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Genes, Fossils, and Culture. An Overview of the Evidence for Neandertal–Modern Human Interaction and Admixture

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This paper re-examines current arguments concerning the evidence for Neandertal–modern human interaction and admixture. While most researchers now agree that the ancestry of all present day humans can be traced back to African late Middle Pleistocene populations, at a time when the remainder of Eurasia was inhabited by 'archaic humans', most notably the Neandertals, issues that remain to be resolved are the tempo and mode of early modern human dispersal and interaction with archaic humans.

This paper focuses on what happened at the time of contact in Europe, and assesses the level of admixture that may have occurred, as well as the extent to which such level may have varied in both time and space. It explains how the available mtDNA evidence does not preclude admixture at the time of contact, and is in fact consistent, depending on a number of parameters, with a possibly substantial Neandertal contribution to the initial modern human population of Europe. It is argued that the absence of Neandertal mtDNA lineages among present Europeans is likely, on dating evidence, to be simply a particular case of generalised loss of Pleistocene mtDNA lineages. Although the full range of interaction types (mutual avoidance, hostile confrontation, full integration) is conceivable, there is plenty of archaeological evidence to suggest that admixture must have been the general rule, and that the paleontological evidence for the generalised presence of archaic traits among Europe's earliest moderns implies the transmission of genes, and indicates that mixed groups should have been reproductively viable. In this context, it would seem that the most parsimonious explanation for the disappearance of the Neandertal mtDNA lineage is genetic swamping.

After more than two decades of controversies, most researchers now agree that the ancestry of all present day humans can be traced back to African late Middle Pleistocene populations such as those represented by the Omo-Kibish and Herto fossils of Ethiopia (for a recent review, see Trinkaus 2005b). At that time, the remainder of Eurasia was inhabited by 'archaic humans', the archetype of which, given the poorer eastern Asian record, are the Neandertals. Remaining issues are the tempo and mode of early modern human dispersal and interaction with archaic humans, the two mutually exclusive models that dominated the field for a long time – 'total continuity' (Neandertals evolve anatomically modernity on their own) versus 'total replacement' (Neandertals become extinct and their territory is occupied by immigrating anatomically modern humans of ultimate African origin) – having been effectively superseded (but see Wolpoff 2002). The focus now is on what happened at the time of contact in Europe, and on assessing the level of admixture (if any) that may have occurred, as well as the extent to which such level may have varied in both time and space.

This trend is apparent in the genetic (Serre *et al.* 2004; Currat & Excoffier 2004; Weaver & Roseman 2005), the paleontological (Hublin 2000; Stringer 2002; Trinkaus & Zilhão 2002; Trinkaus 2005b), and the archeological (d'Errico *et al.* 1998; Mellars 1999; 2004a; 2005; Zilhão & d'Errico 1999; McBrearty & Brooks 2000; Zilhão 2001; d'Errico 2003; Henshilwood & Marean 2003; Klein 2003) literatures. The different genetic studies, in particular, have tried to quantify the extent to which admixture at the time of contact could have been possible given the combined observations that 1) Neandertal mtDNA lineages are not found among extant humans; 2) Neandertal mtDNA is quite different from that of

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extant humans; and 3) Neandertal mtDNA was not found in any of the early modern human fossils so far analysed for aDNA. The conclusions one can derive from these studies, however, are dependent upon a number of parameters for which the genetic evidence alone lacks the required resolution: for instance, the exact time of contact, the duration of the coexistence interval, or the dynamics of population growth before, during, and after the time of contact. In this regard, Weaver and Roseman (2005) emphasise 'the importance of fully integrating archeological, fossil, and genetic evidence in investigations of modern human origins'. Here, I answer their call by offering my view of the problems in current genetic models, and my own estimations, based on the archaeological and fossil evidence, of the values to be used when parametrising the different variables that have to be considered.

DOES CURRENT aDNA EVIDENCE EFFECTIVELY PROVIDE LIMITS TO THE LEVEL OF ADMIXTURE?

Serre *et al.* (2004) report that the characteristic Neandertal mtDNA sequence is absent from five early modern humans analysed, and use phylogenetic arguments suggesting that all present day mtDNA can be traced back to approximately five lineages 25,000 years ago; from these data they generate a sample of ten European early moderns for comparison with eight Neandertal sequences. Under the assumption that the population of modern humans was in expansion at the time of their dispersal into Europe, they calculate that a contribution greater than 25% of Neandertals to the gene pool of Europeans 30,000 years ago can be rejected; however, they note that if the expansion had taken place only after the time of contact, then the Neandertal contribution could have been higher. These results highlight the importance of demographic parameters (on which more will be said below), but are also heavily dependent on the age of both the early modern human fossils analysed and of the mixing event, as well as on the actual authenticity of the early modern human DNA. As pointed out by Cooper *et al.* (2004) 'if the mixing event was earlier or the early human fossils younger, the maximum reasonable Neandertal contribution could be substantially larger', and 'if some of the human fossils did not actually contain any ancient DNA, the loss of a data point reduces the rejection power of the analysis'.

Where issues of chronology are concerned, a directly dated mandible from the site of Oase, in Romania (Fig. 1), places anatomically modern humans *c.* 35 kyr BP (radiocarbon years ago) (Trinkaus *et al.* 2003a; 2003b; 2005; see below); ie, using currently available calibration software (Weninger & Jöris 2004), >40 kyr cal BP (calendar years ago); the implication is that the mixing event was earlier, ie, that it occurred at least 10,000 years before modelled by Serre *et al.*, as is also suggested by other lines of evidence (see below). The five modern humans analysed, in turn, are assumed to represent the population of Europe *c.* 25,000 years ago, but only one can in fact be considered to date to that time: the specimen from Abri Pataud, presumably a sample from the Protomagdalenian (=Late Gravettian) levels of the site, the only ones that yielded human remains. The sample from La Madeleine, a rock shelter spanning the Magdalenian IV–VI stages of the classical French culture-stratigraphic sequence, cannot be older than some 15,000 years ago, and post-dates by many millennia the Last Glacial Maximum (a major historical and demographic threshold associated with a significant genetic bottleneck; Richards *et al.* 2000). The other three samples (one from Cro-Magnon and two from Mladeč), in turn, are considerably older than *c.* 25 kyr cal BP: the Cro-Magnon humans date to *c.* 31.5 kyr cal BP (Henry-Gambier 2002), and the Mladeč ones to *c.* 36 kyr cal BP (Wild *et al.* 2005). In sum, the five 'early modern humans' analysed by Serre *et al.* span a total of 20,000 years and cannot be taken as a chronologically homogeneous sample set to have lived *c.* 25 kyr cal BP; the time of the admixture event, in turn, was not *c.* 30 kyr cal BP but ≥ 40 kyr BP, and only two of the early modern humans are within five millennia of it, the others being much later.

The chemistry of the collagen extracted for radiocarbon dating indicates, moreover, that one of the Mladeč specimens (Mladeč 25) was contaminated (Wild *et al.* 2005). This problem is further compounded by the fact that, as pointed out by Pääbo (commenting on the aDNA of two early modern Gravettian individuals from the Italian cave site of Paglicci, dated to *c.* 29 kyr cal BP; Caramelli *et al.* 2003): 'Cro-Magnon DNA is so similar to modern human DNA that there is no way to say whether what has been seen is real' (Abbott 2003); put another way,

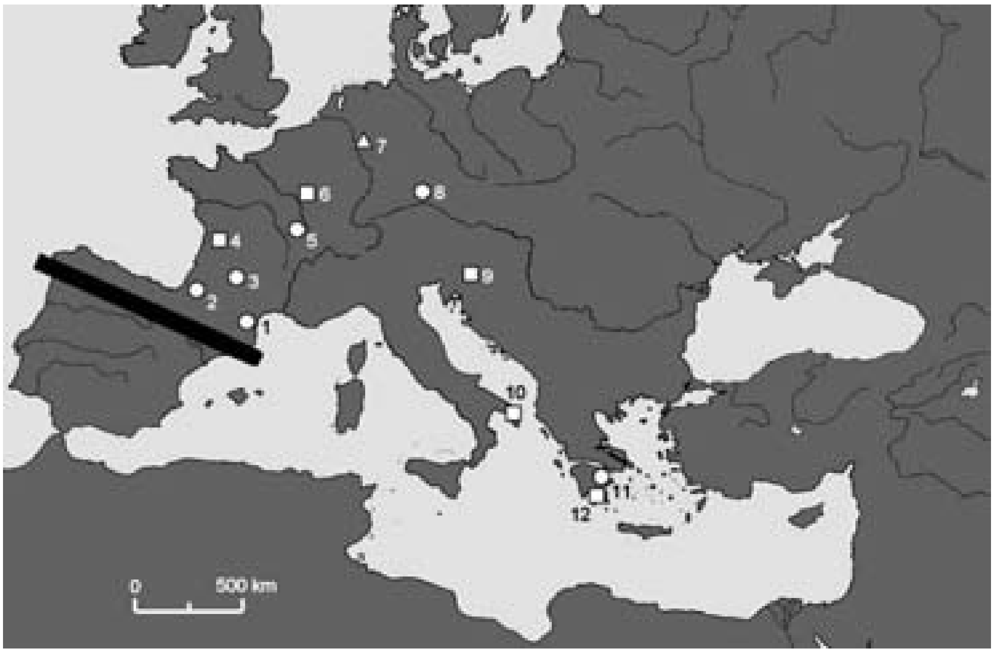
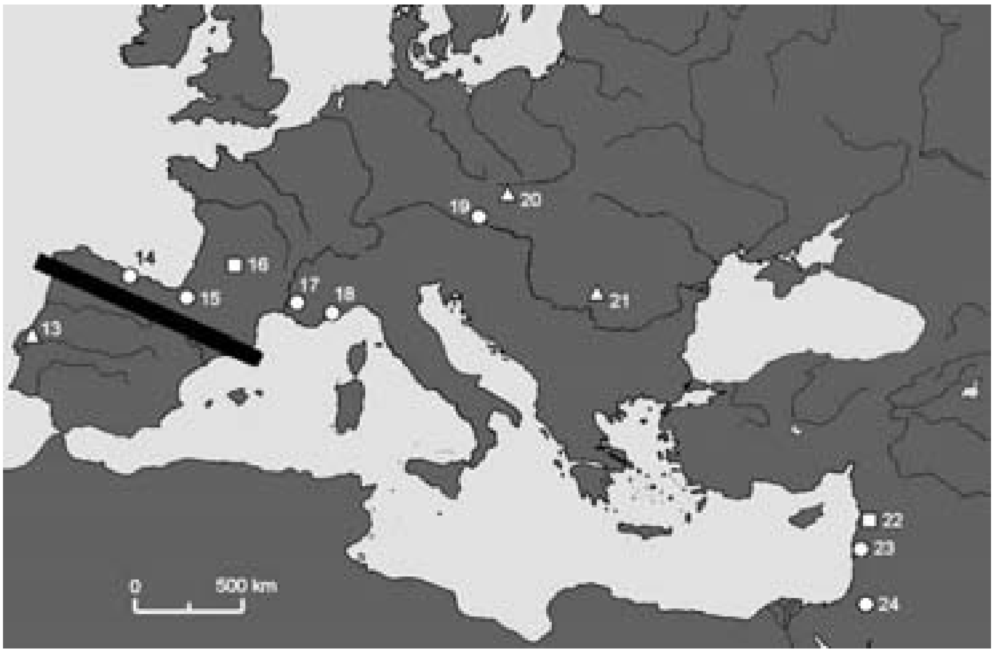


Fig. 1.
Location of key sites for the Neandertal-Modern contact in Europe, immediately before and after the 42nd millennium cal BP (in Iberian regions south of the Ebro river basin, the process was delayed for at least five and possibly as much as eight millennia).
Above: latest reliably dated Châtelperronian, late Micoquian and Uluzzian sites (circles); sites with Neandertal remains reliably directly dated to <45 kyr cal BP (triangles); sites with Neandertal remains in Châtelperronian, late Micoquian, Szeletian, Uluzzian, or late (reliably dated to <45 kyr cal BP) Middle Paleolithic archeological contexts (squares). 1. Caune de Belvis; 2. Abri Dubalen (Brassempouy). 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.
Below: reliably dated Protoaurignacian and Early Ahmarian sites (circles); sites with modern human remains reliably directly dated to within five millennia of the time of contact (triangles); sites with modern human remains in Evolved Aurignacian and Early Ahmarian archeological contexts (squares). 13. Lagar Velho; 14. Morin; 15. Isturitz; 16. Les Rois and La Quina; 17. Esquicho-Grapaou; 18. Riparo Mochi; 19. Krems-Hundsteig; 20. Mladeč; 21. Muierii; 22. Ksar 'Akil; 23. Kebara; 24. Boker A



as reviewed by Pääbo *et al.* (2004) and Willerslev and Cooper (2005), current methodology does not allow determination of whether DNA extracted from a modern human fossil is indeed ancient or simply modern contamination. The implications of this issue are well illustrated in a paper by Malmström *et al.* (2005). They extracted mtDNA from 24 samples of Swedish Neolithic dogs housed in museum collections and showed that 1) all samples contained human DNA; 2) on average, the levels of human DNA (65%) exceeded those of authentic ancient dog DNA (35%); 3) contaminating human DNA was in the dog bones, it did not come from a carrier effect inherent to the PCR process; and 4) hence, recognised criteria for authenticating aDNA (namely, independent replication of the results in a second laboratory) cannot separate ancient human DNA from contamination.

The first implication of the above for the study by Serre *et al.* is that failure to identify Neandertal mtDNA in a given fossil warrants two different interpretations: that it had no Neandertal mtDNA; or that the DNA extracted is modern contamination entirely, explaining the failure. Since the second interpretation cannot be rejected, and even if one were to accept that the early modern humans so far analysed for aDNA are indeed representative of the population of Europe *c.* 25,000 years ago, the assertion that no Neandertal mtDNA lineages have been found among Europeans of that time is not supported. A related implication is that, because current authentication criteria will reject as contaminated any Neandertal fossil yielding modern-looking mtDNA, our understanding of the genetic variability of the Neandertals and of the extent to which they actually differed from extant humans is strongly biased.

WOULD SIGNIFICANT ADMIXTURE NECESSARILY IMPLY THE SURVIVAL OF THE NEANDERTAL mtDNA LINEAGE TO THE PRESENT?

In order to assess admixture, we are thus forced to work back in time on the basis of only two lines of evidence: the apparent distinctiveness of Neandertal mtDNA, and its absence among today's humans. Cooper *et al.* (2004) showed that, depending on a number of genetic parameters, these two observations are in fact consistent with levels of admixture where the Neandertal contribution could have been anywhere between 1% and 53%.

In a more recent study, however, Currat and Excoffier (2004) criticised the models used by Serre *et al.* for estimating the likelihood of different degrees of admixture under an assumption of post-contact panmixia; instead, they used subdivided populations, overlapping ecological niches, and a progressive range expansion of moderns resulting from a density-dependent competition with the Neandertals. Under these assumptions, the absence of Neandertal mtDNA sequences in extant Europeans would lead to a maximum initial Neandertal input into the modern gene pool of 0.1%, and to no more than 120 individual admixture events throughout the period of coexistence, implying almost complete sterility between Neandertal females and modern human males. Higher values would imply the presence in extant Europeans of visible proportions of Neandertal genes; with only one admixture event per 100 demes, for instance, the percentage of Neandertal mtDNA lineages today would be 5%, and values of 99% would be reached with one such event per deme. These conclusions, however, are already contained in the premises of the model underlying the simulations.

In fact, Currat and Excoffier postulate a unique 'colonisation' event, where a single deme of moderns is pitched against the entire Neandertal population of Europe in consecutive iterations of a process consisting in a fight for territory played one cell at a time, at an exclusively local level (ie, with no consequences beyond the boundaries of each of the model's territorial cells), and resolved in favor of moderns within a few generations at most (200–300 years). In these circumstances, two things are obviously inevitable. First, the small groups of moderns migrating into any given territory can only succeed against the invaded, initially more numerous local Neandertals, if a massive competitive advantage is assumed, because otherwise no territory could be occupied (the sensitivity of the model to this parameter is apparent in that simply decreasing the advantage of moderns from the base line of 40:10 to a more 'moderate' value of 25:10 causes a 2.4 fold increase in the maximum number of possible admixture events per deme); in sum, if no competitive advantage is postulated (and the archeological evidence from the time of contact has indeed so far failed to detect any – more on this below), the model

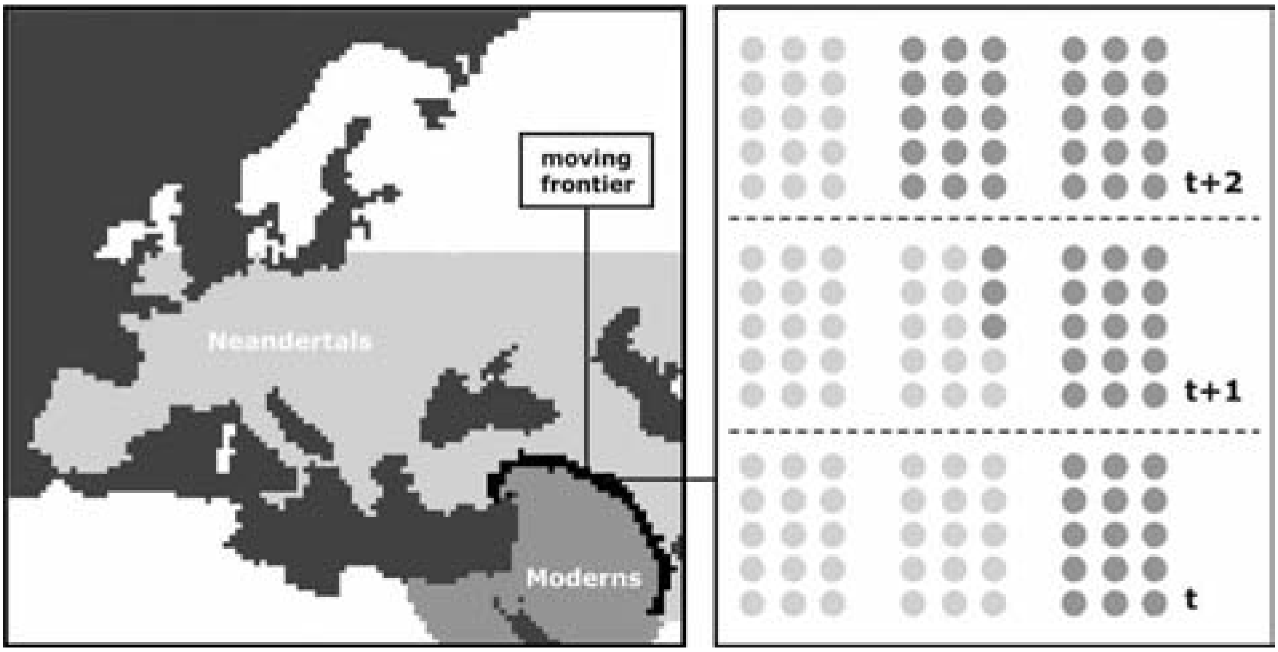


Fig. 2.
Currat and Excoffier's (2004) model of frontier admixture. The range of moderns expands through the penetration of pioneer individuals or families in territorial cells occupied by Neandertals (time t+1); after a period of competition (2–5 centuries), during which admixture is allowed but only within the boundaries of the cell, moderns take over that territory (time t+2)

simply does not work. Second, very low rates of admixture have to pertain, otherwise the modern immigrants would be simply absorbed into the Neandertal pool, and no global change could take place at the biological level in either side of the narrow frontier to which the model limits contact and potential admixture (Fig. 2).

By modelling such largely impermeable gene reservoirs, Currat and Excoffier assume as a premise their conclusion that Neandertals and moderns were different biological species involved in a competition for territory caused by the range expansion of one of them. They do not consider and, hence, do not refute, the more realistic alternative of contact between interacting populations of hunter-gatherers operating under the rules of exogamic marriage. The latter imply that, in order for any given individual to be sure of finding an appropriate mate at the appropriate time, alliance networks extending for thousands of square kilometres have to be established and maintained (Wobst 1974; 1976); as a result, when two previously geographically separated populations make durable contact and females are exchanged, the flow of mtDNA will affect gene pools well beyond the pre-contact frontier. Ethnographic data (Tindale 1953), for instance, indicate that the mean rate of intertribal marriages among Australian aboriginals was about 15%, and that this related principally to women (ie, the transmitters of mtDNA lineages) moving into neighbouring groups. Thus, factors such as genetic drift and differential fertility rates between the subpopulations of such large breeding networks become of paramount importance in explaining genetic histories (Zubrow 1989; Relethford 2001; 2003). The implication is that, in spite of their not considering population structure, the use of panmictic models such as those of Serre *et al.* is still much more realistic than Currat and Excoffier's simulations based on density-dependent, one-cell-at-a-time competition.

A related issue is that Currat and Excoffier model the history of the European gene pool after the time of potential admixture in complete isolation from the rest of the world. As the archeological evidence – artistic styles, burial rituals (Soffer *et al.* 2000; Zilhão & Trinkaus 2002) – particularly well shows for the Gravettian period (between *c.* 31 and *c.* 24 kyr cal BP),

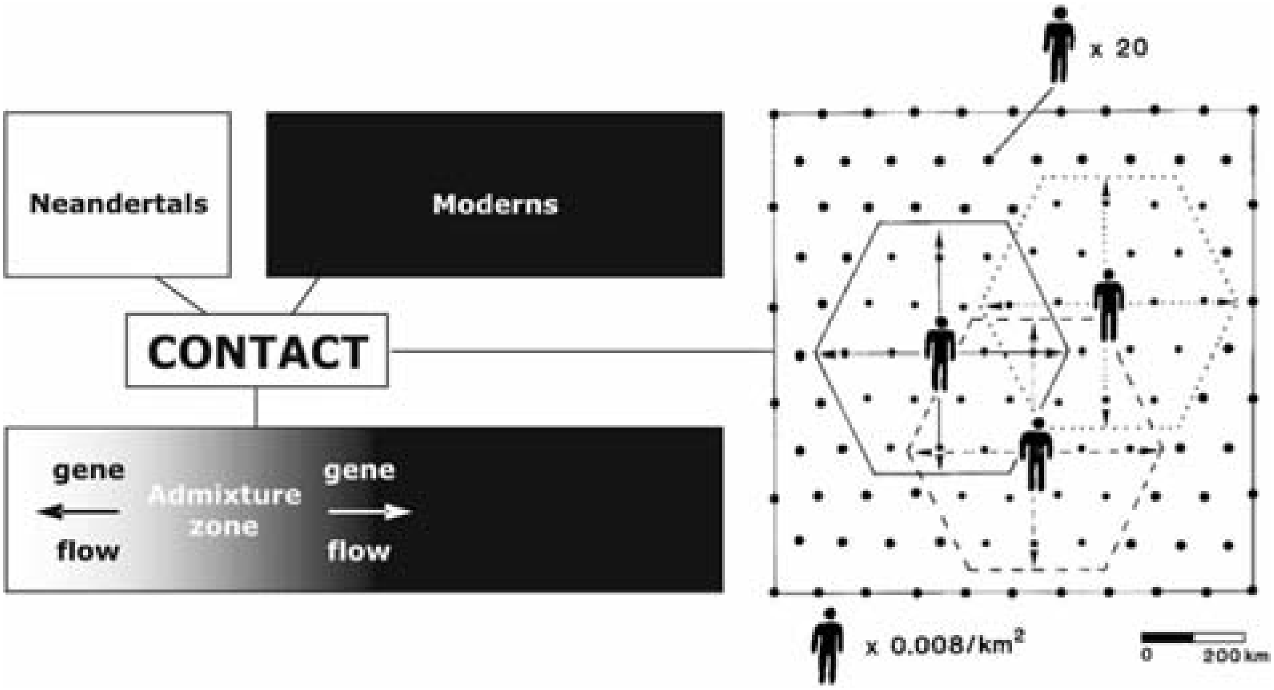


Fig. 3.
Contact between Neandertals and moderns under the rules of exogamic marriage. The exchange of females across extensive breeding networks spreads mtDNA lineages well beyond the frontier, effectively uniting two previously isolated gene reservoirs (based on Smith 1992, fig. 2.1, modified)

the flow of information exchange at that time encompassed vast areas of Eurasia, from Portugal in the west to central Siberia in the east. The relevance of this point is that, once the admixture process was over, the number of females carrying Neandertal mtDNA could only expand to become dominant or exclusive in the present (the inevitable outcome under Currat and Excoffier's rules) if Europe were to be conceived as a sealed, isolated gene reservoir. In a scenario where the continent is part of much wider breeding networks, such an expansion could happen only if both the fertility of those females and the rates of growth of the population of Last Glacial Europe had been much higher than elsewhere in the Old World, which clearly cannot have been the case.

In order to support Currat and Excoffier's conclusions, simulation studies would need to start from the null hypothesis that Neandertals and moderns behaved as different hunter-gatherer groups, contact leading to uninterrupted gene flow across extensive areas (Fig. 3). Only if ultimate 'replacement', as a result of the full integration of a smaller gene reservoir in a larger one could not be obtained in such circumstances, would one be justified in rejecting that null hypothesis and search for alternative ways of explaining the evidence. For now, the null hypothesis is not refuted and, in fact, there seems to be ample evidence from nuclear DNA studies suggesting hybridisation between expanding anatomically modern humans spreading from Africa and archaic Eurasians (Templeton 2002; Garrigan *et al.* 2005).

HOW EXCEPTIONAL WAS THE LOSS OF THE NEANDERTAL mtDNA LINEAGE?

A major source of confusion in the modern human origins debate is the often non-explicit assumption that the phylogeography of extant mtDNA lineages mimics the history of the actual spread of past anatomically modern human populations (Forster 2004). In fact, however, that phylogeography 1) simply represents the coalescence in space and time of the mtDNA lineages that survived, and 2) does not preclude that some such lineages are in fact related to inputs from archaic populations.

For instance, the 'mitochondrial Eve' herself is assumed to have belonged to the African group that underwent the speciation event at the origins of 'moderns-as-a-species'. In actual fact, it simply represents the deepest point in time to which we can trace back the maternal ancestry of living humans; thus, she may well have belonged to an archaic form (such as *Homo heidelbergensis* or *Homo helmei*, depending on which taxonomic scheme is favoured). By the same token, the fact that the L1 haplogroup represents the deepest branch of extant mtDNA phylogeography does not necessarily mean that it represents the first post-speciation *Homo sapiens* populations; it may simply represent an mtDNA lineage that was already in existence among anatomically archaic African populations of the late Middle Pleistocene and was passed on to the gene pool of extant humans.

More importantly, one cannot assume that the variation observed in the present is representative of that which existed in the past. This point has been made before, for instance by Lahr and Foley (1998), who noted that 1) 'the diversity of modern humans

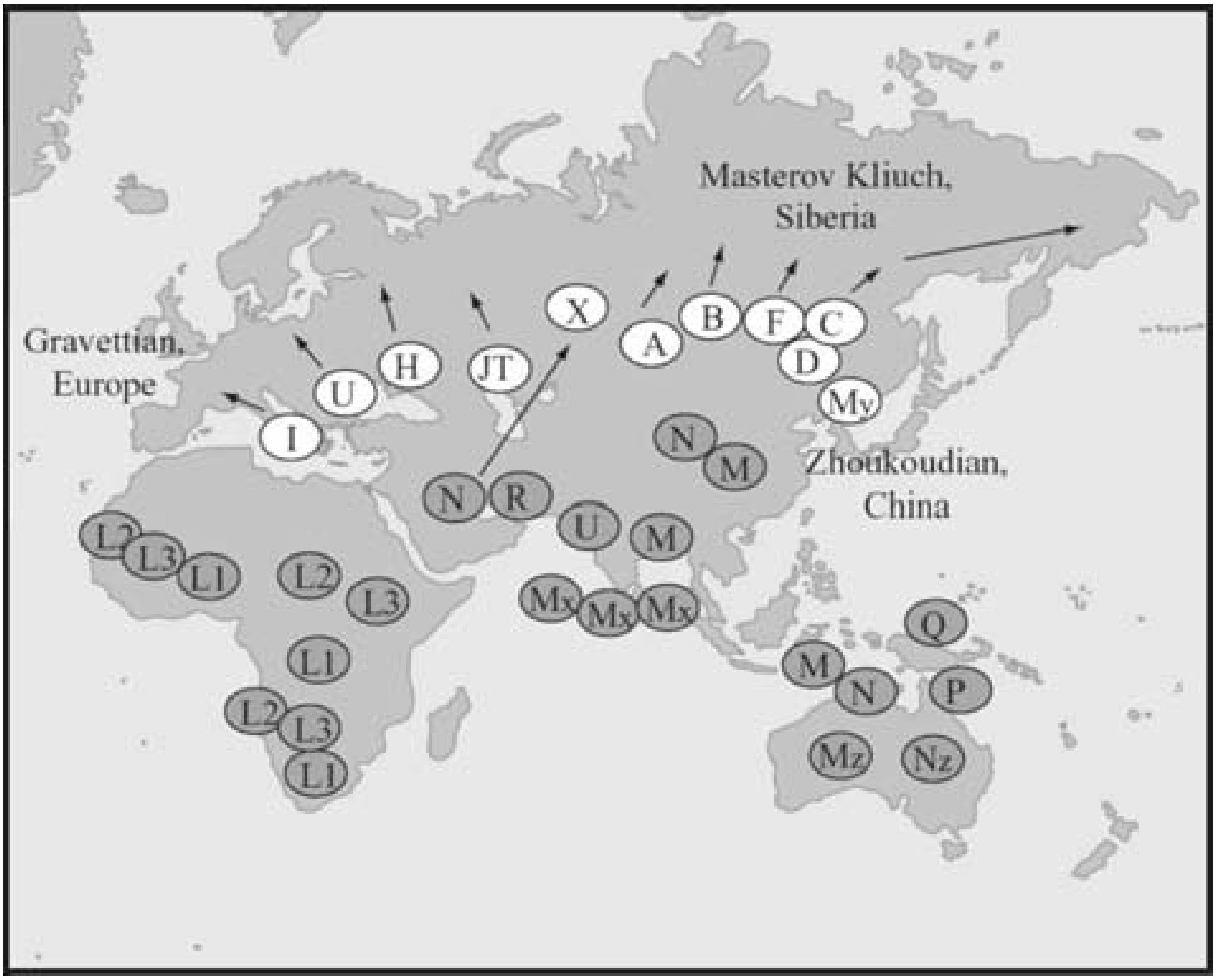


Fig. 4.
The spread into Europe of the continent's founder lineages H, I, and U takes place after 30,000 years ago, at the time of the Gravettian (after Forster 2004, fig. 2d, modified)

today is likely to be just a subset of *Homo sapiens* diversity that could have been sampled across the last 100,000 years', and 2) 'patterns of diversity, particularly the relationship between inter- and intrapopulation diversity, are likely to have varied considerably over time'. The implications of these points, however, have seldom been considered, even if they are of critical importance in the assessment of the observation that the Neandertal mtDNA lineage is not found among extant humans. For instance, in the models of Serre *et al.* (2004), the probability is very low (p<0.007) that any of the five modern human fossils they analysed and assumed to date to *c.* 25,000 years ago was among the ancestors to extant European lineages, while founder analysis (Richards *et al.* 2000; Forster 2004) places the differentiation of Europe's most ancient haplogroups (H, I, and U) in south-west Asia, between 60 and 30 kyr cal BP, with the actual dispersion/colonisation event taking place only after 30,000 years ago (Fig. 4). Although it is assumed that, before, Europe was still inhabited by Neandertals, this simply is not the case, as noted above. If anatomically modern people are documented in Europe since at least 40 kyr cal BP but the immigration of the founder lineages of extant Europeans only happened after 30 kyr cal BP, then the implication must be that the mtDNA lineages to which those first European moderns belonged have since been lost.

In sum, the evidence from extant humans indicates that the mtDNA lineages of the earliest European moderns are as extinct as that of the Neandertals. In the light of this, far from being a special case in need of a special explanation, the extinction of the Neandertal mtDNA lineage becomes simply a particular instance of a generalised process of loss of Pleistocene lineages as a consequence of genetic drift and mutation. If so, then the mtDNA of extant humans carries no information on population dynamics in Europe during the period between 30,000 and 45,000 years ago, and, therefore, cannot help in assessing issues of admixture. Put another way, mtDNA studies have been very useful in confirming the fossil evidence for an African ancestry of extant humans, and in showing that Neandertals did not contribute to the mtDNA gene pool of the present; but they seem to provide little information on what happened at the time of contact. Although this issue may one day be illuminated by studies of the nuclear genome, one must conclude that, for now, the most relevant evidence available is that provided by the anatomy of the fossils and by the cultural features of the associated archeological remains, to which I now turn.

ESTABLISHING THE TIME OF CONTACT AND THE DURATION OF THE COEXISTENCE PERIOD

Direct dating of the Oase 1 mandible first yielded an Oxford date of >35.2 kyr BP; a second, finite Gröningen measurement led to a combined date of 34,950/+990/-890 C BP (OxA-11711/GrA-6165). The standard deviation implies that an age as recent as 33 kyr BP cannot be excluded, but, given the initial Oxford result, the fossil is most likely to date to the 35–37 kyr BP range. A maximum age of 37 kyr BP is in any case indicated by the stratigraphy of the deposit, which shows that both the skull and the mandible came into the site at a time when it was no longer being used by cave bears, direct dating of the latter indicating that such an use lasted until 38–37 kyr BP at the latest (Zilhão & Trinkaus 2005). In calendar years, the age of Oase 1 thus most likely falls within the 42nd millennium cal BP.

On the other hand, over the last five years, direct dating has shown that many of the purported early modern human fossils from central and western Europe (Hahnöfersand and Vogelherd, Germany; Velika Pećina, Croatia; Koněprusy-Zlatý kūň and Svitávka, Czech Republic) in fact dated to Magdalenian, Mesolithic, or even later prehistoric times (Smith *et al.* 1999; Svoboda *et al.* 2002; Svoboda 2003; Terberger & Street 2003; Conard *et al.* 2004; Trinkaus 2005b). As a result, in these regions, no other early modern human remains are securely dated (either directly or, as in the case of the juvenile mandibles from La Quina and Les Rois, by reliable stratigraphic association) to before *c.* 32–31 kyr BP (*c.* 37–36 kyr cal BP), the age of the Mladeč sample (Wild *et al.* 2005). Two lines of reasoning, however, suggest that, at the time of Oase, modern human populations had already extended into European regions west of Romania (with the exception of Iberia, where their penetration was delayed for several millennia; Zilhão 1993; 1998; 2000; Hublin *et al.* 1995).

First, there is the fact that, north of the Ebro river basin, no Neandertal remains are known for which an age post-dating *c.* 36 kyr BP (*c.* 42 kyr cal BP) is acceptable. The single conceivable exception is that

TABLE 1. RELIABLE RADIOCARBON DATES FOR THE EARLY AHMARIAN (BOKER A AND KEBARA, ISRAEL), THE PROTOAURIGNACIAN (KREMS-HUNDSTEIG, AUSTRIA; MOCHI, ITALY; ESQUICHO-GRAPAOU AND ISTURITZ, FRANCE; MORIN, SPAIN), AND THE OASE 1 MODERN HUMAN FOSSIL, CALIBRATED WITH THE CALPAL SOFTWARE (WENINGER & JÖRIS, 2004).

Site	*Provenance*	*Lab number*	*Determination* BP	*Date cal* BP (2σ)
Boker A	1	SMU-578	37,920±2810	46,590–37,390
Kebara	IIIBf (Q16d, 5.38m, hearth)	OxA-1567	35,600±1600	43,400–37,600
Krems-Hundsteig	brown layer with hearths	KN-654	35,500±2000	43,800–36,480
Riparo Mochi	east trench 1959; G, Cut 56–57	OxA-3590	34,680±760	42,280–38,640
Riparo Mochi	east trench 1959; G, Cut 59	OxA-3591	35,700±850	42,850–39,210
Riparo Mochi	east trench 1959; G, Cut 60	OxA-3592	34,870±800	42,420–38,700
Esquicho-Grapaou	SLC 1b	MC-2161	34,540±2000	43,400–35,600
Isturitz	U27, level 4d	GifA-98232	36,510±610	42,510–41,510
Isturitz	V1 26, level 4d	GifA-98233	34,630±560	42,130–38,930
Morin	8	GifA-96263	36,590±770	42,660–41,380
Peştera cu Oase	Modern human Oase 1	OxA-11711/GrA-6165	34,950/+990/-890	42,540–38,500

represented by the direct radiocarbon dates of *c.* 29–28 kyr BP (*c.* 34 kyr cal BP) reported for material from level G1 of the Croatian cave site of Vindija (Smith *et al.* 1999). These results, however, are likely to represent minimum ages only. The associated archeological material comprises a bifacial foliate point of Szeletian type (the closest indicator of the cultural affiliation of the level's Neandertal remains), as well as an Early Aurignacian split-based bone point. On one hand, this association suggests that the level is a palimpsest accumulated over several millennia but, on the other hand, given the ages obtained everywhere else for secure stratigraphic contexts containing such kinds of diagnostic items, it also indicates that the contents of G1 must be older than *c.* 33 kyr BP (*c.* 39 kyr cal BP). Therefore, the radiocarbon results for the Neandertal remains found therein are at least five millennia younger than they should be (and probably much more), the nature of the very small samples used (cancellous bone scraped from the inside the ramus of a mandible and the inner face of a parietal), and the fact that the specimens were coated with preservative, probably explaining, through incomplete decontamination, such a marked rejuvenation. A similar problem most certainly explains the equally rejuvenated *c.* 29 kyr BP result obtained for the Neandertal infant burial of Mezmaiskaya cave, in the northern Caucasus (Ovchinnikov *et al.* 2000): the skeleton was found below intact Mousterian deposits whose age has been established by several reliable dates to be in excess of *c.* 36 kyr BP (Golovanova *et al.* 1999).

Second, there is the fact that, in the time range to which the Oase 1 mandible has been dated, the Protoaurignacian, an archaeological entity with Near Eastern affinities (see below), is found across both the Mediterranean coast and the Danube basin, in marked discontinuity with the cultural geography of preceding times (Table 1; Fig. 5). The latter features several regionally differentiated entities rooted in local Middle Paleolithic traditions, such as the Uluzzian of Greece and Italy, the Bachokirian of Bulgaria, the Bohunician of Moravia, the late Micoquian or Altmühlian of Germany, and the Châtelperronian of

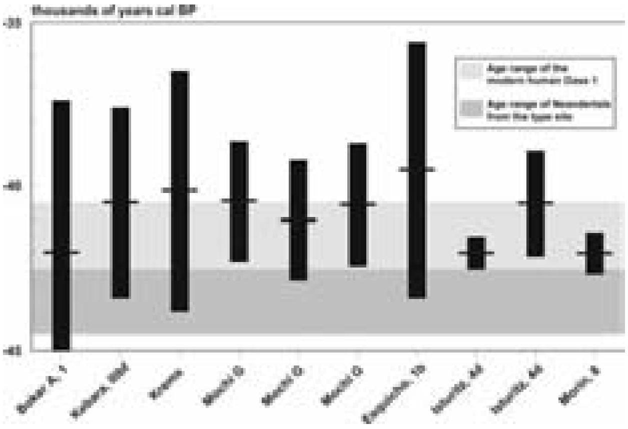


Fig. 5.
Two-sigma plot of the reliable calibrated radiocarbon dates for the Early Ahmarian and the Protoaurignacian in Table 1. Note the overlap with the most likely age range of the Oase 1 modern human fossil

TABLE 2. MOST RECENT RELIABLE RADIOCARBON DATES FOR THE NEANDERTAL-ASSOCIATED TECHNOCOMPLEXES OF EUROPE AND DIRECT DATES FOR NEANDERTAL REMAINS FROM THE TYPE SITE, CALIBRATED WITH THE CALPAL SOFTWARE (WENINGER & JÖRIS 2004). KLISOURA 1 AND LAKONIS I — ULUZZIAN AND LATE MIDDLE PALEOLITHIC OF GREECE; SESSELFELSGROTTE — LATE MICOQUIAN/ALTMÜHLIAN OF GERMANY; CHÂTELPERRON, ROC-DE-COMBE, COMBE-SAUNIÈRE, GROTTE XVI, LA QUINA, ABRI DUBALEN — CHÂTELPERRONIAN OF FRANCE.

Site	*Provenance*	*Lab number*	*Determination BP*	*Date cal BP (2σ)*
Klisoura 1	V, hearth 42	GifA-99168	40,010±740	44,690–42,570
Lakonis I	Unit 1a, base	RTT 3847	38,240±1160	43,900–41,700
Sesselfelsgrotte	Inside, E3	GrN-7153	37,100±1000	43,060–41,380
Châtelperron	B5	OxA-13622	39,150±600	43,860–42,380
Châtelperron	B5	OxA-14320	39,240±380	43,700–42,540
Châtelperron	B5	OxA-13621	40,650±600	45,090–42,930
Roc-de-Combe	square K9, level 8	Gif-101264	39,540±970	44,630–42,230
Roc-de-Combe	square K9, level 8	Gif-101266	40,000±1300	45,450–42,130
Combe Saunière	X	OxA-6503 (tripeptide)	38,100±1000	43,590–41,790
Grotte XVI	B	AA-2997	38,100±1670	44,540–40,980
Grotte XVI	B	GifA-95581	35,000±1200	42,780–37,940
La Quina, aval	4	OxA-10261/Ly-1367	35,950±450	42,230–41,390
Caune de Belvis	7	AA-7390	35,425±1140	42,920–38,480
Abri Dubalen	EBC2	GifA-101045	36,130±690	42,480–41,080
Kleine Feldhofer Grotte	Neandertal 2	ETH-19660	39,240±670	44,000–42,360
Kleine Feldhofer Grotte	Neandertal NN4	ETH-19661	40,360±760	45,040–42,680
Kleine Feldhofer Grotte	Neandertal 1	ETH-20981	39,900±620	44,440–42,640

France. These technocomplexes are in all likelihood related to Neandertals, as shown for the Micoquian (Schmitz *et al.* 2002), the Châtelperronian (Hublin *et al.* 1996), and the Uluzzian (Churchill & Smith 2000), by the associated human remains. The implication is that the most recent dates obtained for such Neandertal-associated early Upper Paleolithic technocomplexes of southern, central, and western Europe can be considered as a sound *terminus post quem* for the disappearance of Neandertals. And, in spite of claims to the contrary (for a review of the evidence, cf. Zilhão & d'Errico 1999; 2003), the most recent such dates are in the 37–36 kyr BP range, ie, *c.* 42,000 calendar years ago, overlapping with the Oase 1 date (Table 2; Fig. 6).

The poor precision of radiocarbon dating in a time range where the method is already working at the limits of applicability, and available calibration tools are still experimental, means that any conclusions are necessarily tentative. But the combined weight of the evidence clearly goes to suggest that the initial dispersal of moderns into Europe cannot have taken place before 37 kyr BP, and had already begun by 35 kyr BP; put another way, that all the action is taking place in the transition from the 43rd to the 42nd millennium cal BP, and that there is no prolonged

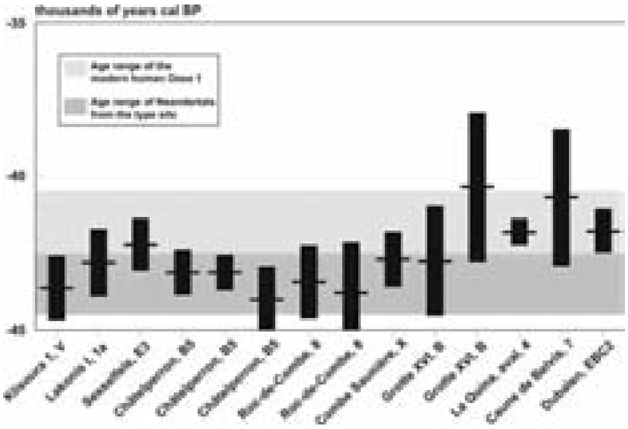


Fig. 6.
Two-sigma plot of the reliable calibrated radiocarbon dates for Neandertal-associated technocomplexes of Europe in Table 2. These results provide a *terminus post quem* for the admixture event across most of Europe (Iberia south of the Ebro excepted), and, combined with the direct date for Oase 1, constrain it around the 42nd millennium cal BP; the overlap of some of the more recent results with the most likely age range for Oase 1 is a byproduct of the uncertainties inherent to radiocarbon dating, not an indicator of long-term contemporaneity between Neandertals and moderns in the same regions

period of overlap. Weaver and Roseman (2005) added further strands of variation to the models put forth by Serre *et al.* (2004) by studying the impact that ten millennia of coexistence might have had on issues of Neandertal-modern admixture. At present, however, the evidence suggests that this is not necessary: whatever the outcome, the interaction game must have been resolved, from the delta of the Danube in the east to the mountains of Asturias in the west, within a couple of millennia at most.

POPULATION DYNAMICS IN OIS-3 EUROPE

Simulations of admixture are greatly impacted by demographic parameters. Weaver and Roseman (2005), for instance, have shown that, in a rapid disappearance scenario, the per generation Neandertal contribution could have been as high as 73.8% under constant population size, but no more than 24.3% under population growth. Currat and Excoffier's (2004) simulations are equally sensitive to this parameter; for instance, in a variant of the model where, for each given territory, all potential admixture occurs within one generation only, and under conditions of demographic equilibrium with no subsequent logistic growth, the maximum number of possible admixture events increases to 1 per every 2 demes, and the maximum initial Neandertal input to the modern human gene pool to 1.33%, ie, 37 times more than in the basic scenario. How does the archeological evidence contribute to clarify issues of population dynamics at this time?

It is clear that population growth must have occurred as both humans and their environment recovered from the OIS-4 colds, and that such growth must go a long way into explaining the Out-of-Africa expansion of modern humans and attendant interaction with Eurasian archaic populations. In Europe proper, a similar growth happened among aboriginal Neandertals, as indicated by the fact that parts of the continent that were depopulated during OIS-4, such as northern Germany or central England, are again settled by humans up to the latitude of 53°N, as documented by the Micoquian site of Lichtenberg (Lower Saxony), and the blade-point sites in the Creswell Crags (Peak District) respectively. On the other hand, using carbon and nitrogen isotope evidence to study palaeonutrition patterns across the Middle–Upper Paleolithic transition, Richards *et al.* (2001) detected a shift towards a more broad-spectrum subsistence economy, including significant consumption of fresh-water resources (fish, molluscs, birds). They concluded that this process of going down the food chain is likely to be associated with population increase, as has been argued by others on the basis of the evidence for similar processes in other times and places (cf. Stiner 2001, for a review). Using the line of reasoning developed by Gamble (1983), Gilman (1984), and Shennan (2001), one could also argue that the emergence of figurative art and the explosion in the use of personal ornaments traditionally associated with the Upper Palaeolithic of Europe relates to processes of social complexity triggered by population expansion and the crossing of significant demographic thresholds. But does this evidence indicate that human populations underwent a steady process of population increase from about *c.* 60,000 years ago onwards?

Where the dietary evidence is concerned, given the provenence and age of the samples, what the data really mean is that the inferred marked demographic increase did not occur in inland Europe until Gravettian times, ie, until after 28 kyr BP (32 kyr cal BP), many millennia after the time of contact between Neandertals and moderns. The emergence of figurative art (painted caves, sculpted figurines) is slightly earlier, but not much; contrary to the widespread notion that such manifestations are closely associated with the immigration of modern humans into Europe (Sinclair 2003), the evidence shows that the phenomenon emerges *c.* 32 kyr BP (*c.* 37 kyr cal BP), ie, some five millennia after the time of contact (Zilhão, in press). The settlement data, in turn, present a very complex picture of expansion and contraction, as might be expected given the palaeoclimatic evidence for frequent and abrupt oscillations from colder to more temperate conditions and back (for a review, cf. van Andel & Davies 2003). The distribution of split-based bone points, for instance, indicates that, in Aurignacian I times, the northern frontier of the human range in Europe had retreated to a line defined by the valleys of the Rhine and the Danube: the northernmost occurrences of that type are in the Belgian Ardennes, whereas southern England, central and northern Germany, as well as most of Poland, seem to have been entirely devoid of human occupation (Fig. 7).

In this particular example of a marked contraction occurring *c.* 35–34 kyr BP (*c.* 40 kyr cal BP), the culprit is likely to have been the major peak of climatic stress

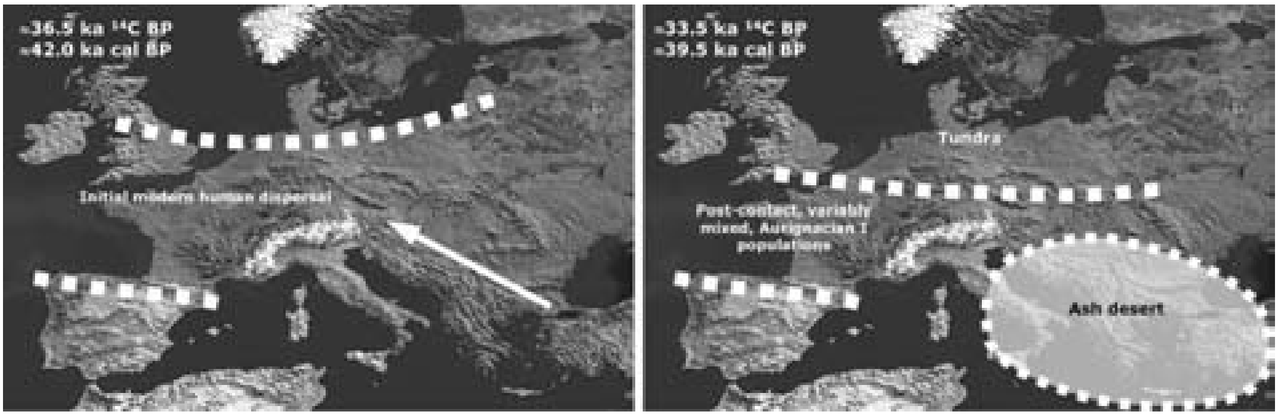


Fig. 7.
Europe before and during Heinrich Event 4. Note the significant contraction in the amount of land available for settlement resulting from the combined effect of the southward advance of the Fenno-Scandinavian ice cap and peripheral tundra, on one hand, and the environmental catastrophe created in the Greater Mediterranean area by the Phlegraean Fields caldera explosion, on the other

represented by Heinrich Event 4 (HE-4) and the attendant episode of glacial advance on land (Stringer *et al.* 2003). Where the greater Mediterranean area is concerned, the environmental impact of that iceberg event may have been enhanced by the catastrophic effects of the explosion of the Phlegraean Fields caldera, in Campania, which is now known to have taken place *c.* 39 kyr cal BP (de Vivo *et al.* 2001); this was the largest such event in the area over the past 200,000 years, and it blanketed the entire region (extending as far East as the Balkans, Greece, Bulgaria, and the Russian/Ukrainian plain) with no less than 200 cubic kilometres of volcanic products, making it unavailable for human habitation for a long time (Fedele *et al.* 2002; 2003). Moreover, this eruption must have played a major role in prolonging at a regional scale, through a 'volcanic winter' effect, the climate-based stress peak affecting European human populations throughout HE-4.

These data indicate a significant contraction (perhaps as much as 30%) of the area available for human settlement in Europe, implying a corresponding contraction in the size of the continent's population and, therefore, that a significant genetic bottleneck must have occurred at this time, ie, soon after modern human immigration and ensuing contact with the local Neandertals. No model of admixture can be considered realistic that, instead of duly considering the impact of such a major demographic crisis, limits itself to the discussion of the 'optimistic' scenarios of either stable or growing human populations.

ISSUES OF ADAPTATION AND COMPETITION

As noted above, Currat and Excoffier's (2004) model can only work if moderns are postulated to have enjoyed a major competitive advantage over Neandertals (4:1, in their basic scenario). This and other estimations used in different variants of their simulations, however, are simply those which are required for moderns to be able to prevail under the model's assumptions. They are not derived from the empirical evidence, although it is true that one can find in the archaeological literature speculations that moderns did hold some kind of competitive edge, residing in either technological superiority or a more productive economy.

It used to be argued, for instance, that Neandertals would have been inefficient, opportunistic hunters, using close-encounter kill strategies, whereas the earliest European moderns would have been logistically-organised, specialised, technologically-aided hunters (cf, for instance, Binford 1983). Over the last two decades, however, a large array of archaeozoological studies have shown that, for the same regions and under comparable environmental constraints, the settlement-subsistence strategies of the late Middle and early Upper Paleolithic Neandertal populations of Europe were as logistically-organised and specialised as those of succeeding modern human groups. For instance, in France, the only part of Europe where the size of the database upon which the issue can be addressed is substantial enough, indicators of niche breadth and hunting efficiency do not change between the Mousterian and the

Aurignacian (Grayson & Delpech 2002; 2003; Morin 2004; but see Mellars 2004b), and much the same has been argued for northern Spain (Pike-Tay *et al.* 1999). And where Germany is concerned, it is particularly striking that the hunting behaviour of the Micoquian Neandertals of 50,000 years ago and of the late Last Glacial Ahrensbourgian moderns of 12,000 years ago, both living off reindeer herds in the northernmost reaches of the human niche, was exactly the same, in spite of the 400 centuries separating the two adaptive systems (Gaudzinski & Roebroeks 2000; 2003).

Recent suggestions have reversed the original argument to postulate that the ability of moderns to exploit faunal resources better than the Neandertals could have consisted in the former's pursuit of a more broad-based subsistence strategy (O'Connell 2006). As the argument goes, encroaching hunter-gatherer groups with a broader diet may be able to occupy the same habitat at higher densities, eventually out-competing local groups exploiting a narrower subset of prey. Supporting evidence would be the significant contrast in the frequency of small animals (molluscs, reptiles, birds, lagomorphs) apparent when Middle and Upper Palaeolithic faunal assemblages are compared. However, as shown by Stiner (2001), the trend towards the incorporation of such prey in human subsistence begins in Europe *c.* 50 kyr cal BP, ie, well *before* the time of contact, and only displays a significant increase in relation to the impact of the Last Glacial Maximum, ie, 20,000 years *after* the time of contact. In sum, when the profiles of hunted faunas are compared for the same region and under similar environmental circumstances, no difference exists between the patterns of big game exploitation by the latest Neandertal and the earliest modern European groups, and the same applies to the exploitation of smaller prey animals.

Where technology is concerned, O'Connell (2006) suggests that the inferred shift toward a broader subsistence base should have technological correlates, because of the need to counteract through improved efficiency the fall in average return rates involved in the process of going down the food chain. Because of preservation issues, arguments about trapping, clothing, shoe-wear, locomotion, and transportation equipment are likely never to be resolved satisfactorily. Available direct evidence relates to the Gravettian: the textile imprints in Dolní Věstonice ceramics suggest the use of textiles and nets (Adovasio *et al.* 2001), and the marked reduction in the robusticity of the lesser toes, in the context of little or no reduction in overall lower limb locomotor robusticity, suggests shod feet (Trinkaus 2005a). Given thermoregulatory constraints (Aiello & Wheeler 2003), and the palaeoclimatic evidence for average winter temperatures in Central Europe reaching –20°C during OIS-3, it is evident, however, that late Neandertals inhabiting this part of the world must have relied on efficient insulating technology. A trend to increased mobility, suggesting some level of technologically-aided locomotion (at least across snowed landscapes), is also apparent in the femoral morphology of late Neandertal populations of western Europe, in parallel with that seen among the continent's earliest modern humans (Trinkaus *et al.* 1998; 1999; Beauval *et al.* 2005). In any case, it is clear that no evidence exists for Neandertal and modern populations of the relevant time period (ie, that of contact) to display any visible contrast at this level.

The same applies to projectile weaponry. The possession of spears, javelins, and sagaies, some of which equipped with stone points and barbs, are all that can be inferred from Uluzzian and Châtelperronian tool-kits, but the same is true of the Protoaurignacian and, indeed, of all extra-European modern human archeological contexts of this time. McBrearty and Brooks (2000) speculate that spear-throwers and even the bow and arrow could have been in use in Africa since the Middle Stone Age (MSA), providing the technological basis for the competitive advantage of moderns over archaic Eurasian populations. These speculations are based on the size, weight, and symmetry of the MSA points, as well as on the similarity between the lunates of the Howiesons' Poort industries and the microliths of Mesolithic Europe. However, the exact same argument can be made for the lithic points of the Châtelperronian, the Szeletian, and the Altmühlian, or the lunates of the Uluzzian. In actual fact, no direct evidence for spear-throwers exists before the Solutrean, and the earliest documented use of the bow and arrow is in Late Glacial times (Clarke 1978).

At broadly the time of contact in Europe, thus, the single instance of what may have been a significant technological development, resulting in improved hafting or greater endurance and durability of projectile points (through greater resharpening potential), is the exclusive use of antler (not bone or ivory) for the manufacture of the split-based points characteristic of Aurignacian I industries. This bone tool type is found from Cantabrian Spain in the west to northern Israel in the east, but the evidence suggests that this is also a post-contact phenomenon. Since most dates for Aurignacian I contexts indicate contemporaneity with HE-4, a reasonable interpretation is that European populations of that time responded with significant technological improvements to the extreme challenge represented by prevailing environmental conditions. But since the earliest modern humans of the continent pre-date such developments, therein cannot lay the explanation for the eventual disappearance of the Neandertals.

THE PALAEONTOLOGICAL AND ARCHAEOLOGICAL EVIDENCE OF ADMIXTURE

The weeded fossil record broadly dated to the time of contact or soon thereafter is much reduced. Four sites only yielded palaeontological material sufficiently complete and described falling within five millennia after the most recent Neandertals of their regions (Trinkaus 2005b): from east to west, they are Oase and Muierii, in Romania, Mladeč, in the Czech Republic, and, because contact was so much later in Iberia, Lagar Velho, in Portugal.

The now rejected fossils were used to argue against admixture on the basis of their remarkably modern appearance and the marked discontinuity with the immediately preceding Neandertals; with the benefit of hindsight, this is not surprising, given that they were all so much more recent. The validated fossils, in contrast, convey the opposite message. All display traits that, in potential ancestor populations, are found only among Neandertals and other archaic humans; for instance, the large and complex third molars, the unilateral bridging of the mandibular foramen, and the Neandertal-like frontal/parietal curvature of the Oase remains (Fig. 8); the thick, projecting supraorbitals and occipital buns of the Mladeč male crania; or the suprainiac fossa and arctic body proportions of the Lagar Velho child. Those traits are in particular absent from the Qafzeh and Skhul remains, the sample that best characterises what the modern human, African ancestors of these early modern Europeans, are supposed to have looked like (Duarte *et al.* 1999; Trinkaus & Zilhão 2002; Wolpoff 2002; Trinkaus *et al.* 2003a; 2003b; 2005; Trinkaus 2005b). On the basis of this evidence, the conclusion that such traits must have been inherited along an archaic, Neandertal line of descent is the most parsimonious reading of the evidence.

That significant admixture occurred at the time of contact is also indicated by the archaeological evidence, particularly where personal ornaments are concerned (Figs 9–10). As discussed by Kuhn and Stiner (1998), Stiner (1999), Kuhn *et al.* (2001), and Vanhaeren (2002), traditions relating to the choice of ornaments are long lasting and often cut across the divisions of regional culture-stratigraphic sequences. In this context, the fact that the only personal

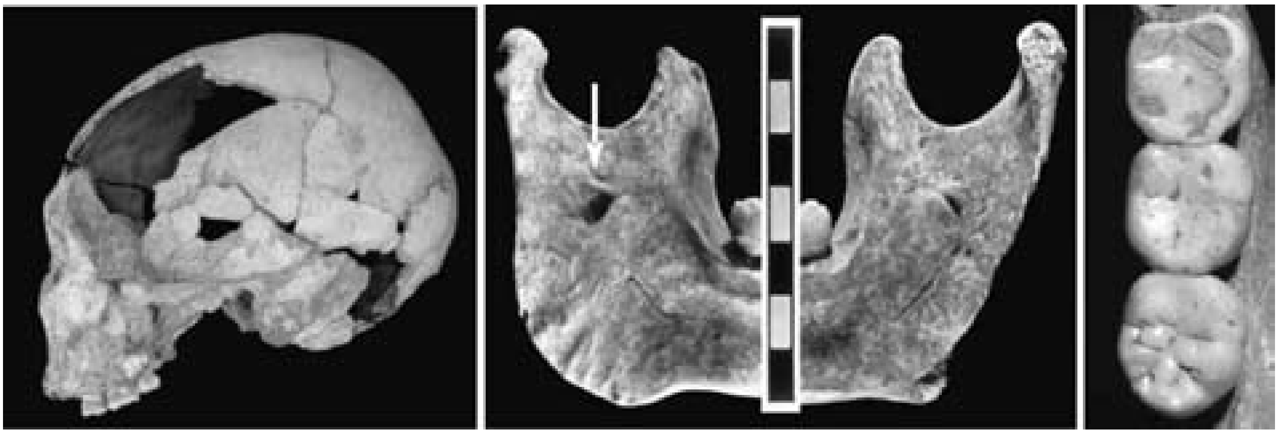


Fig. 8.
The human remains from Oase. Left, lateral view of the Oase 2 skull. Center, the mandibular foramen of Oase 1 (note the unilateral lingular bridging). Right, the right lower row of molars of Oase 1

ornaments known from the Initial Upper Palaeolithic (IUP) and the Early Ahmarian of the Near East are marine shell beads, 90% of which made of *Nassarius gibbosula* (or of *Columbella rustica*, whose size and shape are similar), is consistent with the notion that these technocomplexes represent an expansion into the Near East of an African (and, hence, modern human) tradition of personal ornamentation, going back to the assemblage recovered in level M1 of Blombos cave, South Africa (Henshilwood *et al.* 2004). Dated to *c.* 75 kyr cal BP, this assemblage is exclusively made up of shell beads of *N. kraussianus*, a slightly smaller species of *Nassarius* of broadly the same shape and appearance, whereas other, somewhat later African MSA inventories are entirely made up of ostrich eggshell beads of comparable size. This suggests, in turn, that the two kinds of items (*Nassarius* and ostrich eggshell) may have been interchangeably used, depending on availability, for the manufacture of composite beadworks, as proposed by d'Errico and Vanhaeren (2005).

By the same token, one is allowed to conclude that European assemblages of personal ornaments from the time of contact (Protoaurignacian) or immediately post-dating it (Aurignacian I) that contain *Nassarius gibbosula*, *Columbella rustica*, and other marine shells of similar appearance (from such genera as *Homalopoma*, *Cyprea*, *Trivia*, *Littorina*, etc) represent that African tradition's penetration of the continent. However, such assemblages also incorporate *Dentalium* tubes, pierced animal teeth, and beads made of bone, ivory, or soft stone, ie, kinds of ornaments that, so far, remain undocumented in modern human archeological contexts prior to the time of contact. Together with grooved bones and teeth, and grooved and pierced fossils (gastropods with elongated shells, such as *Turritella* or *Bayana*, as well as belemnites and brachiopods), such novelties correspond to the exact kinds of personal ornaments that, to the complete exclusion of *Nassarius* and similar marine shells, are represented in late Neandertal European sites. Since the differences between the range of ornaments used by late Neandertals and early moderns in Africa and the Near East cannot be explained by raw-material availability, they must reflect cultural choices; and the fact that two separate traditions of personal ornamentation are blended in both Protoaurignacian and succeeding Aurignacian I assemblages must thus be taken as an indication that, in the realm of culture, the contact between Neandertals and moderns did indeed result in admixture (Zilhão, in press).

CONCLUSION

The discussion above can be summarised in a few main points. Available mtDNA evidence does not preclude admixture at the time of contact, and is in fact consistent, depending on a number of parameters, with a Neandertal contribution to the initial modern human population of Europe of up to 73.8%. The

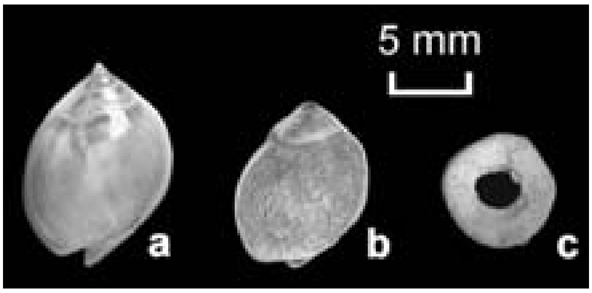


Fig. 9.
Personal ornaments of early African moderns: a. modern shell of *Nassarius gibbosula*; b. modern shell of *Nassarius kraussianus*; c. ostrich eggshell bead from the Middle Stone Age site of Loiyangalani (Tanzania), after Hathaway (2004)

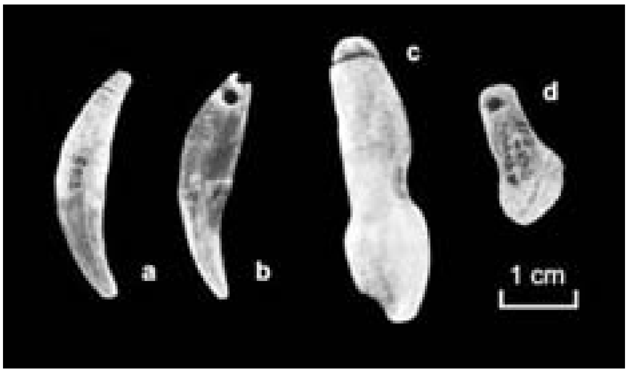


Fig. 10.
Pierced and grooved pendants made of animal bone and teeth, the most common personal ornaments of Europe's late Neandertals, all from basal Châtelperronian level X of the Grotte du Renne, (Arcy-sur-Cure, France) (after Baffier 1999): a–b. fox canines; c. bison incisor; d. lateral phalange of reindeer

absence of Neandertal mtDNA lineages among present Europeans is likely to be simply a particular case of generalised loss of Pleistocene mtDNA lineages, given that the penetration of the continent by the founder lineages of present Europeans is dated to between 30 and 20 kyr cal BP, whereas Europe's earliest modern humans, documented by fossils, go back to *c.* 42 kyr cal BP; one particular demographic crisis *c.* 40–39 kyr cal BP, caused by the combined impact of HE-4 and the Phlegraean Fields caldera explosion, may be of especial relevance in such a process of lineage loss. Iberian regions south of the Ebro basin excepted, no Neandertals are known after *c.* 42 kyr cal BP, which suggests a rather short period of coexistence and a rapid resolution of contact situations (within a few generations at the local and regional scale, within at most a couple of millennia at the continental scale).

Although the full range of interaction types (mutual avoidance, hostile confrontation, full integration) is conceivable, there is plenty of archaeological evidence to suggest that admixture must have been the general rule. Such admixture need not have genetic consequences if the ensuing offspring were sterile, as hypothesised in Björn Kurtén's 'Ice Age Novels' (Kurtén 1980; 1986); the palaeontological evidence for the generalised presence of archaic traits among Europe's earliest moderns, however, implies the transmission of genes, and indicates that mixed groups should have been reproductively viable, as might be expected on the basis of the successful hybridisation observed among extant species and even genera of higher Primates (Jolly 2001). In this context, it would seem that the most parsimonious explanation for the disappearance of the Neandertal mtDNA lineage is genetic swamping, for instance along the lines suggested by Relethford (2001).

Given this situation, which direction should genetic modeling take in order to further contribute to elucidating modern human origins and the fate of the Neandertals? One possible avenue is that of taking the constraints outlined above and, instead of asking whether admixture happened, accept generalised admixture as a matter of fact and model the demographic, genetic, and populational parameters that could explain, at different points in time, the subsequent loss of Neandertal mtDNA. Once the contamination problems are sorted out, the different possible alternatives could then be tested along the lines of the experiment reported by Serre *et al.* (2004). Refined simulations, along the lines of Currat and Excoffier's (2004) but using more realistic parameters, may also be used to try to refute genetic swamping, or establish the limits within which it represents an acceptable explanation. Alternatively, it may well be that the detail of late OIS-3 population history is too complicated for the level of resolution permitted by mtDNA. In that case, one might be led to suggest that significant progress must await reconstruction of the Neandertals' nuclear genome (if technically feasible), or further historical insights derived from the nuclear genome of extant humans. But one conclusion at least seems safe: that no genetic modeling will be useful that is not solidly grounded on the available archeological and paleontological evidence.

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