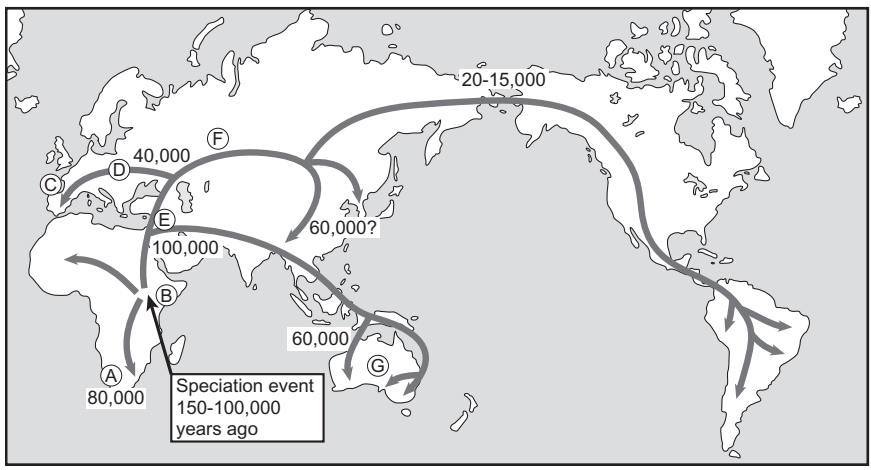
I

THE ORIGIN OF THE SPECIES

Speciation, migration and symbolic representation



Ⓐ South Africa: Blombos cave (red ochre engraving 80,000 BP)
Klasies River (blade technology 70,000 BP)
Border cave (engraved bone and wood 36,000 BP)

Ⓑ Tanzania: Mumba (LSA industry 50,000 BP)
Kenya: Enkapune ya Muto (LSA industry 50,000 BP; perforated beads 40,000 BP)

Ⓒ France: Cromagnon (decorative grave goods 31,000 BP)
Cave paintings: Chauvet (31,000 BP), Lascaux (17,000 BP),
Pech-merle (22,000 BP)
Spain: Cueva Morin (grave goods 37,000 BP)
Altamira (cave paintings 18,000 BP)

Ⓓ Czech Republic: Mladec (ceremonial burial 18,000 BP)
Dolni V stonice (engraved mammoth tusk 26,000 BP)

Ⓔ Israel: Skhul, Qafzeh (symbolic grave goods 110-90,000 BP)

Ⓕ Russia and Ukraine: Sungir (painted ivory pendant 28,000 BP)
Kostenki (drilled beads 36,000 BP)

Ⓖ Australia: Kakadu (rock shelter art 40,000 BP)
Lake Mungo (ceremonial red ochre burials 60,000 BP)

BP = Years Before Present LSA = Late Stone Age

The Morphological and Behavioural Origins of Modern Humans

CHRIS STRINGER

Summary. The majority of the fossil and genetic evidence favours an African origin for modern humans during the later part of the Middle Pleistocene (prior to 130,000 years ago), and one or more range expansions out of Africa after that date. However, a number of uncertainties remain. If there was a speciation event at the appearance of modern humans, what was its nature? Furthermore, did the evolution of modern human behaviour occur gradually or punctuationally? In this chapter, I will examine the difficulties faced in defining what is meant by 'modern' humans, and in reconstructing the morphological and behavioural origins of our species.

INTRODUCTION

THIS IS A GOOD TIME to be writing about the morphological and behavioural origins of *Homo sapiens*. Although the Late Pleistocene fossil human record has not been greatly extended over the last few years, provocative new interpretations of it have appeared, as well as new or revised dating of important evidence. In addition, genetic data from both recent and fossil humans are allowing increasingly detailed reconstructions of early human history. The archaeological record has not expanded markedly, but key discoveries have focused debate on critical areas concerning the capabilities of Middle Palaeolithic humans, and on the concept of a behavioural 'human revolution' at the Middle–Upper Palaeolithic transition (Holden, 1998).

It is now generally accepted that modern humans had a recent African origin (Stringer, 2001a). The Multiregional Model, under which *H. sapiens* evolved across the inhabited Old World throughout the Pleistocene (Thorne & Wolpoff, 1992), has now given way to variants of Out of Africa models (Stringer, 1994). However, these have differing time-scales for the origin and dispersal of *H. sapiens*, and varying scenarios of replacement or gene flow during dispersal phase(s) outside of Africa. In the rest of this chapter I will

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assume that the morphological and behavioural origins of modern humans were African, but will review recent data and the current debate about the tempo and mode of that origin. In particular I will address the following issues.

1 What is meant by 'modern humans'?
2 How has the application of new dating techniques affected the debate?
3 Was speciation in humans gradual or punctuational?
4 When did modern human behaviour evolve?

WHAT IS MEANT BY 'MODERN' HUMANS?

No agreement exists among palaeoanthropologists on how to recognise ancient examples of 'modern' humans, morphologically or behaviourally. I previously favoured the use of recent skeletal variation to diagnose whether a fossil could be termed 'modern' (Stringer, 1994), but it is now apparent that modern skeletal variation is smaller than that recognised for *H. sapiens* in even the Late Pleistocene, and members of the *H. sapiens* clade in the African Late–Middle to Early–Late Pleistocene were even more distinct and diverse (Stringer, 1992; Lahr, 1996). While there seems little doubt that Aurignacian- and Gravettian-associated humans from over 25,000 years ago in Europe share enough morphological and behavioural features with recent populations to warrant the application of the term 'modern', problems soon arise as we move further back in time. The samples from Skhul and Qafzeh in Israel appear to represent a primitive form of *H. sapiens* (Stringer, 1992; Lahr, 1996). However, they are associated with Middle Palaeolithic artefacts, comparable with those made by Neanderthals, and with only disputed evidence of 'modern' symbolic behaviour. The contrast between their morphology and their inferred behaviour is sufficient for Klein (2000) to employ the term 'near-modern' for them, implying that they represent an evolutionary stage where modern anatomy was evolving *prior* to truly modern behaviour. In the case of the late Neanderthals of south western France, dating from about 35,000 years ago, an inversion of that situation has been posited by d'Errico *et al.* (1998). They argue that these Neanderthals were developing 'modern' symbolic behaviour independently of *H. sapiens*, thus producing a contrasting decoupling of modern anatomy and behaviour from that envisaged by Klein, since the Neanderthals were apparently evolving aspects of 'modern' behaviour separately from the appearance of 'modern' anatomy.

It seems to me that these different ideas, whether ultimately accurate or not, are important for the way that they highlight difficulties inherent in any absolute concept of 'modernity'. Was modernity (morphological and/or behavioural) a package that had a unique African origin in one time, place and

population, or was it a composite whose elements appeared at different times and places, and were then gradually assembled to assume the form we recognise today? In the rest of this chapter I will review the evidence that leads me to favour the second alternative, one which does, however, bring with it other difficulties.

HOW HAS THE APPLICATION OF NEW DATING TECHNIQUES AFFECTED THE DEBATE?

The majority of the fossil human record can still only be relatively dated. However, over the last 15 years new or improved physical dating techniques have allowed better age estimates for sites that were previously at, or beyond, the limits of radiocarbon dating (approximately 35,000 years) (Stringer, 2001b). When I began my doctoral studies some 30 years ago, Europe and the Americas were the only continents that could be said to have reasonably accurate time-scales for the appearance of modern humans. The Neanderthal–modern interface in Europe appeared to occur at about 35,000 years, while in the Middle East it was estimated to be only slightly older. The time-scale for the appearance of modern humans was poorly known in eastern Asia and Australasia, perhaps occurring at less than 30,000 years. Africa, although central to hominid origins, was considered to have lagged behind regions such as Europe during later human evolution. Now, however, African fossils such as Florisbad, Singa and Guomde can be seen more appropriately as relics of the early evolution of the modern human clade, since they all probably date beyond 130,000 years (Grün *et al*., 1996; McDermott *et al*., 1996; Bräuer *et al*., 1997). In the Middle East, the Skhul and Qafzeh samples of early modern (or near-modern for Klein, 2000) humans probably date to more than 100,000 years, while anatomically modern humans were apparently even present in south-eastern Australia prior to 60,000 years (Thorne *et al*., 1999; Grün *et al*., 2000). Thus Europe can no longer be seen as crucial for an understanding of the early evolution of *H. sapiens*, although it is clearly important for what it reveals about the extent of human behavioural complexity 30,000 years ago.

WAS SPECIATION IN HUMANS GRADUAL OR PUNCTUATIONAL?

There is no agreement about the number of human species that have existed through the Pleistocene. For some workers (multiregionalists) there may have been only one: *H. sapiens.* For others, there may have been at least eight. My preference lies between these extremes, and for the rest of this chapter I will use four species names: *Homo erectus*, its probable descendant *Homo heidelbergensis*,

and the two probable descendant species of *heidelbergensis*, *Homo neanderthalensis* and *H. sapiens.* However, it should be recognised that any discussion of speciation processes in humans presupposes a workable species recognition concept for the fossils that will allow speciation events to be examined. An additional complication is that some workers confuse different species concepts; for example, some multiregionalists insist on applying biological species concepts in an attempt to show that *H. neanderthalensis* and *H. sapiens* must have been conspecific. However, even if we accept controversial claims for the existence of supposed Neanderthal–modern hybrids (for example Duarte *et al*., 1999), it is well known that many closely related mammal species, including primates, can hybridise, and may even produce fertile offspring. But if this is not a widespread behaviour, it may have little or no impact on the populations that constitute the core of the different species. Thus in fossils, morphological criteria are necessarily the mode of species recognition.

However, some genetic data are now available from Neanderthal specimens (Krings *et al*., 2000), and these can be compared with the fossil record. Both support the idea of a separation between the Neanderthal and modern human lineages during the Middle Pleistocene, and both suggest that Neanderthal–modern human differences were of the order of two or three times that found within modern humans. But even in this case, where morphological differences are clear-cut, the genetic data can be used to support either a conspecific or specific difference between Neanderthals and modern humans.

If we assume that the Neanderthal–*sapiens* separation was a specific one occurring in the middle part of the Middle Pleistocene, what can we say about the nature of the origins of these species? The European fossil record of this period can now be interpreted as showing a gradual accretion of Neanderthal characteristics. This is best exemplified in the rich fossil sample from the Sima de los Huesos at Atapuerca, dating from about 300,000 years ago (Arsuaga *et al*., 1997). Individual specimens show mosaic *heidelbergensis* and *neanderthalensis* characters, and the sample as a whole can be interpreted as a derived form of *heidelbergensis* or a primitive form of *neanderthalensis.*

The relatively rich and well-dated European Middle Pleistocene record thus appears to demonstrate the gradual, local, nature of Neanderthal evolution. If this model of gradual, regional, evolution can also be applied to the African fossil record, an accretional mode of *sapiens* evolution would consequently be expected (Stringer, 1998). However, acceptance of a gradualistic scenario for the origin of modernity means that diagnosing 'modernity' will be dependant on the particular criteria selected. Additionally, while individual anatomical characters may be used to recognise which fossils belong to the *sapiens* clade, membership of this clade will not necessarily be synonymous with modernity as an assemblage, since this may have evolved long after the cladistic origin of *H. sapiens* (which, in my view, was at the *neanderthalensis–sapiens* cladogenetic

event). Thus fossils such as Skhul, Qafzeh, and even those from Singa and Florisbad, probably belong to *H. sapiens* cladistically, but do not necessarily represent 'modern' humans.

WHEN DID MODERN HUMAN BEHAVIOUR EVOLVE?

If the characteristic morphology of modern humans evolved in a gradual, mosaic, fashion, what of modern human behaviour? The concept of a 'human revolution', demarcating a punctuational origin of a package of modern human behaviours, such as complex language, symbolism and specialised technologies, has been central to much archaeological debate over the last 10 years (Klein, 2000). Originally focused on apparent contrasts between the Middle and Upper Palaeolithic records in Europe, this concept has now been extended to the Middle Stone Age–Later Stone Age transition in Africa. It is argued that the major changes in the whole of human behavioural evolution occurred there about 50,000 years ago (possibly related to changes in cognition or language). In turn, this led to the successful expansion of modern humans and now-modern behaviour beyond Africa, and the replacement of the remaining archaic populations. Thus morphological and behavioural evolution were decoupled, and 'morphological modernity' may have evolved before 'behavioural modernity'. This pattern is counterintuitive for those who argue that behavioural change lay behind the transformation of the archaic skeletal pattern into that of modern humans.

However, McBrearty & Brooks (2000) have argued that this view of events displays a Eurocentric bias and a failure to appreciate the depth and breadth of the African Middle Stone Age record that precedes the supposed 'human revolution' by at least 100,000 years. In their view, 'modern' features such as advanced technologies, increased geographic range, specialised hunting, aquatic resource exploitation, long-distance trade and the symbolic use of pigments, occur across a broad spectrum of Middle Stone Age industries. This suggests to them a gradual assembly of the package of modern human behaviours in Africa during the Late Middle–Early Late Pleistocene, and its later export to the rest of the world. Thus the origin of our species, behaviourally and morphologically, was linked with the appearance of Middle Stone Age technology, dated in many parts of Africa to more than 250,000 years ago.

CONCLUSIONS

It is still too early to determine definitively when and where 'modern' morphology and behaviour developed, especially when these concepts are apparently

also so fluid. In my view, Africa was the ultimate source of the basic elements of both our anatomy and our behaviour. But it has also become evident that some supposedly unique attributes of modern human behaviours were present even in the Lower Palaeolithic outside of Africa (witness the evidence for systematic hunting of large mammals from sites such as Boxgrove and Schöningen). And the debate about Neanderthal, and specifically Châtelperronian, capabilities highlights the issue of potential versus performance. Were the Neanderthals developing complex behaviours independently of modern humans, or only because of contact with them (compare d'Errico *et al.*, 1998 with Mellars, 1999)? If we could bring up a Neanderthal child in a modern human society, could it achieve what we achieve, or would it be limited by its genetic and developmental endowment? Did behavioural innovations regularly and independently arise in different populations in human prehistory, but were often lost during population crises or extinctions, or did such innovations diffuse widely, even between distinct populations or species? Was the apparently unique role of Africa in modern human origins a result of a particular evolutionary pathway, or more a consequence of larger population size (Relethford & Jorde, 1999), with less bottlenecking, more continuity, and a greater potential both to make and to accumulate behavioural innovations?

While the (admittedly limited) evidence seems to point to a gradual assembly of modern human morphology and behaviour in Africa during the period from 300 to 100,000 years ago, rather than major punctuational events, genetic data continue to suggest that this may be too simple a story. A number of different genetic data sets suggest that there were major population bottlenecks during this period of time (Jorde *et al.*, 2000; Ingman *et al.*, 2000), with effective population size reduced to only a few thousand individuals. Such population crashes might indeed have produced saltational changes in morphology and behaviour within what must have been a very diverse *sapiens* clade. It will be exciting to see the evidence developing for or against these scenarios during this new century (for discussion of some new data see Balter, 2002).

DISCUSSION

Questioner: Why did they leave Africa?

Stringer: We don't know. Perhaps it was climatic and environmental changes, or population pressure, leading to range expansions. Global climate was highly variable during the later Pleistocene, over both long and short time-scales. Another interesting possibility is that the use of marine resources may be part of the reason, or at least provided new opportunities. There is growing evidence that humans (both *H. sapiens* and Neanderthals) were adapted or adapting to coastal life during the later Pleistocene. Early modern populations could

have dispersed along littoral zones from North East Africa at times of Late Pleistocene low sea levels, taking them all the way to Indonesia. Australia would then have been within reach, as well as inland colonisations up river valleys.

Questioner: When did modern humans get to Australia?

Stringer: Probably at least 60,000 years ago, based on new dating for the Mungo 3 burial site and for archaeological sites in northern Australia. Sea-going craft would have been needed for repeated island hops, so boats must have existed by this time, despite the lack of direct evidence. The Mungo 3 burial is associated with the use of red ochre (possibly ceremonial). If the new datings are accurate, this would be the oldest known burial with red ochre, about double the age of examples from Europe. It is possible to argue that these early colonisers were not the ancestors of today's Aborigines, and that fully modern human behaviour arrived later, but in my view the earliest Australians were probably essentially 'modern', both anatomically and behaviourally.

Questioner: What is your view of evidence for the peopling of the island of Flores, 800,000 years ago?

Stringer: If the archaeological interpretations are accurate, primitive water craft were apparently used to get there, but the distances involved may have been much less than today. We know little of the exact palaeogeography at that time. I think the move to Australia would have been a much bigger jump, and I think that was only achieved by modern humans.

Questioner: Was *H. erectus* in Java?

Stringer: Yes, *H. erectus* was definitely in Java throughout much of the Pleistocene, and may have even overlapped with the arrival of *H. sapiens* in the region. There were regular land connections between South East Asia and Java during the Pleistocene, and numerous fossils of *erectus* have been discovered there.

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