Research News

Africa: Cradle of Modern Humans

A combination of new fossil evidence and even newer molecular biological evidence is pointing to Africa as the source of modern humans, perhaps within the past 200,000 years

ALTHOUGH discoveries of "early man" fossils remain the great headline catchers of paleoanthropology, one of the hottest current topics in the science focuses on much more recent times: namely, the origin of modern humans, *Homo sapiens sapiens*. The reasons for the excitement are several, but one key ingredient is the introduction of molecular biological evidence into what previously has been the sole province of bone and stone buffs. "This new line of evidence has been extremely healthy for the science," says Christopher Stringer, an anthropologist at the British Museum (Natural History), London. "But not everyone is happy about it."

The story the molecular biology seems to be telling is that modern humans evolved in Africa about 200,000 years ago, from where they migrated throughout the rest of the Old World, probably replacing more primitive humans as they went. This version of human prehistory is at variance with the view held by many anthropologists: namely, that modern humans evolved on a broad geographic front, absorbing rather than replacing most existing populations of more primitive humans.

For many researchers, therefore, there is a head-on conflict between the molecules and the fossils. "If the molecular evidence is correct, then the fossils become inexplicable," states Milford Wolpoff of the University of Michigan. "But I believe the fossil evidence shows that the molecular biology is being wrongly interpreted."

There is something of a sense of déjà vu about this disagreement, recalling as it does a similar molecules-versus-bones conflict during the 1970s and early 1980s. This one was at the other end of the anthropological scale, on the date of the first member of the human (hominid) family. "The anthropologists said the first hominid evolved at least 15 million years ago," says Allan Wilson, a biochemist at Berkeley who helped promote molecular anthropology, "and we said it was more like 5 million years. It took a decade and a half before the anthropologists realized they were wrong."

Wilson, with his colleagues Rebecca Cann and Mark Stoneking, is now pushing one of the molecular biology approaches to solving the date of the origin of modern humans: namely, the use of mitochondrial DNA (mtDNA) as a fast-ticking molecular clock. "Some people don't like our conclusions," observes Wilson, "but I expect they will be proved wrong again."

"If it is the origin of modern humans you are interested in, then Western Europe is something of a backwater."

Although most anthropologists have had an opportunity to try to assess the molecular biology evidence recently published in the scientific literature, it is so new that few have been more directly exposed to it. The first occasion at which this was possible, in the format of a scientific meeting, was at a recent gathering at the University of Cambridge, England.* "It was useful for both sides to see that the other wasn't quite as secure about its results as they might have imagined," comments Stringer who coorganized the meeting with Cambridge University archeologist Paul Mellars.

In addition to the novel introduction of molecular biology into the program, the meeting was further innovative in having contributions from a population geneticist, an ecologist (see box on page 1295), and a demographer. "We wanted to place the problem in the widest possible scientific context," explains Mellars. The result was that each of these three research perspectives produced further support for the notion of a recent African origin of *Homo sapiens sapiens*, followed by replacement.

The origin of *Homo sapiens sapiens* has long been an issue in anthropology, tied up as it is with the fate of everyone's favorite caricature of cavemen, the Neandertals. Broadly speaking, two opposing hypotheses have been proposed over the decades, each of which has been the subject of majority support at different times as facts and fantasies have shifted anthropological opinion.

The first, termed the candelabra model by Harvard University's William Howells, proposes that ancestral populations—specifically, *Homo erectus*—throughout the Old World each independently evolved first to archaic *Homo sapiens*, then to fully modern humans. This model, which has also been called the Neandertal phase hypothesis, therefore envisages multiple origins of *Homo sapiens sapiens*, and no necessary migrations. One consequence would be that modern geographic populations would have very deep roots, having been separated from each other for a very long time, perhaps as much as a million years.

The second, which Howells called the Noah's Ark model, envisages a geographically discrete origin, followed by migration throughout the rest of the Old World. In this model, populations of Archaic sapiens might be completely replaced by the newcomers. So, by contrast with the candelabra model, here we have a single origin and extensive migration. Moreover, modern geographic populations would have relatively shallow roots, having derived from a single source in relatively recent times.

If the candelabra model were correct, then it should be possible to see in modern populations echoes of anatomical features that stretch way back into prehistory: this is known as local continuity. In addition, the appearance in the fossil record of advanced humans might be expected to occur at more or less the same time throughout the Old World. By contrast, the Noah's Ark model predicts little local continuity and the appearance of modern humans in one locality before they spread into others.

These two models represent extremes, of course, and it is possible to envisage intermediates. For instance, there might have been a single geographic origin, followed by migrations in which the newcomers interbred with established populations of Archaic sapiens. And there could have been a great deal more gene flow between different geo-

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graphic populations than is allowed for in the strict candelabra model. The result of all this would be a much less clear-cut signal in the fossil record, because there would be a melange of evidence for migration and evidence of local continuity, both of which might appear to be diluted.

Until relatively recently there was a strong sentiment among anthropologists in favor of extensive local continuity. In addition, Western Europe tended to dominate discussions, for several cogent reasons. First, the best fossil record for the immediate pre-modern era comes from this part of the world: namely, the remains of more than 300 Neandertal individuals found in sites from Western Europe to the Near East. Second, there are many splendid archeological sites that, in combination, appear to document the transition of pre-modern, Middle Paleolithic, tool technologies to the much more extensive and sophisticated Upper Paleolithic technologies of modern humans. Last, the spectacular painted caves of southern France and northern Spain dazzled people into believing that Europe was where all the action was in the emergence of *Homo sapiens sapiens*, people like us.

"In fact," says Fred Smith of the University of Tennessee, "if it is the *origin* of modern humans you are interested in, then Western Europe is something of a backwater. One of the things that is becoming clear is that the real action was elsewhere." Smith's comment reflects one of the few areas upon which most people agreed at the recent Cambridge meeting. "If there is good evidence for replacement, then it is in Western Europe," he says. In other words, the Neandertals, whose extraordinary facial architecture and overall skeletal robusticity was so very different from the relatively athletic build of the first modern humans in the area, almost certainly became extinct. They were ancestral to nothing, and disappeared from that part of the world 32,000 years ago.

At the other end of their range, in the Near East, the disappearance of the Neandertals began much earlier, about 45,000 years ago. It looks as if a wave of extinction spread east to west over a period of 13,000 years or so. Some anthropologists think that the replacement was not complete, however, that there must have been some interbreeding. "There is a whole suite of Neandertal characters in modern humans," says Wolpoff, "and this is an argument for some kind of ancestry." But, as University of New Mexico anthropologist Erik Trinkaus has pointed out, "the limb proportions of the first modern humans in Europe are typical of equatorial people, not people adapted to cold climates, as Neandertals were."

In addition to the classic Neandertals, the

A Sharp Competitive Edge

"For several years, I have been interested in modeling the extinction of Neandertals," says Ezra Zubrow of the State University of New York at Buffalo. "I believe I can show that only a small demographic advantage is necessary for the modern forms to grow rapidly and for the archaic forms to become extinct. This advantage may be as paltry as a 1% difference in mortality and the extinction as rapid as 30 generations, or a single millennium."

By addressing demographically the question of the replacement of Archaic sapiens by modern forms, Zubrow was putting on a quantitative footing something that has troubled many people: namely, under what circumstances could one closely related species wipe out another? "Anthropologists have always had difficulty grappling with that," says Christopher Stringer, of the British Museum (Natural History), London.

Contrary to the graphic and gory confrontations recently portrayed on screen and in printed fiction, the succession of *Homo sapiens sapiens* over *Homo sapiens neanderthalensis* might have been a swift but unremarkable affair. "The key conclusion from my model," notes Zubrow, "is that rapid extinction of the Neandertals could have resulted from a very small difference in mortality only, nothing dramatic."

Central to Zubrow's demographic modeling is the interaction of the archaic and modern populations, an interaction that left one of them—the Neandertals—at a slight disadvantage. How realistic is this? "Well, the archeological evidence tells you that the archaic and modern humans were rather different creatures," says Zubrow. "Although Neandertals were relatively sophisticated in many ways—for instance, they survived huge climatic fluctuations, they manufactured an extensive stone tool technology, and they buried their dead—modern humans outstripped them at every step." For instance, several archeologists argue that Neandertals were intellectually less sophisticated in planning and implementing their daily foraging for meat, that they were poor hunters compared with modern humans.

Given this kind of competitive edge, says Zubrow, and given that Neandertals and modern humans overlapped in their foraging territories, a slightly increased mortality of one group in relation to the other is quite conceivable. "You don't have to have all out warfare between the two groups, though of course this could have happened."

Zubrow worked with several demographic approaches, but eventually used linked stable and stationary population models. "I decided initially to test what changes in life expectancy would occur if there were changes in the mortality pattern," explains Zubrow. The result of a 2% increase in mortality among the Neandertal populations is, as one would expect, a diminishing life expectancy. "This process continues generation by generation with each subsequent generation's life expectancy being less than the one preceding it."

By tying the increase in Neandertal mortality to a linked decrease in mortality among modern humans, the relative fates of the two populations was further exaggerated. And in the final stage of the model, not only was the mortality rate for each subsequent generation related to the age structure and mortality in the previous generation of their own group but of the opposing group too.

"One sees the same processes as in the case of limited interaction," explains Zubrow. "Given a slight advantage, increased mortality operates to the benefit of *Homo sapiens sapiens* more than to the benefit of *Homo sapiens neanderthalensis*. . . . The increase in life expectancy for modern humans is much greater and more rapid than the contemporaneous decrease in life expectancy for Neandertals."

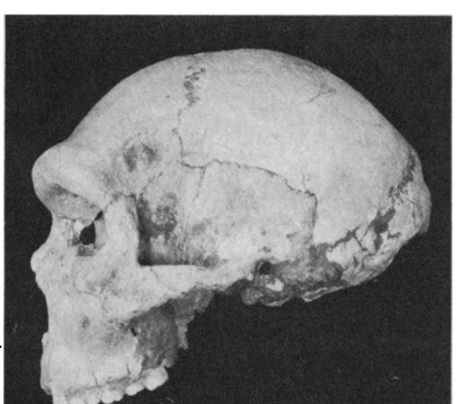
Advantages in fertility and population size in favor of the Neandertals have little impact in this model. Imposed mortality rate is the key. "The increment in mortality need only be between 1 and 2%," concludes Zubrow. "If one has an initial increment of 7%, extinction within 15 generations is assured. If one is talking of a band of 50 people, it only requires that 4 people die. It is not difficult to imagine this happening a multiplicity of times where and when *Homo sapiens neanderthalensis* and *Homo sapiens sapiens* came into contact." ■ **R.L.**

fossil evidence most immediately relevant to the origin of modern humans is to be found throughout Europe, Asia, Australasia, and Africa, and goes back in time more than 300,000 years. Many of these fossils—which are principally more or less complete crania—look like a mosaic of ancient (*Homo erectus*) and modern (*Homo sapiens sapiens*) features, and are generally termed Archaic sapiens. "I think it is a very poor term," says Stringer, "because it is not specific and almost certainly includes different groups that were separate from each other." Whatever they are called, these fossils are the ones in which signs of local continuity are sought.

Although there are still problems of the incompleteness of the record, and uncertainties about dating of specific specimens, recent years have seen changes in how this evidence is interpreted. "Several years ago I was an adherent of the idea that modern human morphology seemed to have appeared roughly at the same time worldwide," says Smith. "I said there was no good evidence of a discrete source area, where modern morphology appeared earlier than elsewhere. But the evidence from southern Africa convinces me I was wrong."

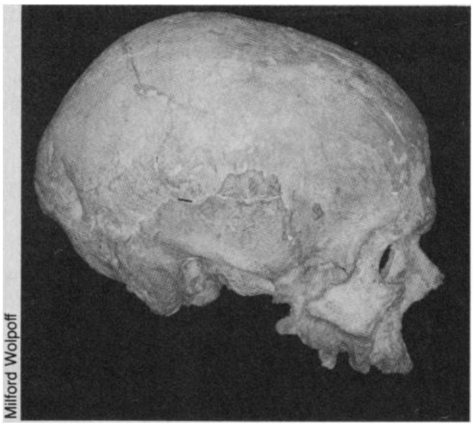
That evidence comes from five sites, each of which has question marks of one sort or another. "The most convincing case can be made with Klasies River Mouth," says University of Chicago anthropologist Richard Klein, who has worked at most of the sites. The human fossils from this site are "totally modern in all observable respects," says Klein, "including the presence of a strongly developed chin." Although the dating of the site is still disputed in some quarters, the human fossils seem to be between 115,000 and 80,000 years old, which makes them much earlier than anything in Western Europe, and probably in the Near East too.

"This evidence convinced me that Africa was probably the source of modern human populations," says Smith, "but I still don't accept the idea of complete replacement." The reason is that he sees anatomical evidence for continuity in central Europe, and probably in North Africa too. "I would argue that there is a balance between continuity and new genetic elements coming in," he says, "a blending of old and new in these areas."



Milford Wolpoff

Petralona: *this 300,000-year-old fossil, found in Greece, is a mosaic of old and new.*



Milford Wolpoff

Cro-Magnon: Homo sapiens sapiens, *found in France, dated at about 25,000 years.*

Wolpoff takes the local continuity argument further, and includes much of Australasia. He cites a small suite of anatomical characters that, he says, links modern aboriginal populations with fossil specimens that go back deep into *Homo erectus* times, a span of as much as a million years. "That looks like good continuity," says Stringer, "but when you look at the characters they are all primitive, things that you will find in fossil populations throughout the Old World." Hence, there is no unique link between the fossil and modern populations in Australasia, argues Stringer. Wolpoff acknowledges that the individual characters are primitive, but says that the combination of them is unique, and therefore provides the required link.

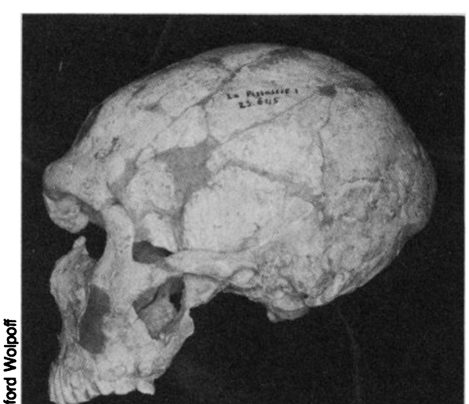
"It is significant that in the area where you have the best fossil evidence—in Western Europe—you see a clear signal of replacement," says Stringer. "You can argue for local continuity in other regions, simply because you have less fossil evidence. A lot of the supposed evidence for local continuity is based on shared primitive characters. Once you realize this, the argument for continuity begins to disappear."

Stringer, whose position based on the fossil evidence is close to the Noah's Ark model, welcomes the independent evidence offered by the mtDNA analysis. Wilson and his colleagues turned to mtDNA as a tool because it accumulates mutations much faster than does nuclear DNA, and therefore is a good potential clock for relatively short time periods. In addition, because mtDNA is inherited only through the maternal line, it does not mix and become diluted with paternal DNA, and therefore offers what should be a high fidelity link with ancestral populations.

When the Berkeley biochemists analyzed the mtDNA of 147 women from five different geographic populations—Africa, Asia, Europe, Australia, and New Guinea—they discovered that the differences among the whole set were very small, indicating that they were all of relatively recent origin. The different populations did, however, separate out, with one set being formed by African individuals only and another by individuals from all groups. The conclusion was that all modern humans derive from a population that lived about 200,000 years ago in Africa, from which populations migrated to the rest of the Old World about 100,000 years later. Little or no interbreeding with existing Archaic sapiens populations occurred, suggest Wilson and his colleagues.

"They have calibrated the mutation rate incorrectly," claims Wolpoff. "With a much slower rate they would get a time of origin of 850,000 years ago, which I believe is correct." Smith also hesitates to accept the molecular biology evidence at face value. "I think there are still a lot of problems with the mtDNA work, which other molecular biologists are looking at," he says. "If all these problems were to be solved, yes, I would be prepared to accept their conclusions about replacement." (The mtDNA clock is shortly to be the subject of a separate Research News article.)

Meanwhile, says Smith, "the demonstration of contemporaneity of modern and archaic humans in a region where I see evidence for continuity—like central Eu-



Milford Wolpoff

La Ferrassie: *a classic Neandertal individual, found in France.*

rope for instance—would also be convincing evidence for widespread replacement." Such a demonstration might be difficult, however, even if replacement had in fact occurred, simply because it might have happened very swiftly and therefore not be visible in the fossil record.

"Most people have thought about replacement as a long-term process," says Ezra Zubrow of the State University of New York at Buffalo. "But in my demographic calculations I have shown that, even with very small differences in mortality between modern human and archaic populations, complete replacement can occur locally within 30 generations, or 1000 years." (See box on page 1293.) In most cases 1000 years is too short an interval to be resolved reliably in the fossil record. Smith, and others, might therefore have to rely on the molecular biology evidence to settle the replacement question.

Overall, the Cambridge meeting probably further tilted opinion toward the idea of replacement. But it also illustrated how very complex the issue is, because the issue is in fact made up of several different strands. In addition to the genetic and anatomical strands, there is behavior—specifically, the tools that people made and what they did with them.

The anatomical evidence for the origin of modern humans seems to point to a figure around 100,000 years, which of course must be a minimum date. But, compare that with the genetic evidence, and one is already at twice that date. So, one problem is the relation between the genetic origin of the species and its manifestation in novel anatomy.

How, then, does behavior fit in? Once modern humans were well established, they manufactured a sophisticated tool technology that was based on the production of fine blades and the use of bone, antler, and ivory. This was quite distinct from the flake-based technology of the archaic species. However, definitely in Africa, and probably in other regions too, the earliest anatomically modern humans were manufacturing distinctly pre-modern tool kits. And, according to Klein, their hunting skills were inferior to those of later modern humans. The obverse—association of archaic forms with advanced technology—has also been discovered at two European sites. "Yes, the link between archeology and morphology is very loose," comments Smith.

This raises the question of what it is to be a modern human. Is it, as Wolpoff believes, that "the movement of ideas is more important than the movement of genes"? Or is it that a clearer definition of "modern human" needs to be agreed on? ■ ROGER LEWIN

Ecology of Modern Humans

"Recourse to culture as an all embracing and all pervading explanation has probably done most to obscure the processes by which modern humans evolved," suggests Robert Foley of the University of Cambridge. For many anthropologists, culture has long been perceived as being so important an element in the lives of the ancestors of modern humans that it essentially unified the numerous separate populations distributed throughout the Old World and propelled them all along an evolutionary trajectory to *Homo sapiens sapiens*. "What all this adds up to," says Foley, "is that the origin of modern humans has been treated as a unique event, outside the processes of evolutionary biology." Being an ecologically oriented anthropologist, Foley argues that "understanding the origin of modern humans can now be best served not by stressing the uniqueness of this evolutionary event, but by looking at it in a comparative ecological framework."

By taking this biological, comparative approach, Foley concludes, among other things, that the origin of modern humans was likely to have occurred in a single location, not continent-wide; the woodland-bush-grassland environment of Africa of the late Pleistocene was ideal for promoting the speciation of modern humans, as compared with other regions of the Old World; and the initial, slow evolution of modern humans would have been followed by rapid dispersal by migration.

Foley identifies four areas of evolutionary ecology that might bear on the origin of modern humans: biogeography, environmental dynamics, spatial ecology, and adaptive divergence.

The first of these—biogeography—addresses the question of whether evolution is likely to occur uniformly throughout widespread populations of a primate species. Looking at monkey evolution in Africa, Foley concludes that "populations that disperse across broad geographical areas diverge; they do *not* continue to have a single evolutionary trajectory." It is true that you often see certain parallelisms in widespread populations—such as the increasing brain size in Archaic sapiens populations—but unique changes occur too: in this case, the reduction of cranial robusticity and architectural reorganization occurs only once in the Old World, and it occurs in Africa.

In terms of environmental dynamics, during the fluctuating glaciations of the late Pleistocene, Africa, probably more than any other continent, would have experienced tremendous habitat fragmentation and reformation, processes that enhance the prospects of speciation. Indeed, one genus of monkey—*Cercopithecus*—underwent a radiation into at least 16 species at about the time that modern humans are thought to have evolved.

Referring to the third issue—spatial ecology—Foley notes that, although shifts in habitat may promote speciation, the shifts must not be too rapid or too severe, otherwise the most likely response is for the indigenous species to migrate or become extinct while existing species move in. "Changes in environment during glacial-interglacial cycles in higher latitudes are likely to be very marked and quite rapid," says Foley. "This may explain why the faunal history of Eurasia over the last million years is largely one of changing distributions of animals. In contrast, tropical environments have more mosaic and continuous environmental patterning—a situation in which local evolution is quite likely to occur."

Foley identifies some characteristics of modern humans that would separate them from Archaic sapiens—such as widespread ranging behavior, large social groups with considerable kin-based substructure, and high dietary selectivity—and asks what ecological circumstances might promote such differences. "These characteristics are most likely to occur in patchy environments where food is both of high quality and predictable," he says. Meat is a high-quality, patchy resource, but hardly predictable—unless, of course, a potential predator develops exceptional hunting skills. "The critical variable here might well be the development of a technology that allows predation from a distance—projectiles," speculates Foley. "Increasing planning depth, technological efficiency, foraging organization etc., will reduce the unpredictability of the environment."

Testing this ecological approach to modern human origins will require more data—on paleoenvironments and paleobehavior, for instance. Meanwhile it represents a healthy innovation in a long-established quest. ■ **R.L.**