Neanderthals and the modern human colonization of Europe

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The fate of the Neanderthal populations of Europe and western Asia has gripped the popular and scientific imaginations for the past century. Following at least 200,000 years of successful adaptation to the glacial climates of northwestern Eurasia, they disappeared abruptly between 30,000 and 40,000 years ago, to be replaced by populations all but identical to modern humans. Recent research suggests that the roots of this dramatic population replacement can be traced far back to events on another continent, with the appearance of distinctively modern human remains and artefacts in eastern and southern Africa.

The most significant contributions to these issues over the past decade have come from detailed studies of the DNA structure of present-day human populations in different areas of the world, combined with the gradually accumulating recovery of residual traces of 'ancient' DNA extracted from a number of Neanderthal and early anatomically modern human remains. Studies of both mitochondrial and Y-chromosome DNA patterns in modern world populations (inherited respectively through the female and male lineages) point to the genetic origins of all present-day populations within one limited area of Africa somewhere in the region of 150,000 years before present (yr BP), followed by their dispersal to other regions of the world between about 60,000 and 40,000 yr BP[1–6]. These results are further reinforced by recent discoveries of skeletal remains of anatomically modern populations in different areas. Discoveries at Herto in Ethiopia reported just over a year ago[7] confirm the presence of early forms of anatomically modern humans in Africa by about 160,000 yr BP, whereas the earliest discoveries of distinctively modern populations in both Europe and most parts of Asia can be dated no earlier than 40,000–45,000 yr BP. The one exception is in Israel, where the rich skeletal remains from the Skhul and Qafzeh caves indicate a precocious, and apparently short-lived, incursion of early anatomically modern populations into this region (presumably via the Nile valley) at an early stage in the last glaciation, around 100,000 yr BP[8].

In Europe, the most dramatic support for these patterns has come from the recovery of a number of relatively well-preserved sequences of mitochondrial DNA from a number of actual skeletal finds of Neanderthals and early anatomically modern humans. Analyses of seven separate Neanderthal specimens (including those from the Neanderthal type-site itself) yielded segments of mitochondrial DNA that are radically different from those of all known present-day populations in either Europe or other parts of the world, and that are equally different from those recovered from five early specimens of anatomically modern populations from European sites[9,10]. The conclusion is clear that there was either very little—if any—interbreeding between the local Neanderthals and the intrusive modern populations in Europe, or that if such interbreeding did take place, all genetic traces of this interbreeding were subsequently eliminated from the European gene pool. The mitochondrial DNA evidence recovered from the Neanderthal specimens further suggests that the initial evolutionary separation of the Neanderthals from the populations which eventually gave rise to genetically modern populations must reach back at least 300,000 yr (ref. 9)—a finding that is in good agreement with the surviving fossil evidence from Africa and Europe[1]. Whether this evidence is sufficient to indicate that the Neanderthals belonged to an entirely separate biological species from modern humans is at present more controversial[1,2].

The archaeological record

One important issue in current research is exactly what patterns of culture and technology were associated with the initial dispersal of anatomically and genetically modern populations across Europe[11,12]. The general assumption in the past has been that this dispersal is represented by the widespread distribution of the 'Aurignacian' technologies, which can be traced continuously from the adjacent areas of the Near East (Israel, Lebanon, Syria and so on) through most areas of eastern and central Europe, to the Atlantic coasts of France and Spain—broadly within the time range from around 40,000 to 35,000 yr BP in conventional (that is, uncalibrated) radiocarbon terms[4,6,8,11–16] (see Fig. 1). Significantly, the Aurignacian period shows an apparently sudden flowering of all the most distinctive features of fully 'modern' (or, in archaeological terms, Upper Palaeolithic) cultural behaviour. Such features include: the first complex and carefully shaped bone, antler and ivory tools; a sudden proliferation of perforated animal teeth, far-travelled marine shells, carefully shaped stone and ivory beads and other forms of personal ornaments; and (at least in sites in central and western Europe) remarkably varied and sophisticated forms of both abstract and figurative art—ranging from engraved outlines of animals, to representations of both male and female sex organs, to the remarkable ivory statuettes of animal and human figures from southern Germany (Fig. 2) and the elaborate cave paintings of the Chauvet cave in southeastern France[14–17]. Collectively, this reflects an explosion in explicitly symbolic behaviour among the Aurignacian populations of Europe and western Asia that is conspicuously lacking from the preceding Middle Palaeolithic Neanderthal communities of the region[18,19]. It is generally agreed that symbolic communication and expression at this level of complexity would be almost inconceivable in the absence of complex language systems and in the absence of brains structured very similarly, if not identically, to our own[20–23]. If we add to this the evidence for the striking uniformity of these Aurignacian technologies across Europe, the sharp break occurring between the earliest Aurignacian and the immediately preceding technologies in the different regions, and the apparent chronological cline in the progressive appearance of this technology from east to west across the continent (Fig. 1), the archaeological evidence alone suggests strongly that the Aurignacian period was that of the initial dispersal of anatomically and behaviourally modern populations across central and western Europe[8,13,15,24].

Aurignacian populations

The most frustrating aspect of the current evidence has been the

difficulty of identifying substantial and anatomically distinctive specimens of human skeletal remains in association with Aurignacian technologies[11]. A number of skeletal remains of typically anatomically modern form which were initially attributed to the Aurignacian have recently been shown on the basis of direct radiocarbon dating of the bones themselves to represent intrusive burials into the Aurignacian levels from much later levels—notably those from Velika Pećina in Croatia[25] and those from the remarkable early Aurignacian site of Vogelherd in south Germany (with a range of impressive art objects; see Fig. 2)[12]. The unexpected shock of these discoveries has, perhaps not surprisingly, led some authors to question some of the earlier assumptions about the automatic correlation of the Aurignacian with populations of anatomically modern humans[12,26].

Although understandable, these reactions are nevertheless at best premature and almost certainly unfounded. Even if we implicitly accept the results of all the recent dating evidence, the most we could infer from these results is that the Aurignacians were infuriatingly reluctant to abandon their dead within their main occupation sites—in contrast to the preceding Neanderthals (from whom we now have relatively substantial and well-preserved skeletal remains from at least 20 cave and rock shelter sites), or the populations of the ensuing Gravettian and later stages of the Upper Palaeolithic sequence. To suggest that the scarcity of well-documented skeletal material from the Aurignacian period argues against the association of these populations with anatomically modern humans would be an obvious scientific *non sequitur*. To suggest that this instead favours an association with Neanderthals would be even less defensible.

In reality, the situation is not nearly as bleak as some recent discussions[12,26] have suggested. Despite the elimination of the skeletal material from Vogelherd and Velika Pećina, we now have a range of more fragmentary skeletal remains from at least five or six well-documented contexts in Europe and western Asia which point unmistakably to the presence of diagnostically modern (Cro-Magnon) populations that fall within the time range of the Aurignacian occupation and in several cases are apparently associated directly with Aurignacian archaeological material. The best-dated finds at present are the remains of three typically modern individuals recently reported from the Peştera cu Oase Cave in Romania (directly dated by radiocarbon accelerator measurements to about 35,000 yr BP, although unfortunately not associated directly with archaeological material[26]) and the remains of a complete juvenile skeleton excavated from the levels immediately underlying the long Aurignacian sequence at Ksar Akil in the Lebanon and dated on the basis of both archaeological evidence and overlying radiocarbon measurements to at least 40,000 yr BP[27,28]. From western Europe we have a fragmentary maxilla from Kents Cavern in Devonshire directly dated to 30,900 ± 900 yr BP[11] and the remains of two characteristically modern mandibles from the site of Les Rois in western France, apparently closely associated with the early Aurignacan levels on the site and dating to around 32,000–35,000 yr BP[29]. Churchill and Smith[11] have suggested that the fragmentary mandible and other remains from the initial pre-Aurignacian (Bachokirian) levels at Bacho Kiro in Bulgaria are probably of anatomically modern form, in this case with radiocarbon dates ranging from 39,000 to 43,000 yr BP. Finally, and perhaps most significantly, the two distinctively anatomically modern crania and other skeletal remains from the site of Mladeč in the Czech Republic have recently been dated on the basis of radiocarbon measurements of associated calcite deposits to around 34,000–35,000 yr BP, and are almost certainly associated with a range of typically Aurignacian bone artefacts[11,30].

Clearly, there is an urgent need for further direct radiocarbon dating of all these finds to confirm their precise age and associations with typically Aurignacian material. What is beyond dispute at present is that populations that were in most, if not all, respects fully anatomically modern in form were clearly present in several parts of both Europe and the adjacent areas of the Near East entirely within the time range of the Aurignacian period (that is, before around 30,000 yr BP in radiocarbon terms) and well before the appearance of the succeeding Gravettian and later Upper Palaeolithic technologies[14]. This conclusion is reinforced by all the recent studies of both mitochondrial and Y-chromosome DNA patterns in present-day human populations, which point consistently to a dispersal of fully modern (that is, African-derived) patterns of DNA across Europe by at least 35,000 yr BP and probably between 40,000 and 50,000 yr BP[5,6,31].

And here I should sound a further note of caution. Radiocarbon dating is not without its problems, particularly within the crucial time range of around 30,000–40,000 yr BP under consideration here[32–34]. The problems stem partly from the known fluctuations in the ^{14}C content of the atmosphere over this time range (which can make measured radiocarbon ages up to 3,000–6,000 years younger than the true, calendar ages of the samples involved[32]) and partly from the potentially serious effects of contamination by

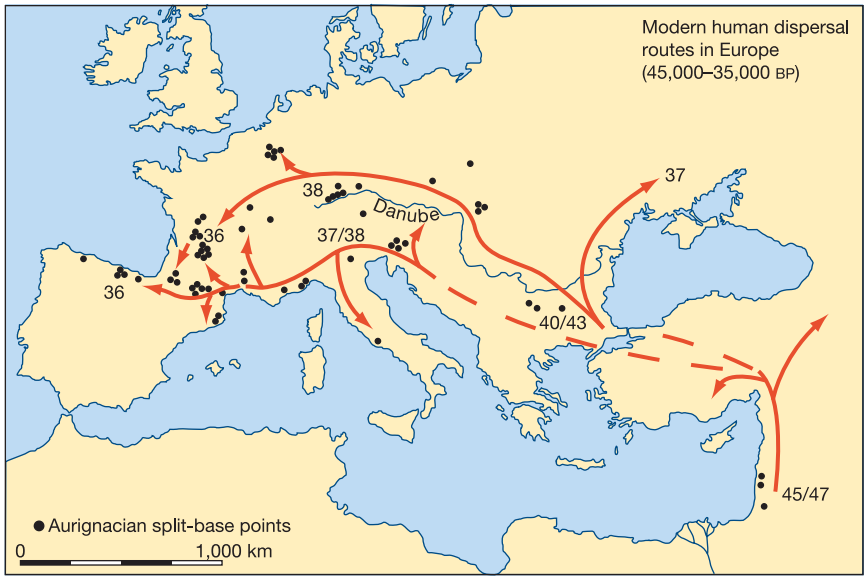

Figure 1 Apparent dispersal routes of the earliest anatomically and behaviourally modern populations across Europe, as reflected in the archaeological data. The northern route (along the Danube) is represented by the 'classic' Aurignacian technologies, while the southern (Mediterranean) route is represented by the 'proto-Aurignacian' bladelet technologies (Fig. 3)—with their inferred origins in the preceding early Upper Palaeolithic technologies in the Near East and southeastern Europe. Dates (in thousands of years BP) indicate the earliest radiocarbon dates for these technologies in different areas, expressed in thousands of radiocarbon years before present (BP). (These are likely to underestimate the true (calendar) ages of the sites by between 2,000 and 4,000 yr; see ref. 32). Dashed lines indicate uncertain routes.

intrusive recent carbon in the dated samples. For a sample 40,000 years old, contamination by only one per cent of modern carbon would reduce the measured age of the sample by over 6,000 years. This is especially true of dates based on bone or shell samples, which have been shown repeatedly to yield ages that are often several thousand years younger than the true ages, unless extremely rigorous pre-treatment procedures are applied to the samples[33,34]. There is of course no suggestion that the very young ages recently reported for the skeletal remains from Vogelherd and elsewhere can be dismissed in these terms. But in the case of the date of 27,680 ± 270 yr BP reported on a marine shell sample apparently associated with the famous human burials from the Cro-Magnon site in southwest France[35] we cannot exclude the possibility that this represents a true radiocarbon age of >30,000 yr BP, which would put these finds clearly within the Aurignacian time range, as the apparent archaeological associations of the find would suggest[29]. The same caution should be applied to any future applications of direct radiocarbon dating to early Upper Palaeolithic skeletal remains, as well as to those for Neanderthal remains[25]. At least in the case of bone samples, it would be prudent to regard all radiocarbon measurements as minimum estimates for the true age of the samples within the critical range of 30,000–40,000 yr BP (refs 33, 34).

Patterns of population dispersal

One of the most significant features that has emerged from recent archaeological research is the evidence for an apparently dual pattern of colonization by early anatomically modern populations across Europe, along two different routes. The first route is represented by the distribution of the 'classic' Aurignacian technologies discussed above—that is, those represented at Aurignac itself and marked by a range of distinctive tool forms, including typical nosed and carinated scraper forms, heavily edge-trimmed Aurignacian blades and perhaps most significantly the highly distinctive split-base bone and antler spear-head forms[13–16] (Fig. 3). As shown in Fig. 1, these technologies are distributed across a broad arc of western, central and southeastern Europe and extend into the immediately adjacent areas of the Near East. At no other point in the Upper Palaeolithic sequence do we observe such a striking similarity in stone and bone technology extending over such a wide diversity of environmental zones. Although the available radiocarbon dates for these technologies show a broadly similar pattern across this region (centred on about 38,000–34,000 yr BP), there are strong indications that the origins of this technology can be identified significantly earlier at sites in southeastern Europe (as at Bacho Kiro and Temnata in Bulgaria) and in the eastern Mediterranean region (as at Ksar Akil in Lebanon) than anywhere in central and western Europe—in both areas extending back to at least 40,000 radiocarbon yr BP[8,13,28,36]. As noted above, the appearance of the new Aurignacian technologies in central and western Europe invariably occurs as an abrupt break with the immediately preceding Neanderthal technologies, strongly supporting their association with new, intrusive populations[13–16].

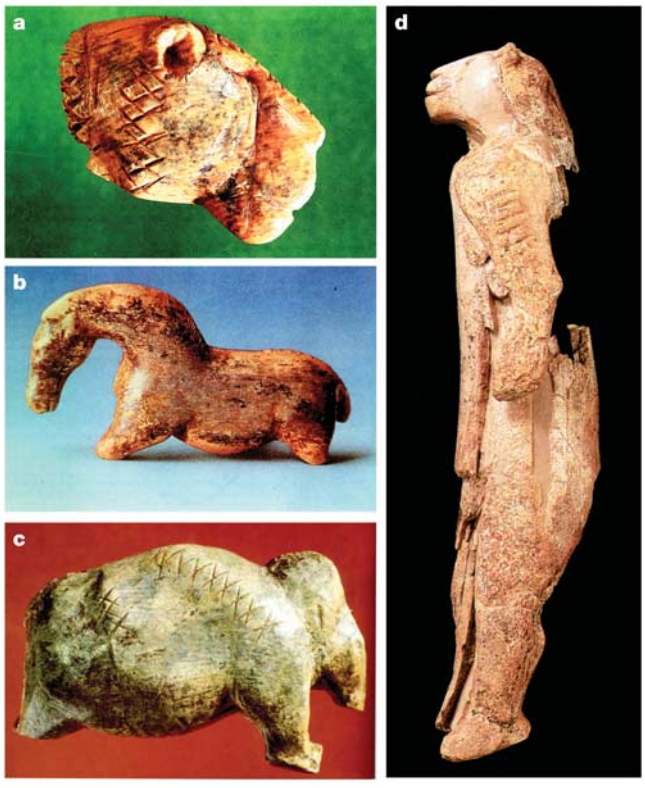

Figure 2 Early Aurignacian carved ivory animal and human figures from sites in southern Germany. **a**–**c**, Vogelherd Cave; **d**, Hohlenstein–Stadel Cave. The carvings represent the head of a cave lion (**a**), a horse (**b**), a mammoth (**c**) and a male human figure with the head of a cave lion (**d**).

The second route of dispersal is distributed mainly along the Mediterranean coast of Europe, extending from at least north-eastern Italy to the Atlantic coast of northern Spain. Although often referred to in the literature as 'archaic' or 'proto' Aurignacian[13,37], these industries show a very different pattern of technology from that of the classic Aurignacian, dominated mainly by small, carefully shaped bladelets (the Dufour and Font-Yves forms), which probably served as the tips and barbs of composite spear- or arrowheads (Fig. 3). Again, these industries represent a sharp break with the immediately preceding Neanderthal technologies in these areas, and again the most convincing origins for these technologies seem to occur in sites in the Near East (for example, in the lower levels of the Ksar Akil sequence in Lebanon, or at a number of open-air sites such as Boker A in southern Israel) dating back to around 38,000–40,000 yr BP[8,28,36,38]. Both these industries and those of the classic Aurignacian period appear to derive ultimately from the preceding Ahmarian and Emiran technologies of the Near East, clearly represented in the exceptionally long early Upper Palaeolithic sequence at Ksar Akil, and reaching back to at least 45,000–47,000 yr BP[8,28,36]. At Ksar Akil itself these initial Upper Palaeolithic levels are associated with the burial of a typically anatomically modern skeleton[27]. Thus, these levels may well reflect the earliest appearance of fully anatomically modern populations in this region, after their inferred dispersal from Africa shortly before this time.

What is particularly intriguing about these geographical patterns of dispersal of early anatomically modern populations across Europe is their close similarities to the much later dispersal of the earliest agricultural (Neolithic) communities across the continent, between about 10,000 and 6,000 yr BP, that is, comprising a northern route mainly along the Danube valley and a southern route along the Mediterranean coast. To find these close similarities in population dispersal patterns at two widely separated times in European prehistory is one of the most interesting features to have emerged from recent research.

Neanderthal–modern human interactions

Any model of this kind implies that there must inevitably have been numerous episodes of contact—and therefore potential interaction—between the expanding populations of modern humans and the indigenous Neanderthal populations across Europe. There is insufficient space here to review all of the related discussion that has emerged in the recent literature[17,19,39–41]. One point which now seems clear, however, is that the appearance of a number of apparently modern features of technology among some of the final Neanderthal communities of central and western Europe

(notably the simple bone tools and a number of grooved or perforated animal-tooth pendants found in the Chatelperronian levels at Arcy-sur-Cure in Central France[17,39,42]) can be shown to coincide closely with the appearance of early Aurignacian populations in the nearby regions of central Europe, and probably with those along the Mediterranean coast[8,14,37,40,43].

Such patterns of behavioural interaction and technological transfer between the local Neanderthal and intrusive anatomically modern populations are precisely what we would predict on the basis of examples of recent ethnic contact situations[40], regardless of the respective cultural and cognitive capacities of the two populations. Whether the ability of the final Neanderthals to adopt some of these new patterns of technology can be taken to imply that they had brains effectively identical to those of the incoming modern populations is currently a topic of lively but inconclusive debate[22,23,40,44]. All that can be said is that if the evolutionary trajectories of the Neanderthal and modern populations had been separate for at least 300,000 yr—as all available genetic and anatomical evidence suggests—then the possibility of some divergence in neurological structures over this period cannot be ruled out[45,46]. Equally, the possibility of some small degree of interbreeding between the two populations cannot be excluded on the basis of either the current anatomical or DNA evidence[1,10] and would again seem plausible in anthropological and demographic terms.

However we visualize this situation, the reality is that all traces of distinctively Neanderthal patterns of mitochondrial DNA, as well as the distinctive anatomical features of Neanderthals, disappeared relatively rapidly from European populations[1,2,9,10]. This probably reflects a straightforward case of direct competition for space and resources between the two populations, in which the demonstrably more complex technology and apparently more complex organization of the anatomically modern populations would have given them a strong competitive advantage over the Neanderthals. Some of the rapid climatic oscillations that have been documented over this time range may also have played a critical part in this demographically competitive situation[47–49].

The human revolution?

That the Neanderthals were replaced by populations that had evolved biologically, and no doubt behaviourally, in the very different environments of southern Africa makes the rapid demise of the Neanderthals even more remarkable, and forces us to ask what other cultural or cognitive developments may have made this replacement possible. The rapidly accumulating archaeological evidence for highly symbolic patterns of culture and technology within African populations dating back to at least 70,000 yr BP (marked by the appearance of complex bone technology, multiple-component missile heads, perforated sea-shell ornaments, complex abstract 'artistic' designs and abundant use of red ochre—recently recorded from the Blombos Cave and other sites in southern Africa[50–53]) may provide the critical clue to new patterns of cognition, and probably complex linguistic communication, linked directly with the biological evolution of anatomically and genetically modern populations[1,3]. Perhaps it was the emergence of more complex language and other forms of symbolic communication that gave the crucial adaptive advantage to fully modern

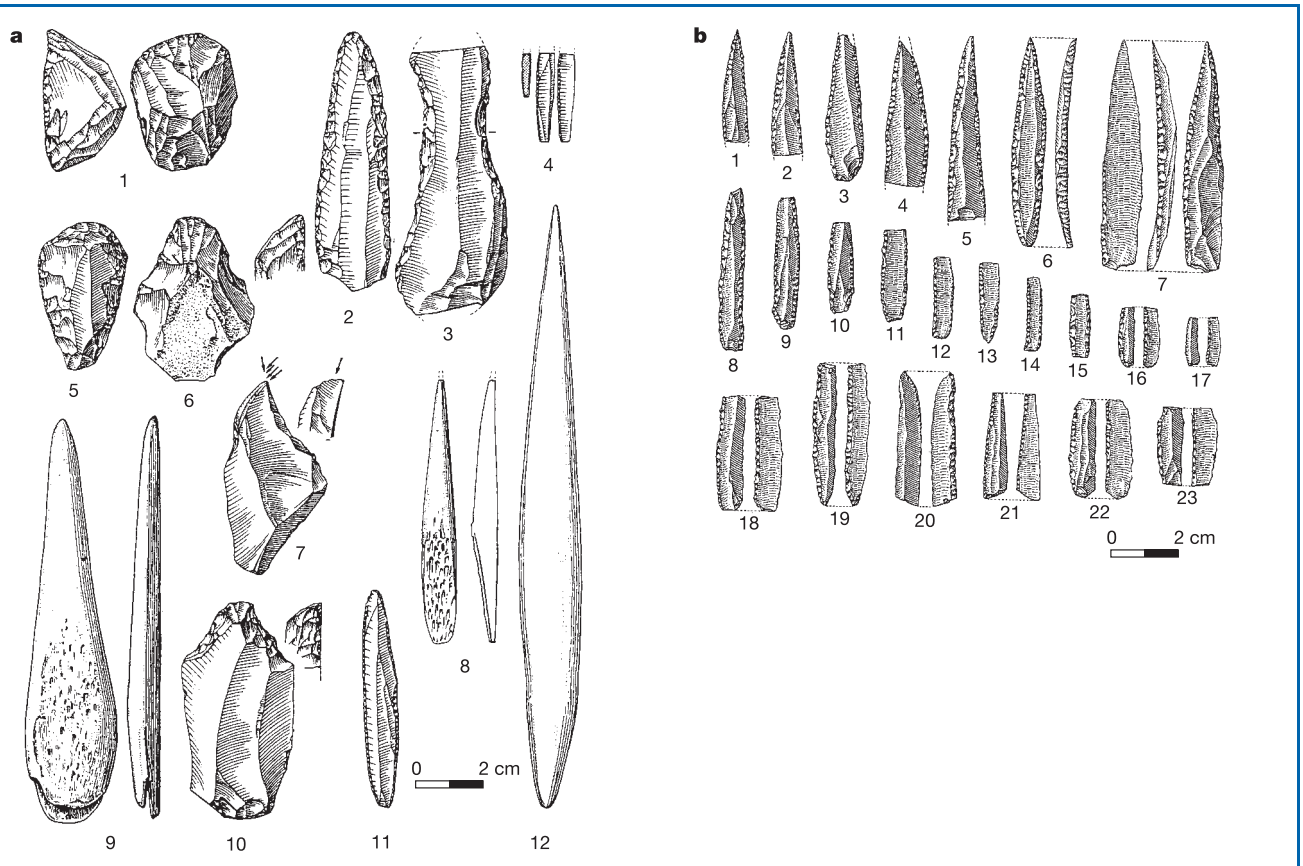

Figure 3 Tool forms from classic Aurignacian and proto-Aurignacian sites. **a**, Characteristic tool forms of the 'classic' Aurignacian technologies in Europe and the Near East. 1, 6 and 10 are carinated and nosed scrapers; 2 and 3 are Aurignacian blades; 9 is a split-base bone point; 4 and 11 are retouched bladelets. **b**, Retouched bladelet forms characteristic of the Mediterranean 'proto-Aurignacian' technologies in Europe, probably representing the tips and barbs of hafted missile heads. 1–7 are Font-Yves bladelets; 8–23 are Dufour bladelets.

populations and led to their subsequent dispersal across Asia and Europe and the demise of the European Neanderthals. The precise mechanisms and timing of this dramatic population dispersal from southern Africa to the rest of the world remains to be investigated[1,3,4]. □

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1. Stringer, C. Modern human origins: progress and prospects. *Phil. Trans. R. Soc. Lond. B* **357,** 563–579 (2002).
2. Tattersall, I. in *The Speciation of Modern* Homo sapiens (ed. Crow, T. J.) 49–59 (British Academy, London, 2002).
3. Forster, P. Ice ages and the mitochondrial DNA chronology of human dispersals: a review. *Phil. Trans. R. Soc. Lond. B* **359,** 255–264 (2004).
4. Lahr, M. M. & Foley, R. Towards a theory of modern human origins: geography, demography and diversity in modern human evolution. *Yb. Physical Anthropol.* **41,** 127–176 (1998).
5. Richards, M. *et al.* Tracing European founder lineages in the near Eastern mitochondrial gene pool. *Am. J. Hum. Genet.* **67,** 1251–1276 (2000).
6. Underhill, P. *et al.* The phylogeography of the Y-chromosome binary haplotytes and the origins of modern human populations. *Ann. Hum. Genet.* **65,** 43–62 (2001).
7. White, T. D. *et al.* Pleistocene *Homo sapiens* from Middle Awash, Ethiopia. *Nature* **423,** 742–747 (2003).
8. Bar-Yosef, O. in *The Geography of Neandertals and Modern Humans in Europe and the Greater Mediterranean* (eds Bar-Yosef, O. & Pilbeam, D.) 107–156 (Peabody Museum, Harvard Univ., Cambridge, Massachusetts, 2000).
9. Krings, M. *et al.* A view of Neanderthal genetic diversity. *Nature Genet.* **26,** 144–146 (2000).
10. Serre, D. *et al.* No evidence of Neandertal mtDNA contribution to early modern humans. *PLoS Biol.* **2,** 0313–0317 (2004).
11. Churchill, S. E. & Smith, F. H. Makers of the early Aurignacian of Europe. *Yb. Physical Anthropol.* **43,** 61–115 (2000).
12. Conard, N., Grootes, P. M. & Smith, F. H. Unexpectedly recent dates for human remains from Vogelherd. *Nature* **430,** 198–201 (2004).
13. Kozlowski, J. K. & Otte, M. The formation of the Aurignacian in Europe. *J. Anthropol. Res.* **56,** 513–534 (2000).
14. Conard, N. J. & Bolus, M. Radiocarbon dating the appearance of modern humans and timing of cultural innovations in Europe: new results and new challenges. *J. Hum. Evol.* **44,** 331–371 (2003).
15. Mellars, P. A. Archaeology and the population-dispersal hypothesis of modern human origins in Europe. *Phil. Trans. R. Soc. Lond. B* **337,** 225–234 (1992).
16. Mellars, P. A. in *The Peopling of Britain: the Shaping of a Human Landscape* (eds Slack, P. & Ward, R.) 39–67 (Oxford Univ. Press, Oxford, 2001).
17. White, R. Personal ornaments from the Grotte du Renne at Arcy-sur-Cure. *Athena Rev.* **2,** 41–46 (2001).
18. Mellars, P. A. *The Neanderthal Legacy: an Archaeological Perspective from Western Europe* (Princeton Univ. Press, Princeton, New Jersey, 1996).
19. d'Errico, F. The invisible frontier: a multiple species model for the origin of behavioral modernity. *Evol. Anthropol.* **12,** 188–202 (2003).
20. Donald, M. *The Origins of the Modern Mind* (Harvard Univ. Press, Cambridge, Massachusetts, 1991).
21. Pinker, S. *The Language Instinct* (Penguin, London, 1994).
22. Mithen, S. *The Prehistory of the Mind* (Thames & Hudson, London, 1996).
23. Lewis-Williams, D. *The Mind in the Cave* (Thames & Hudson, London, 2002).
24. Davies, W. A very model of a modern human industry: new perspectives on the origins and spread of the Aurignacian in Europe. *Proc. Prehist. Soc.* **67,** 195–217 (2001).
25. Smith, F. H., Trinkaus, E., Pettitt, P. B., Karavanić, I. & Paunović, M. Direct radiocarbon dates for Vindija G1 and Velika Pećina Late Pleistocene hominid remains. *Proc. Natl Acad. Sci. USA* **96,** 12281–12286 (1999).
26. Trinkaus, E. *et al.* An early modern human from Peştera cu Oase, Romania. *Proc. Natl Acad. Sci. USA* **100,** 11231–11236 (2003).
27. Bergman, C. A. & Stringer, C. B. Fifty years after: Egbert, an early Upper Palaeolithic juvenile from Ksar Akil, Lebanon. *Paléorient* **15,** 99–111 (1989).
28. Mellars, P. A. & Tixier, J. Radiocarbon-accelerator dating of Ksar'Aqil (Lebanon) and the chronology of the Upper Palaeolithic sequence in the Middle East. *Antiquity* **63,** 761–768 (1989).
29. Gambier, D. in *The Human Revolution: Behavioural and Biological Perspectives on the Origins of Modern Humans* (eds Mellars, P. & Stringer, C.) 194–211 (Edinburgh Univ. Press, Edinburgh, 1989).
30. Svoboda, J., van der Plicht, J. & Kuželka, V. Upper Palaeolithic and Mesolithic human fossils from Moravia and Bohemia (Czech Republic): some new ^{14}C dates. *Antiquity* **76,** 957–962 (2002).
31. Sherry, S. T. *et al.* Mismatch distributions of mtDNA reveal recent human population expansions. *Hum. Biol.* **66,** 761–775 (1994).
32. Shackleton, N. J., Fairbanks, R. G., Chiu, T. & Parrenin, F. Absolute calibration of the Greenland time scale: implications for Antarctic time scales and for Δ^{14}C. *Quat. Sci. Rev.* **23,** 1513–1522 (2004).
33. Aitken, M. J. *Science-based Dating in Archaeology* (Longmans, London, 1990).
34. Bronk Ramsey, C., Higham, T., Bowles, A. & Hedges, R. Improvements to the pretreatment of bone at Oxford. *Radiocarbon* **46,** 155–163 (2004).
35. Henri-Gambier, D. Les fossiles de Cro-Magnon (Les Eyzies-de-Tayac, Dordogne): nouvelles données sur leur position chronologique et leur attribution culturelle. *Bull. Mém. Soc. Anthropol. Paris* **14,** 89–112 (2002).
36. Ohnuma, K. & Bergman, C. A. in *The Emergence of Modern Humans* (ed. Mellars, P.) 91–138 (Edinburgh Univ. Press, Edinburgh, 1990).
37. Le Bon, F. *L'Aurignacien Entre Mer et Océan. Réflexions sur l'unité des phases anciennes de l'Aurignacien dans le Sud de la France* (Société Préhistorique de France, Paris, 2002).
38. Monigal, K. in *More than meets the Eye: Studies on Upper Palaeolithic diversity in the Near East* (eds Goring-Morris, A. N. & Belfer-Cohen, A.) 118–133 (Oxbow books, Oxford, 2003).
39. d'Errico, F., Zilhão, J., Julien, M., Baffier, D. & Pelegrin, J. Neanderthal acculturation in western Europe? A critical review of the evidence and its interpretation. *Curr. Anthropol.* **39,** S1–S44 (1998).
40. Mellars, P. A. The Neanderthal problem continued. *Curr. Anthropol.* **40,** 341–350 (1999).
41. Hublin, J.-J. in *The Geography of Neandertals and Modern Humans in Europe and the Greater Mediterranean* (eds Bar-Yosef, O. & Pilbeam, D.) 157–182 (Peabody Museum, Harvard Univ., Cambridge, Massachusetts, 2000).
42. Hublin, J.-J., Spoor, F., Braun, M., Zonneveld, F. & Condemi, S. A late Neanderthal associated with Upper Palaeolithic artefacts. *Nature* **381,** 224–226 (1996).
43. Haesaerts, P. & Teyssandier, N. in *The Chronology of the Aurignacian and of the Transitional Complexes* (eds Zilhão, J. & d'Errico, F.) 133–151 (Instituto Português de Arqueologia, Lisbon, 2003).
44. Coolidge, F. L. & Wynn, T. A cognitive and neuropsychological perspective on the Chatelperronian. *J. Anthropol. Res.* **60,** 55–73 (2004).
45. Klein, R. G. Archaeology and the evolution of human behavior. *Evol. Anthropol.* **9,** 7–36 (2000).
46. Enard, W. *et al.* Molecular evolution of $FOXP_2$, a gene involved in speech and language. *Nature* **418,** 869–872 (2002).
47. Mellars, P. A. in *Neandertals and Modern Humans in Western Asia* (eds Akazawa, T., Aoki, K. & Bar-Yosef, O.) 493–508 (Plenum, New York, 1998).
48. Mellars, P. A. in *Explaining Social Change: Studies in Honour of Colin Renfrew* (eds Cherry, J., Scarre, C. & Shennan, S.) 27–43 (McDonald Institute for Archaeological Research, Cambridge, 2004).
49. Finlayson, C. *Neanderthals, Modern Humans* (Cambridge Univ. Press, Cambridge, 2004).
50. Henshilwood, C. S. *et al.* Emergence of modern human behavior: Middle Stone Age engravings from South Africa. *Science* **295,** 1278–1280 (2002).
51. Henshilwood, C. S., d'Errico, F., Vanhaeren, M., Van Niekerk, K. & Jacobs, Z. Middle Stone Age shell beads from South Africa. *Science* **304,** 404 (2004).
52. McBrearty, S. & Brooks, A. The revolution that wasn't: a new interpretation of the origin of modern human behavior. *J. Hum. Evol.* **39,** 453–563 (2000).
53. Mellars, P. A. in *The Speciation of Modern* Homo sapiens (ed. Crow, T. J.) 31–47 (British Academy, London, 2002).

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