[15,16] Contamination is another unresolved issue, particularly where the aDNA of early moderns is concerned.[17,18] As Pääbo[19] pointed out, "Cro-Magnon DNA is so similar to modern human DNA that there is no way to say whether what has been seen is real."

Thus, failure to identify Neandertal mtDNA in a given early modern human fossil may simply result from the fact that the extracted DNA is entirely modern contamination, not from the fact that no Neandertal mtDNA originally existed in that specimen. When such a failure occurs with material that, on paleontological grounds, is clearly Neandertal, current criteria of authentication[17] dictate rejection of the results, not the conclusion that the material belonged to a genetically modern Neandertal. The logical implications are, first, that early modern aDNA data cannot at present be considered and, second, that current perceptions of Neandertal aDNA variability may well be artificially constrained. Given these problems, it is clear that the current framework of aDNA research is inherently biased against admixture, which makes it all the more significant that the combined fossil and extant genetic evidence is consistent with levels of Neandertal contribution to Europe's earliest modern humans as high as 73.8%.[14,20–23] A recent simulation study suggests that such levels must have been negligible if not nil (at most, 0.1%),[24] but this conclusion is already contained in the anthropologically flawed premises of the tested admixture model.[25]

Genetics, therefore, does not reject Neandertal-modern admixture. But is there any positive evidence that it occurred? Arguably, that is exactly what the most recent developments in the field of human paleontology suggest.[26] Over the last five years, direct dating of the remains has demonstrated that the large majority of Europe's purported early modern human finds were instead of Holocene age. Their marked morphological modernity and contrast with even such late Neandertals as Saint-Césaire supported suggestions of major physical anthropological discontinuity and hence, complete population replacement at the Middle-to-Upper Paleolithic transition. The illusory nature of such a contrast is now apparent. Moreover, the few finds that are sufficiently complete to be taxonomically diagnostic and, in the process of that determination were shown to date to within a few millennia of the time of contact, feature a diverse array of anatomically archaic, often specifically Neandertal traits unknown in the Middle and early Upper Pleistocene of Africa. These fossils finds are Oase (Romania), Mladeč (Czech Republic) and Lagar Velho (Portugal), the latter being of relevance here despite its significantly later chronology, because Neandertals survived in Iberia for much longer than elsewhere in Europe.[27,28]

Where the Mladeč crania are concerned, the existence of traits such as prominent occipital buns, broad interorbital breadths, and juxtamastoid eminences is well known.[29] In the Lagar Velho child skeleton (Fig. 1), the list includes, among others, a low crural index and arctic body proportions, a retreating symphyseal profile, and the presence of a suprainiac fossa.[30] In the Oase fossils, the list includes lingular bridging of the mandibular foramen, a parietal/frontal curvature fully in the Neandertal range, and third molars that display a complex cusp morphology, are larger than the second molars, and more than two standard deviations above the average for the Middle Pleistocene (Fig. 2).[31,32] Since these features relate to aspects of skeletal morphology that are not susceptible to change during the ontogenetic cycle, they must reflect inheritance, the persistence in these overall modern individuals of genes transmitted by archaic ancestors—in Europe, the Neandertals. Although this proposition initially faced a certain level of inevitable skepticism,[33] the body of data and arguments subsequently brought to support it remain unchallenged.

In sum, nothing in the genetic and fossil evidence reviewed here suggests the existence of fundamental biological barriers preventing fruitful interaction between Neandertals and moderns at the time of contact. At least, most now agree that the issue should be approached with no preconceptions, and that it is up to the

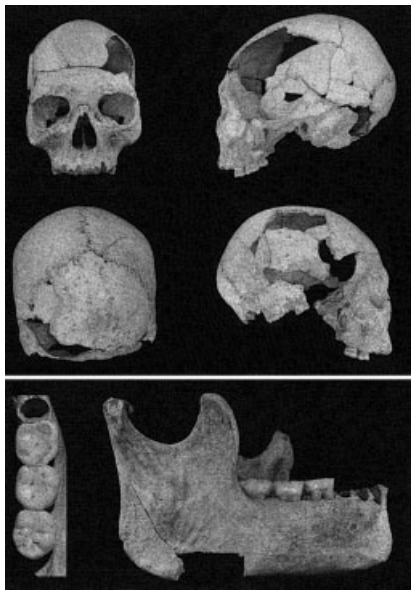


Figure 2. The Oase 2 cranium (above) and the Oase 1 mandible and right molar row (below).

empirical record to decide whether such admixture actually occurred.[34] How can archeology contribute to this debate? Because the transmission of cultural traits follows different rules (it depends on human volition, not natural selection), detecting a biological contribution from the Neandertals to later populations does not necessarily entail that an equivalent signature must exist in the realm of culture. However, if such a signature is found to exist, then the case for admixture is strengthened. Throughout the 1990s, any assessment of this issue was bound to be controversial because there was no consensus on the chronology of the archeological entities providing a cultural background for the relevant human fossils. Recent advances have substantially clarified the picture.

CULTURES

The Oase fossils are of particular importance in this context because, at ca. 40.5 kyr calBP, they are Europe's oldest modern human remains and likely represent the first such people to enter the continent. Under a model of admixture, the notion that the Oase people are very close to the time of contact is consistent with their archaic traits, and finds additional support in the patterns of spatio-temporal distribution of the latest Neandertal remains. In fact, nowhere north of the Ebro divide, from El Sidrón, Spain, in the west to Lakonis, Greece, in the east, do Neandertal remains or cultural manifestations that can be securely associated with them, such as the Châtelperronian of France, the Uluzzian of Italy, or the Micoquian of Germany, postdate the 42nd millennium calBP.[35]

The two putative exceptions are no more. That the ca. 29-28 kyr ^{14}Cbp results for the Neandertal material in level G1 of Vindija could only be minimum ages[25] has now been vindicated by reanalysis of the samples.[36] This gives further credence to the notion that the ca. 29 kyr ^{14}Cbp result for the Mezmaiskaya cave infant[37] must also be a vast underestimation of its true age; this burial, in fact, was covered by intact Mousterian deposits with multiple reliable dates in excess of 36 kyr ^{14}Cbp.[38] The notion that the Châtelperronian and the Uluzzian survived for many millennia after moderns are first recorded in Europe was based, in turn, on the radiocarbon dating of bone samples having a geological context and chemical characteristics that indicated incomplete decontamination.[39,40] The impact of such factors on the chronology of samples from this period is now widely accepted.[41]

Radiocarbon results for the Klisoura 1 cave in Greece place the Uluzzian at ca. 44 kyr calBP.[42] They are corroborated by the fact that in Italian cave sites the Uluzzian stratigraphically underlies a region-wide chronostratigraphic marker, the Campanian Ignimbrite, consistently dated by ^{39}A/^{40}A to ca. 39 kyr calBP, and is further separated from that marker by Aurignacian levels or by levels with a mix of Uluzzian and Aurignacian material.[43,44] Where the Châtelperronian is concerned, all accelerator mass spectrometry results recently obtained—for the sites of Brassempouy, Caune de Belvis, Grotte XVI, La Quina, Roc-de-Combe and Châtelperron—place it before ca. 42 kyr calBP.[35] In the light of these results, it is clear that the key site of the Grotte du Renne can be no exception (Box 1). Moreover, the notion that a very late Châtelperronian would be demonstrated by the patterns of interstratification observed at El Pendo, Roc-de-Combe, Le Piage, and Châtelperron is now all but abandoned. Careful geological and taphonomical analysis of these sites, coupled with some reexcavation, showed that the El Pendo sequence is entirely redeposited; that the putative Châtelperronian lens sandwiched between Aurignacian deposits at Le Piage is in fact a mixed deposit in secondary position; and that excavation error and faulty intrasite correlations lay behind the Roc-de-Combe pattern.[45,46] At Châtelperron itself, the study of the museum collections and associated documentation shows that the "Châtelperronian" levels putatively situated above a lens of Aurignacian material are no more than backdirt from the nineteenth-century excavations.[47]

Because the transmission of cultural traits follows different rules (it depends on human volition, not natural selection), detecting a biological contribution from the Neandertals to later populations does not necessarily entail that an equivalent signature must exist in the realm of culture. However, if such a signature is found to exist, then the case for admixture is strengthened.

In western Europe, the Châtelperronian and the Uluzzian are followed by the Aurignacian, associated with diagnostic modern human remains at La Quina and Les Rois.[26] The features of the lithic and bone assemblages and the radiocarbon dates obtained for the La Quina sequence indicate that these remains can be no older than ca. 38 kyr calBP.[35] The dental material from the Aurignacian of Brassempouy, dated to ca. 37 kyr calBP, is also of modern human affinities,[48] although the issue remains controversial.[49] On the basis of cultural continuity, it is in any case reasonable to assume that the same people who manufactured the Aurignacian ca. 38-37 kyr calBP were also responsible for earlier manifestations of the technocomplex. This inference is certainly consistent with the fact that the Oase finds place people of overall modern anatomy in Europe during the earlier part of the Aurignacian, and with the traditional view of the latter as a long-lasting archeological entity united by strong elements of cultural continuity. New excavations and in-depth technological studies have now vindicated this view and the validity of the tripartite Aurignacian I, II, and III–IV succession.[45,50–52]

Box 1. Grotte du Renne (Arcy-sur-Cure)

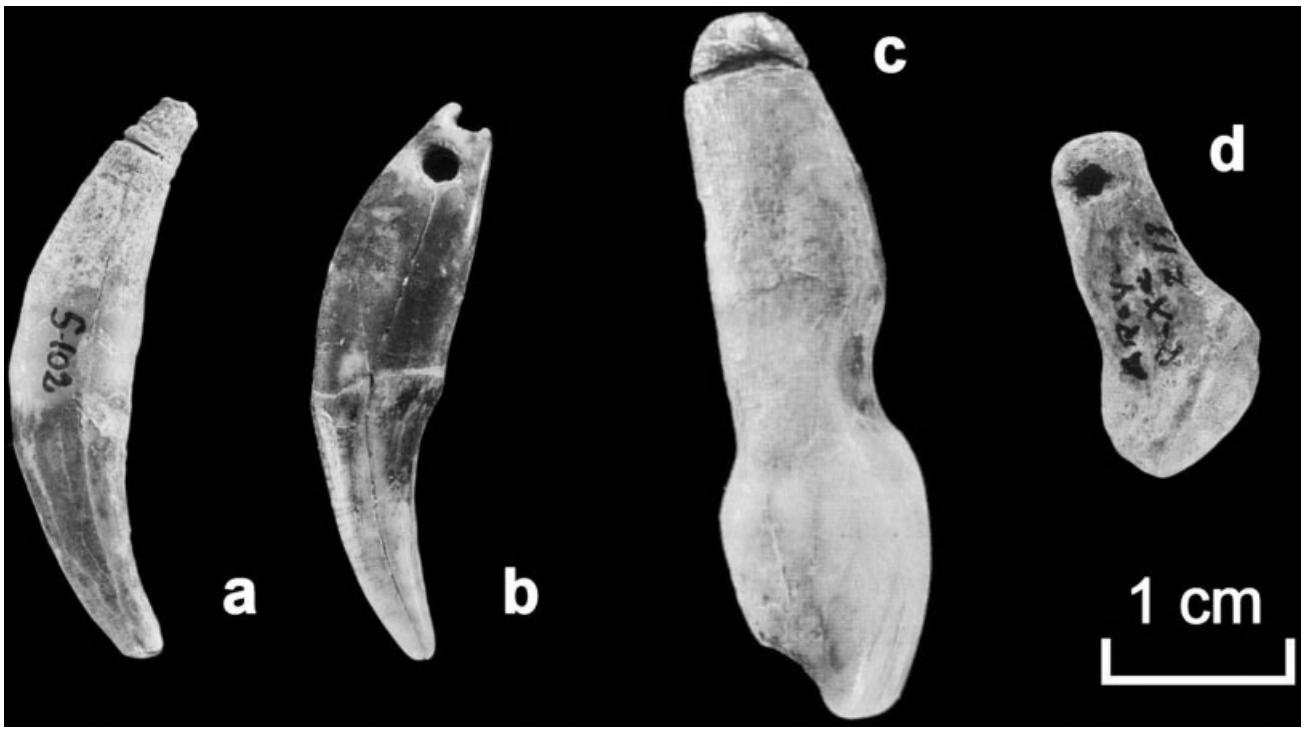
Among the sites that yielded Châtelperronian ornaments, the Grotte du Renne stands out. Following recognition that the human remains from the corresponding levels were of Neandertals, it was suggested that the ornaments reflected trade with or scavenging from abandoned sites of contemporary Aurignacian modern humans, if not simply intrusion from an overlying Aurignacian level.[91]

Because most ornaments come from basal level X, not from level VIII, which is in direct contact with the Aurignacian, these interpretations are inconsistent with the stratigraphic distribution of the finds and with the manufacture byproducts indicative of the *in-situ* production of ornaments, bone tools, and decorated bird bone tubes.[92,93] Moreover, the often-quoted ca. 32-33 kyr ^{14}Cbp dates are clearly rejuvenated. As indicated by the discrepancy between results for "outside" and "inside" areas of the same levels at Fumane (Italy) and Sesselfels (Germany), the cause is bone diagenesis after occupation, when collapse of the roof transformed the Renne's inhabited cave porch into an open air site.[40] The ca. 43 kyr calBP result for level Xb is consistent with the chronology of the Châtelperronian elsewhere in France and provides the most reliable indicator of its age here.

Recent developments have strengthened the view that we are not dealing with an epigonical Aurignacian-impacted phenomenon restricted to a peripheral region inhabited by residual Neandertal survivors. The notion that incomplete decontamination systematically rejuvenates bone samples from this time range, specifically in the examples given, is now accepted even by those who most vocally opposed it.[41] Study of the human teeth confirmed their Neandertal affinities.[94] Publication of the lithic assemblages[95,96] yielded quantitative data that greatly strengthen the inconsistency of the hypothesis that the ornaments are intrusive. The conclusion that these pierced and grooved teeth, bones, and fossils stand for the emergence of symbolic behavior among Neandertals before modern human immigration is further supported by similar finds from Quinçay,[97] where contamination from later occupations can be completely excluded because none exists.

Vertical Distribution of the Archeological Finds in the Grotte du Renne[92–96]

Level	Culture	Lithics	%	Ornaments	%	Bone Awls	%	Neandertal Teeth	%
VII	Aurignacian	11,901	12.50	7	17.50	8	15.09	—	—
VIII	Châtelperronian	8763	9.20	4	10.00	4	7.55	1	3.45
IX	Châtelperronian	11,856	12.45	4	10.00	5	9.43	3	10.34
X	Châtelperronian	62,684	65.84	25	62.50	36	67.92	25	86.21
Total		95,204		40		53		29	



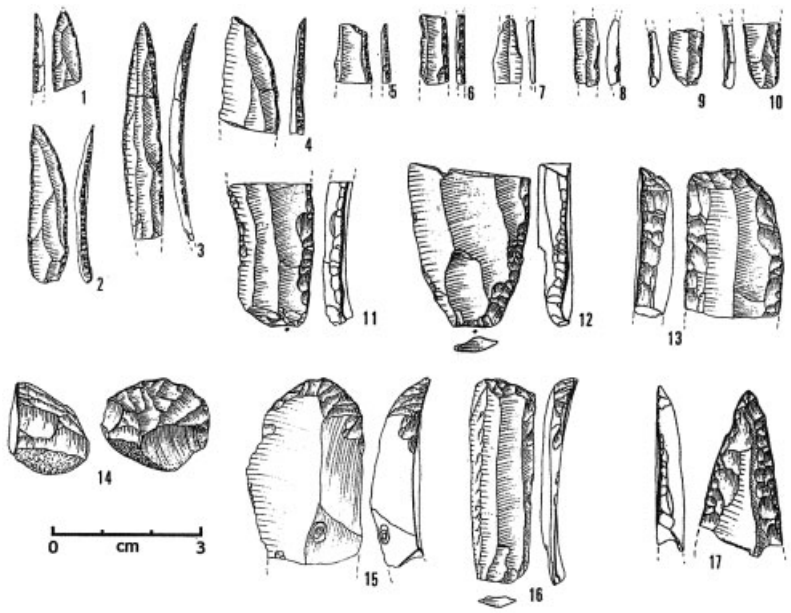


Figure 3. Lithics from the Protoaurignacian of Tincova (Banat, Romania).[98] 1–3, Font-Yves points; 4–10, Dufour bladelets (Dufour subtype); 11–12, retouched blades; 13, endscraper on retouched blade; 14, bladelet core; 15–16, simple endscrapers; 17, pointed blade.

This work has also made it clear that the so-called Protoaurignacian, characterized by large numbers of Font-Yves points and Dufour bladelets of the long, slender Dufour subtype, both made on blanks extracted from unidirectional prismatic cores in the framework of a single, continuous reduction sequence (Fig. 3), previously considered to be a Mediterranean variant of the classical Aurignacian,[52] is instead a chronological phase.[35] The recent reexcavation of the key cave site of Isturitz[53] and the revision of the stratigraphy of Le Piage show that, in France, as in Italy or Spain, this Protoaurignacian stratigraphically precedes the Aurignacian I with split-based bone points and carinated scrapers. These developments, combined with detailed critiques of the available corpus of radiocarbon results,[35,39,40] eliminated the apparent discrepancy between stratigraphic and chronometric patterns: At ca. 42-41 kyr calBP (Table 1), the Protoaurignacian postdates the Châtelperronian and the Uluzzian. The Aurignacian I is nowhere earlier than ca. 40.5 kyr calBP.

Suggestions that at least some Aurignacian occurrences could actually predate the Neandertal-associated early Upper Paleolithic cultures of Europe are based on four sites only.[54,55] At Châtelperron, the claim is that spit B4 of Delporte's 1950s excavations places the Aurignacian beyond 43 kyr calBP. However, that level contained both Châtelperronian and Aurignacian material and yielded two dates, ca. 41 and ca. 44 kyr calBP. The only reasonable interpretation of this evidence is that the earlier relates to the Châtelperronian component and the later to the Aurignacian one.[47] At Willendorf II, Austria, the evidence comes from level 3, which yielded a small assemblage of artifacts in secondary position sitting on an eroded surface that yielded soliflucted charcoal dated to ca. 43 kyr calBP. However, as recently acknowledged by the site's researchers, "dating small charcoal fragments dispersed in soliflucted layers must be avoided" because of the "lateral supply of older charcoal fragments."[56] Such a supply clearly explains the anomalous results, which simply provide a *terminus post quem* for the lithics, the affinities of which lie with the Aurignacian I. A related situation exists at Keilberg-Kirche, Germany, where most finds come from surface collections and displaced deposits.[57] The mixed lithic assemblage contains Middle Paleolithic and early Upper Paleolithic items (*blattspitzen*). The charcoal dated to ca. 43 kyr calBP likely relates to one of these components, as further indicated by the fact that the Aurignacian diagnostics are carinated burins characteristic of the Evolved Aurignacian (II-IV), everywhere else dated to <ca. 37.5 kyr calBP. Where the Geissenklösterle is concerned, the controversies[2,40] surrounding the definition and age of its lower Aurignacian level are now settled, with all parties involved agreeing that the level dates to ca. 40.5 kyr calBP,[58] in good accord with the Aurignacian I affinities of the lithics.

A recent proposition is that the pre-Aurignacian Upper Paleolithic entities of central and eastern Europe, such as the Bachokirian of Bulgaria or the Bohunician of Moravia and Poland, which are dated to the ca. 44-42 kyr calBP interval, represent a precocious extension of the modern human range into the Danubian basin[59] (Fig. 4). This scenario is based on perceived similarities with a Levantine entity, the Emiran or Initial Upper Paleolithic (IUP), assumed to be a product of modern human culture. The assumption is reasonable, but the link with the Danube is extremely weak. It rests on the observation that Levallois blade production is unknown in Moravia before the Bohunician, and that the latter's reduction strategy of aiming at the extraction of morphologically Levallois points via non-Levallois prismatic methods is akin to that in the basal levels of Boker Tachtit, Israel. These arguments assume that the technological transition observed at Boker Tachtit is a unique event, but the independent emergence and disappearance of prismatic blade technologies is recorded at different moments in time and space over the last 200,000 years. Moreover, the diffusion of technologies can occur with no migration being involved. In fact, the apparently intrusive nature of the Bohunician in Moravia simply reflects the large time gap currently separating it from the local Micoquian. In nearby southern Poland, the sites of Piekary IIa and Księcia Józefa document the *in-situ* development of volumetric Upper Paleolithic methods of blade debitage out of Levallois flake-

TABLE 1. Reliable Radiocarbon Dates[35] for the Latest Neandertal and Earliest Modern Human Remains and Associated Cultural Manifestations: the Uppermost IUP Level of Uçağizli Provides a *terminus post quem* for the Early Ahmarian

Site	Culture/Fossil	Level	Sample	Method	Lab Number	Result	calBP 2σ
Üçağizli	IUP (=Ksar Akil XXI)	G	Charcoal	AMS	AA37626	39100 ± 1500	45350 – 41630
Kebara	Early Ahmarian	IIIBf hearth	Charcoal	AMS	OxA-1567	35600 ± 1600	43460 – 37580
Boker A		1	Charcoal	Conventional	SMU-578	37920 ± 2810	46920 – 37320
Oase	Early Modern Human	—	Bone	AMS	OxA-11711/GrA-6165	34950/+990/−890	42490 – 38410
Krems-Hundsteig	Protoaurignacian	Brown layer	Charcoal	Conventional	KN-654	35500 ± 2000	43990 – 36310
Grotta di Fumane		A2	Charcoal	AMS	UtC-2048	36500 ± 600	42620 – 41300
Riparo Mochi		G	Charcoal	AMS	OxA-3591	35700 ± 850	42890 – 38930
Esquicho-Grapaou		SLC1b	Charcoal	Conventional	MC-2161	34540 ± 2000	43430 – 35550
Isturitz		U274d	Burnt bone	AMS	GifA-98232	36510 ± 610	42640 – 41280
Morin		8	Charcoal	AMS	GifA-96263	36590 ± 770	42850 – 41050
Kleine Feldhofer Grotte	Neandertal	—	Bone	AMS	ETH-19660	39240 ± 670	44650 – 42290
El Sidrón		—	Tooth	AMS	Beta 192067	38240 ± 890	44290 – 41730
Klissoura 1	Uluzzian	V	Burnt bone	AMS	GifA-99168	40010 ± 740	45110 – 42630
Abri Dubalen	Châtelperronian	EBC2	Bone	AMS	GifA-101045	36130 ± 690	42920 – 39800
Châtelperron		B5	Bone	AMS	OxA-13622	39150 ± 600	44590 – 42270
Grotte du Renne		Xb1-Y10	Bone	AMS	OxA-8451/Ly-894	38300 ± 1300	44720 – 41440
Caune de Belvis		7	Bone	AMS	AA-7390	35425 ± 1140	42900 – 38380
Combe Saunière		X	Bone	AMS	OxA-6503 (tripeptide)	38100 ± 1000	44320 – 41600
Grotte XVI		B	Bone	AMS	GifA-95581	35000 ± 1200	42730 – 37890
La Quina, aval		4	Bone	AMS	OxA-10261/Ly-1367	35950 ± 450	42600 – 40280
Roc-de-Combe		Square K9, level 8	Bone	AMS	Gif-101264	39540 ± 970	45030 – 42230

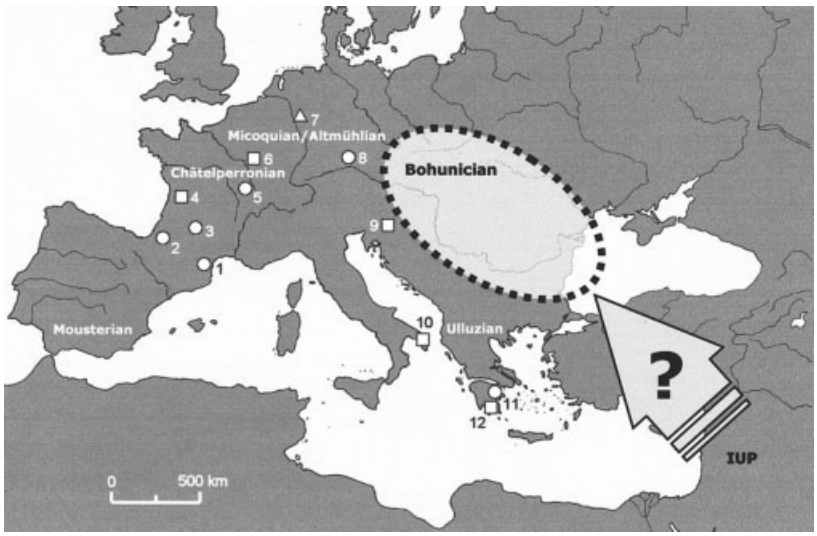


Figure 4. The latest evidence of Neandertals north of the Ebro divide and the "IUP = Bohunician hypothesis" of a Danubian wedge of modern human settlement ca. 45 ka calBP. The cultural continuity between the Bohunician and the regional Middle Paleolithic contradicts the hypothesis, but the issue remains open due to the lack of associated human remains. Circles: latest Châtelperronian, Micoquian and Uluzzian sites. Triangles: Neandertal remains directly dated to <45 kyr calBP. Squares: Neandertal remains in Châtelperronian, Micoquian, Szeletian, Uluzzian, or late Middle Paleolithic contexts. 1. Caune de Belvis, 2. Abri Dubalen, 3. Grotte XVI and Roc-de-Combe, 4. Saint-Césaire, 5. Châtelperron, 6. Grotte du Renne, 7. Kleine Feldhofer Grotte (Neander valley), 8. Sesselfelsgrotte, 9. Vindija, 10. Cavallo, 11. Klisoura 1, 12. Lakonis I.

based technologies during the time interval of the Moravian hiatus (ca. 53-43 kyr calBP)[60] (Fig. 5). Parsimony dictates that there is no need to look into the Middle East for the source of the Bohunician if a better local alternative is available.

Given the lack of associated human remains, the authorship of the Bohunician must remain an open issue, but the evidence for cultural continuity with the regional Middle Paleolithic suggests that it relates to Neandertals. The same reasoning pertains to the Bachokirian of Bulgaria. Although aspects of size, shape, and crown morphology align the dental material from the type-site with modern humans,[61] this conclusion only applies to the Aurignacian levels, the single human remain from the Bachokirian ones being a taxonomically undiagnostic left mandibular fragment with deciduous first molar. Moreover, the recent review of the relevant collections fully confirmed previous reservations concerning the diagnosis of the relevant assemblages from Bacho Kiro and Temnata as Aurignacian or pre-Aurignacian. In fact, technologically, these are Middle Paleolithic assemblages where, in contrast with the IUP and the Bohunician, blade production is fully within the Levallois concept.[62–64]

This evidence indicates that Europe remained entirely a Neandertal continent until ca. 43 kyr calBP and that, southwestern Iberia excluded,[27,28] contact was established and subsequent interaction was resolved within the one or two millennia centered around 42 kyr calBP (Fig. 6), broadly coinciding with the onset of Greenland Interstadial (GIS) 11. In terms of archeological entities, these conclusions have two corollaries of crucial importance:

1. Any manifestations of human behavior predating the 43rd millennium BP must be attributed to Neandertals, who were therefore the authors of the Châtelperronian, the Uluzzian, the Bohunician, and equivalent early Upper Paleolithic cultures of Europe displaying features of regional continuity with the preceding Middle Paleolithic.

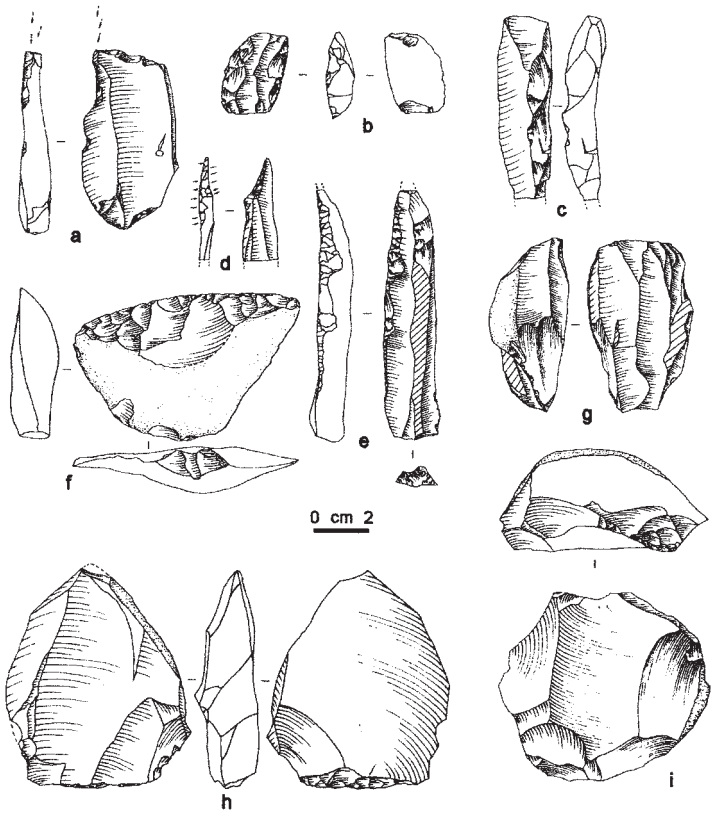


Figure 5. Lithics from level 7b of Piekary IIa, thermoluminescence dated to ca. 53 ka BP.[60] a. burin, b. truncated-faceted scraper, c. crested blade, d, e. backed blades, f. transversal sidescraper, g. bidirectional, prismatic blade core, h. Levallois blank, i. Levallois core.

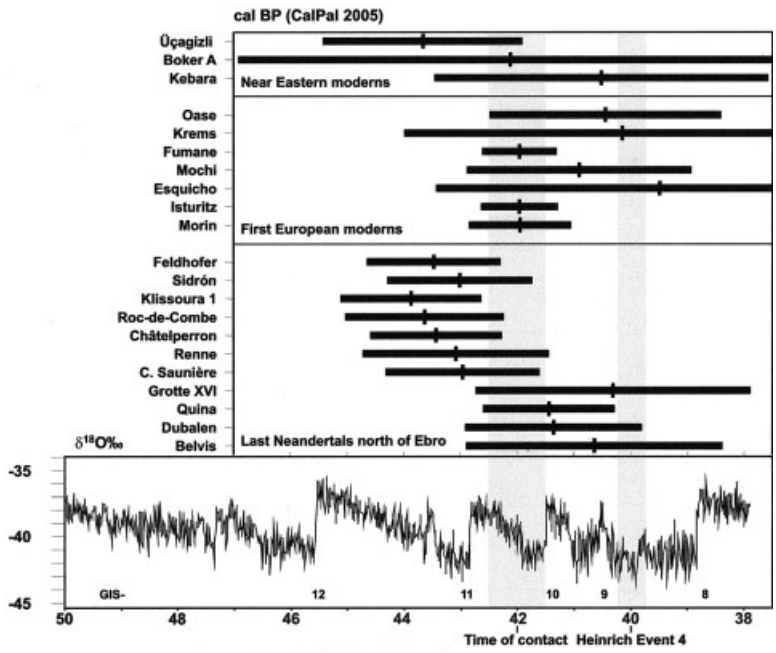


Figure 6. Plot of the calibrated dates in Table 1. The tail of younger Châtelperronian results illustrates the impact of incomplete decontamination on bone samples, not long-term contemporaneity with the Aurignacian. (At Grotte XVI, for instance, two other results for the same level place it firmly beyond 43.5 kyr calBP). Assuming Oase and the Protoaurignacian as proxies, the first modern human dispersals into Europe coincide with the onset of GIS-11, ca. 42 kyr calBP.

2. Any manifestations of human behavior postdating the 41st millennium BP must be attributed to modern humans, who were therefore the authors of the Aurignacian I and the Aurignacian II, including at Vindija, where level G1 is a palimpsest covering an extended interval of time. The Neandertal remains are in all likelihood associated with that level's Szeletian material, not with the split-based point also found there.

INTERACTION

Given the preceding, ambiguity is now restricted to the particular archeological entity that available dates place in the exact interval during which, by whatever mechanism, Neandertals were replaced by modern humans, the Protoaurignacian. In fact, depending on potentially regionally variable patterns of interbreeding (extensive, negligible, or nonexistent), manifestations of human behavior from the time of contact may relate to modern humans, Neandertals, or variously mixed populations. That the dispersal of modern humans into Europe is clearly involved in the emergence of the Protoaurignacian, is suggested by several lines of evidence:

1. Technologically and typologically, the Protoaurignacian is virtually indistinguishable from the Early Ahmarian of the Levant. Its Font-Yves points, for instance, are exactly the same thing as the latter's El-Wad points.[65]

2. Chronologically, the two entities are broadly contemporary. At Ksar 'Akil, in Lebanon, the Early Ahmarian is undated but lies between the Aurignacian and the IUP; Üçağizli, in southern Turkey, provides a solid chronological framework for the IUP[66] and thus, indirectly, a *terminus post quem* of ca. 43-41 kyr calBP for the Early Ahmarian that is consistent with the single reliable date for Kebara (ca. 40.5 kyr calBP, on hearth charcoal).[67]

3. The now lost juvenile skeleton from the Early Ahmarian of Ksar 'Akil ("Egbert") is modern[68] and, given the preceding, of the same age as the Oase fossils.

4. In marked contrast with the geographical fragmentation of the immediately preceding Neandertal-associated technocomplexes, the Protoaurignacian extends uniformly across Europe, from Romania (Tincova) and Austria (Krems-Hundsteig) in the east to Cantabrian Spain (Morin) in the west.

A further point of cultural similarity resides in the fact that the two entities feature marine shell beads as ornaments.[35] One species in particular, *Nassarius* (= *Arcularia*) *gibbosula,* represents 40% of all beads in the Early Ahmarian of Ksar 'Akil and is also well represented among Protoaurignacian marine shell ornaments; the latter's range of taxa is broader, but all are of pretty much the same size and shape. *Nassarius* beads are also about 90% of the several hundred ornaments now known from the IUP of Üçağizli,[66] suggesting cultural continuity between the two. In fact, the earliest African ornaments, those from the ca. 75,000-year-old Still Bay levels of Blombos,[69] are marine shell beads. Since the single species used, *Nassarius kraussianus* (Fig. 7), is very similar to *Nassarius gibbosula,* it is not unreasonable to speculate that the IUP, the Early Ahmarian, and the Protoaurignacian are lithic technological expressions of a single deeply rooted cultural tradition extending all the way back into the Middle Stone Age of southern Africa and, therefore, mod-

Figure 7. Personal ornaments of early moderns[66,69] above, *Nassarius gibbosula* from the IUP of the Near East; below, *Nassarius kraussianus* from the Middle Stone Age of Blombos. The length of these shells varies between 1.0 and 1.5 cm.

ern human-related. Such speculations are in any case fully consistent with the evidence of the long-term stability of traditions of personal ornamentation, which, throughout the Upper Paleolithic, often remain unchanged for tens of millennia.[70]

Both the Protoaurignacian and the subsequent Aurignacian I however, also have other types of personal ornaments, ones that are as completely unknown in the Early Ahmarian and the IUP of the Levant as in the Middle Stone Age of Africa, which, besides the perforated *Nassarius*, only contains ostrich eggshell beads. The novelties are *Dentalium* tubes, pierced and grooved animal teeth, and beads made of bone, ivory, soft stone, or fossils (Fig. 8; Box 1). Their absence from any modern human cultural complex of preceding times obviously cannot be attributed to raw-material availability, and can only relate to cultural preference. It is thus of great significance that those Protoaurignacian novelties correspond precisely to the only kinds of personal ornaments recorded in the Bachokirian, the Uluzzian, and the Châtelperronian; that is, to the kinds of personal ornaments in use among the Neandertal societies that immigrating modern humans encountered in Europe.[35]

The conclusion that the Protoaurignacian represents the blending of two separate traditions of personal ornamentation thus seems inescapable. In any other archeological or anthropological context, few would question it. Clearly, the alternative view that, after 30,000 years of total and absolute conservatism, moderns would have suddenly decided to adopt such kinds of ornaments at precisely the time of contact with the Neandertals, but independently of any influence from them, amounts to a virtually impossible coincidence.

COGNITION

A corollary of the chronological patterns I have reviewed is that "fully symbolic *sapiens* behavior," as measured by exactly the same standards currently used to assess the African evidence,[71,72] emerged in Europe when the continent was still exclusively inhabited by Neandertals. Many have attempted to define a specifically "modern human behavior" as opposed to a specifically "Neandertal behavior," and all have met with a similar result: No such definition exists that does not end up defining some modern humans as behaviorally Neandertal and some Neandertal groups as behaviorally modern.

In the realm of subsistence, for instance, early OIS-3 Neandertals were logistically organized hunters at Salzgitter-Lebenstedt, in northern Germany, where they exploited reindeer in exactly the same manner as the Ahrensbourgians who recolonized the area 40,000 years later.[73] In the Levant, however, they had a broad-spectrum economy, including significant exploitation of small mammals and plant foods, as revealed by recent studies of phytoliths and macroplant remains from Kebara, Amud, and Tor Faraj.[74–76] In areas of the Iberian Peninsula where the present-day coastline is sufficiently close to theirs, such as the Bay of Malaga, late OIS-3 Neandertal groups left sites featuring shell-midden accumulations that differ from those of the Late Upper Paleolithic and Mesolithic only in that their lithic component is Mousterian.[77] In sum, Neandertal adaptations ranged through the entire gamut of ethnographically documented settlement-subsistence strategies.[78] There is no such thing as "Neandertal behavior."

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It has been argued that modern cognition depended on the acquisition of enhanced working memory (EWM), a cognitive feature associated with the emergence of language and related to the ability to "hold in mind" representations currently not "held in view." This feature is apparent in paleotechnic systems reflecting remote action and contingency planning, such as the production of artificial raw materials requiring procurement in disparate sources and careful control of chemical variables throughout a complex chain of technical operations.[79] Although the proponents of this view claim that such evidence does not appear in the archeological record until about 5,000 years ago, the birch-bark pitch found in the Micoquian site of Königsaue, in Germany, fully matches their requirements for EWM in the archeological record: It was produced through a several-hour smoldering process that required a strict manufacture protocol under exclusion of oxygen and at a tightly controlled temperature between 340°C and 400°C.[80] One can hardly imagine how such Pleistocene high-tech could have been developed, transmitted, and maintained in the absence of symbolic thinking and language as we know them. In a nutshell, when only technological systems are considered, the hallmark of cognitive modernity is documented among Neandertals 40,000 years before comparable examples are offered by modern human societies.

In this regard, one must also note that the widespread notion that "the first modern humans in Europe were in fact astonishingly precocious artists"[81] misrepresents the facts. After 150 years of intensive archeological research, evidence to that effect is actually nonexistent. Where both mobiliary and parietal art are concerned, the earliest anywhere in the world are the figurines of the German Aurignacian[82] and the Chauvet cave paintings.[83] In good agreement with the nature of the associated lithics, the range of dates falls, in both cases, entirely within the Aurignacian II and thus postdates by some 5,000 years

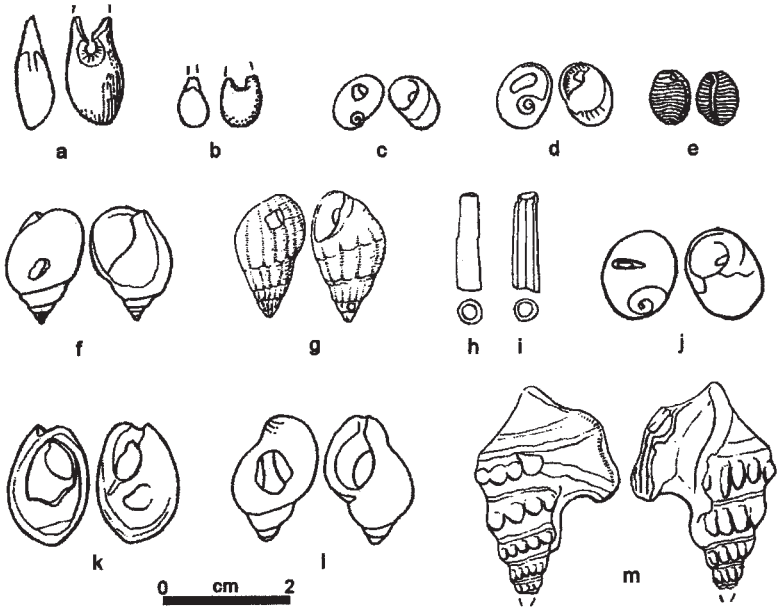

Figure 8. Protoaurignacian beads from the Rothschild rockshelter (France)[99]: a. pierced red deer canine, b. steatite bead, c. *Theodoxus fluviatilis,* d. *Cyclope neritea,* e. *Trivia europaea,* f. *Sphaeronassa mutabilis,* g. *Hinia reticulata,* h, i. *Dentalium,* j. *Littorina obtusata,* k. *Nassarius* (= *Arcularia*) *gibbosula,* l. *Nucella lapillus,* m. *Aporrhaïs pespelecani.*

the arrival of moderns in Europe.[35] This art, therefore, holds the same relevance for the explanation of patterns of cultural interaction at the time of Neandertal-modern human contact as do PowerPoint presentations for the explanation of the rise of Sumerian civilization.

DEMOGRAPHY

Even if a certain level of long-distance stimulus generated by contacts along the frontier with contemporary, presumably modern human societies of the Levant was involved in these processes, the conclusion is obvious: Neandertals and moderns featured similar levels of cognitive development and behavioral "modernity." Such issues can thus be effectively removed from any further consideration as potential barriers to admixture. But if the eventual disappearance of anatomically archaic but behaviorally modern Neandertals was not due to a putative biologically based competitive disadvantage, how do we then explain it?

That no Neandertal mtDNA survives today simply indicates that a particular maternal lineage that existed 50,000 years ago is no more, but tells us little about when and why it disappeared. In fact, given that founder analysis places the actual immigration of the most ancient European haplogroups of today only after 30 kyr calBP,[84] accepting the premises and conclusions of extant mtDNA studies carries the implication that the lineages to which the earliest European moderns belonged are as extinct as the Neandertals'. That this may well be the case should come as no surprise. Although much attention has been paid to the environmental impact of the frequent and dramatic climatic oscillations recorded in the climate proxies of Oxygen Isotope Stage 3 (OIS-3),[85] their demographic corollaries are often overlooked. Most assessments of mtDNA histories through the critical period before and after the time of contact only consider two population scenarios, stability and expansion. It is clear, however, that contractions must also have occurred, producing bottlenecks that must go a long way toward explaining patterns of lineage loss and survival.

A case in point with major implications for the issues at stake here is the environmental crisis associated with the emergence of the Aurignacian I in the archeological record, soon after moderns are first documented in Europe. At this time—Heinrich Event 4, ca. 40-39 kyr calBP—extremely cold conditions prevailed, imposing on human populations the highest level of climatic stress recorded in the entire Upper Pleistocene. Its effects must have been compounded by the catastrophic explosion, ca. 39 kyr calBP, of the Phlegraean Fields caldera.[43,44] As a result, the area available for human settlement in Europe must have contracted by as much as 30%, implying a major population crash (Fig. 9). No modeling of the genetic history of OIS-3 Europe and of the role that Neandertals played in it can be considered realistic if it does not account for a demographic crisis of such significance.

The population crash, however, does not explain why it was those particular lineages that went extinct, whereas others that existed at the same time in Africa and western Asia are still extant; nor does it explain why the biological contribution of Neandertals, still visible in skeletal traits of people dated to within 5,000 years of contact, seemingly all but vanished by ca. 30 kyr calBP. Selection and contingency may well have played a role in the process, but the most parsimonious explanation is demography,[86,87] which suffices to propose a broad historical reconstruction of the process.

Europe is one-third of Africa's size, and during glacial times only a narrow belt of the continent south of 53° N was available for settlement, the loss to mountain glaciation compensated for by the exposure of extended areas of the present-day continental platform. Moreover, as in today's subarctic areas, European territories would have had lower carrying capacities than the subtropical savannahs of Africa, with attendant implications for human population density. In sum, because modern humans were African and Neandertals European, the modern human gene reservoir must have been many times larger than the Neandertal one. As long as the two reservoirs remained largely isolated, Neandertal-ness could be and was maintained. But once populations expanded in the two continents as a result of technological im-

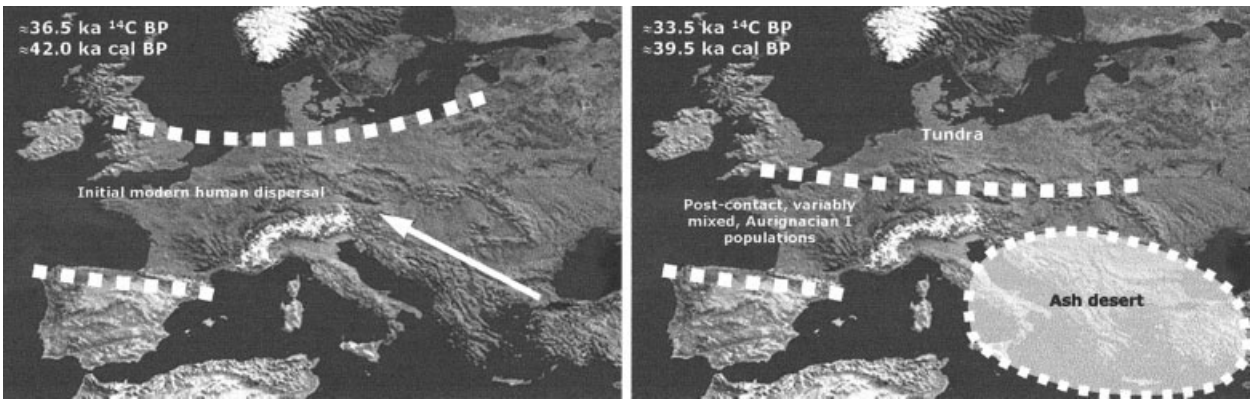

Figure 9. Two millennia after the time of contact, the inhabitable area of Europe significantly shrank as a result of the combined impact of HE-4 and the Phlegraean Fields caldera explosion.

provements that led to major gains in the efficiency of resource exploitation, significant contact and interaction would have begun along what previously had been a largely impermeable frontier. At that time, the two reservoirs effectively merged. In such a situation, even a minor edge of moderns in demographic parameters other than simple numbers, such as fertility, would, in less than one millenium,[86] suffice to bring about the demise of the Neandertals, especially if interbreeding was common. One millenium is the empirically observed interval during which the interaction game was resolved.

As different authors have discussed,[88,89] the fixation of sociotechnic and ideotechnic innovations is best explained by population growth requiring increased levels of intergroup and intragroup social interaction eventually resulting in the emergence of systems of personal and ethnic identification. The ornaments from Blombos show the mechanism in action in southern Africa ca. 75 kyr ago. The lack of evidence for the next 30,000 years suggests that the system may have subsequently collapsed, but by 45,000 calBP we see it again in eastern Africa as well as, for the first time, in the Near East and Europe. The marked differences in the choice of emblems and the biological evidence of reduced contact between Europe and Africa provided by the very fact of Neandertal-ness suggest that the European process was largely independent, and there is no reason to suppose that it was not dictated by similar underlying causes. In fact, vast areas deserted during OIS-4 times, including southern England, Belgium, Germany, and Poland, feature a relatively dense network of OIS-3 sites that, in central Europe, are clearly related to each other by a shared, very particular technology, the Micoquian. This simultaneous emergence or reemergence of personal ornamentation can thus be taken as a proxy for levels of population increase leading to the crossing of a demographic threshold and precipitating contact, followed by admixture and, eventually, absorption of the smaller population by the larger one.

CONCLUSION

When modern humans entered Europe, they encountered people with the same cognitive capabilities and featuring identical levels of cultural achievement. In such a situation, the entire gamut of interaction situations, from conflict to mutual avoidance and full admixture, must have ensued at the local and regional level. But the overall result in the long-term continental perspective was that of biological and cultural blending, the imbalance in the size of the gene reservoirs involved explaining the eventual loss of Neandertal mtDNA lineages among later and extant humans.

It could be argued that such findings are of little or no consequence to the heart of the matter, in that they do not change the basic conclusions derived from genetic studies that a contribution of Neandertals to present Europeans is currently undetectable and, therefore, must be negligible, and that patterns of extant humans' ancestry are essentially related to the recent Out-of-Africa dispersal of anatomically modern people. The European evidence, however, does have a major implication for studies of modern human origins where issues of symbolism, language, and cognition are concerned. The Blombos cave finds effectively refuted the notion[90] that the appearance of ornaments and art could be explained by cognitive developments precipitated by a genetic mutation occurring ca. 50 kyr calBP. By the same token, if Neandertal-associated archeological cultures featuring all elements of behavioral modernity existed in Europe many millennia before the arrival of modern humans, and if contact entailed significant levels of interaction and admixture, then the acquisition of "fully *sapiens* behavior" cannot be construed as the outcome of an anagenetic biocultural process restricted to the African *Homo heidelbergensis* lineage.

The ultimate implication of the European evidence, thus, is that the "hardware" requirements for symbolic thinking must have been in place before the Middle Pleistocene divergence of the Neandertal lineage. This conclusion has three corollaries: first, that the much later appearance of personal ornaments and art represents a qualitative leap in culture, reflecting the operation of demographic and social factors triggered by technological improvements and adaptive success; second, that it is highly unlikely that

the Neandertal-*sapiens* split involved differentiation at the biospecies level; and third, that the search for the genetic and cognitive processes underlying the emergence of language and symbolism in the human lineage needs to be refocused on aspects of the Lower Pleistocene emergence and evolution of *Homo erectus* people.

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