

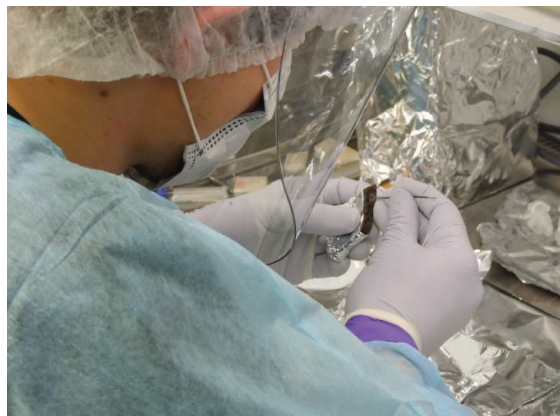


A New View Of the Birth of *Homo sapiens*

New genomic data are settling an old argument about how our species evolved

FOR 27 YEARS, CHRIS STRINGER AND Milford Wolpoff have been at odds about where and how our species was born. Stringer, a paleoanthropologist at the Natural History Museum in London, held that modern humans came out of Africa, spread around the world, and replaced, rather than mated with, the archaic humans they met. But Wolpoff, of the University of Michigan, Ann Arbor, argued that a single, worldwide species of human, including archaic forms outside of Africa, met, mingled and had offspring, and so produced *Homo sapiens*. The battle has been long and bitter: When reviewing a manuscript in the 1980s, Wolpoff scribbled “Stringer’s desperate argument” under a chart; in a 1996 book, Stringer wrote that “attention to inconvenient details has never been part of the Wolpoff style.” At one tense meeting, the pair presented opposing views in rival sessions on the same day—and Wolpoff didn’t invite Stringer to the meeting’s press conference. “It was difficult for a long time,” recalls Stringer.

Then, in the past year, geneticists announced the nearly complete nuclear genomes of two different archaic humans: Neandertals, and their enigmatic eastern cousins from southern Siberia. These data provide a much higher resolution view of our past, much as a new telescope allows astronomers to see farther back in time in the universe. When compared with the genomes of living people, the ancient genomes allow anthropologists to thoroughly test the competing models of human origins for the first time.



Going back in time. A researcher extracts DNA from a fossil.

The DNA data suggest not one but at least two instances of interbreeding between archaic and modern humans, raising the question of whether *H. sapiens* at that point was a distinct species (see sidebar, p. 394). And so they appear to refute the complete replacement aspect of the Out of Africa model. “[Modern humans] are certainly coming out of Africa, but we’re finding evidence of low levels of admixture wherever you look,” says evolutionary geneticist Michael Hammer of the University of Arizona in Tucson. Stringer admits: “The story has undoubtedly got a whole lot more complicated.”

But the genomic data don’t prove the classic multiregionalism model correct either. They suggest only a small amount of interbreeding, presumably at the margins where invading moderns met archaic groups that were the worldwide descendants of *H. erectus*, the human ancestor that left Africa 1.8 million years ago. “I have lately taken to talking about the best model as replacement with hybridization, ... [or] ‘leaky replacement,’” says paleogeneticist Svante Pääbo of the Max Planck Institute for Evolutionary Anthropology in Leipzig, lead author of the two nuclear genome studies.

The new picture most resembles so-called

Ancient abode. A finger and molar (*inset*) of a new type of human were found in Denisova Cave, Siberia.

assimilation models, which got relatively little attention over the years. “This means so much,” says Fred Smith of Illinois State University in Normal, who proposed such a model. “I just thought ‘Hallelujah! No matter what anybody else says, I was as close to correct as anybody.’”

Evolving models

Stringer and others first proposed Africa as the birthplace of modern humans back in the mid-1980s. The same year, researchers published a landmark study that traced the maternally inherited mitochondrial DNA (mtDNA) of all living people to a female ancestor that lived in Africa about 200,000 years ago, dubbed mitochondrial Eve. She caught the attention of the popular press, landing on the cover of *Newsweek* and *Time*.

Additional studies of living people—from Y chromosomes to snippets of nuclear DNA to the entire mtDNA genome—consistently found that Africans were the most diverse genetically. This suggests that modern humans arose in Africa, where they had more time to accumulate mutations than on other continents (*Science*, 17 November 2006, p. 1068). Meanwhile, ancient DNA technology also took off.

Pääbo’s group sequenced first a few bits of Neandertal mitochondrial DNA in 1997, then the entire mitochondrial genomes of several Neandertals—and found them to be distinct from those of living people. So ancient DNA, too, argued against the idea of mixing between Neandertals and moderns. Over the years the replacement model became the leading theory, with only a stubborn few, including Wolpoff, holding to multiregionalism.

Yet there were a few dissenting notes. A few studies of individual genes found evidence of migration from Asia into Africa, rather than vice versa. Population geneticists warned that complete replacement was unlikely, given the distribution of alleles in living humans. And a few paleoanthropologists proposed middle-of-the-road models. Smith, a former student of Wolpoff’s, suggested that most of our ancestors arose in Africa but interbred with local populations as they spread out around the globe, with archaic people contributing to

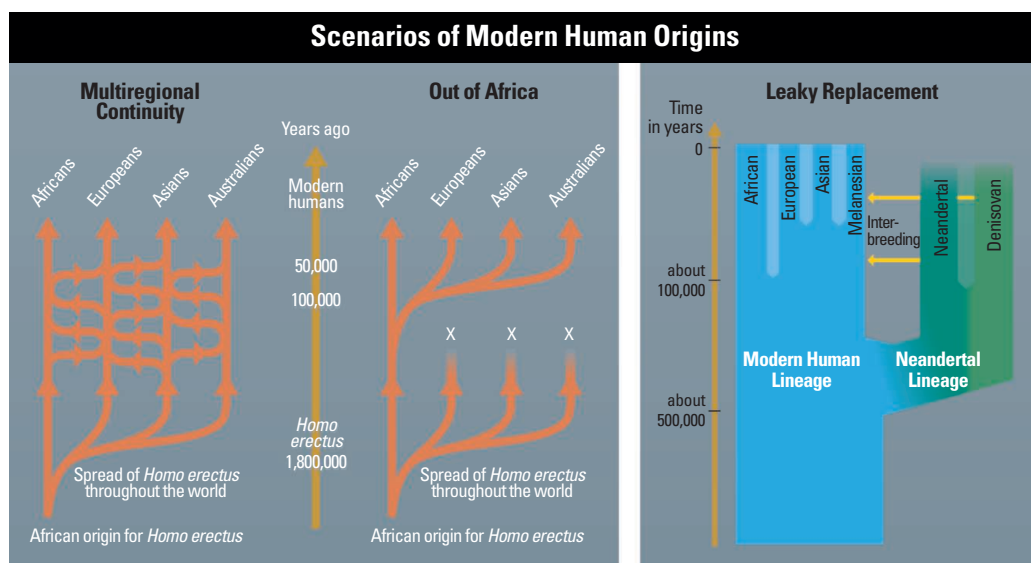
about 10% of living people’s genomes. At the University of Hamburg in Germany, Gunter Brauer similarly proposed replacement with hybridization, but with a trivial amount of interbreeding. But neither model got much traction; they were either ignored or lumped in with multiregionalism. “Assimilation got kicked so much,” recalls Smith.

Over time, the two more extreme models moved toward the middle, with most multiregionalists recognizing that the chief ancestors of modern humans arose in Africa. “The broad line of evolution is pretty clear: Our ancestors came out of Africa,” says biological anthropologist John Relethford of the State University of New York College at Oneonta. “But what happens next is kind of complex.”

the genome was neither a Neandertal’s nor a modern human’s, yet the girl was alive at the same time, dating to at least 30,000 years ago and probably older than 50,000 years. Her DNA was most like a Neandertal’s, but her people were a distinct group that had long been separated from Neandertals.

By comparing parts of the Denisovan genome directly with the same segments of DNA in 53 populations of living people, the team found that the Denisovans shared 4% to 6% of their DNA with Melanesians from Papua New Guinea and the Bougainville Islands. Those segments were not found in Neandertals or other living humans.

The most likely scenario for how all this happened is that after Neandertal and Denisovan populations split about 200,000 years ago,



Changing views. Two models of modern human origins (*left*) are being challenged by new insights based on ancient DNA (*right*), which suggest some limited interbreeding between modern and archaic populations.

Genes from the past

Then in May 2010 came the Neandertals’ complete nuclear genome, sequenced from the bones of three female Neandertals who lived in Croatia more than 38,000 years ago. Pääbo’s international team found that a small amount—1% to 4%—of the nuclear DNA of Europeans and Asians, but not of Africans, can be traced to Neandertals. The most likely model to explain this, Pääbo says, was that early modern humans arose in Africa but interbred with Neandertals in the Middle East or Arabia before spreading into Asia and Europe, about 50,000 to 80,000 years ago (*Science*, 7 May 2010, pp. 680, 710).

Seven months later, on 23 December, the team published in *Nature* the complete nuclear genome of a girl’s pinky finger from Denisova Cave in the Altai Mountains of southern Siberia. To their surprise,

modern humans interbred with Neandertals as they left Africa in the past 100,000 years. Thus Neandertals left their mark in the genomes of living Asians and Europeans, says co-author Montgomery Slatkin, a population geneticist at the University of California, Berkeley. Later, a subset of this group of moderns—who carried some Neandertal DNA—headed east toward Melanesia and interbred with the Denisovans in Asia on the way. As a result, Melanesians inherited DNA from both Neandertals and Denisovans, with as much as 8% of their DNA coming from archaic people, says co-author David Reich, a population geneticist at Harvard Medical School in Boston.

This means *H. sapiens* mixed it up with at least two different archaic peoples, in at least two distinct times and places. To some, that’s starting to sound a lot like multiregionalism. “It’s hard to explain how good I feel

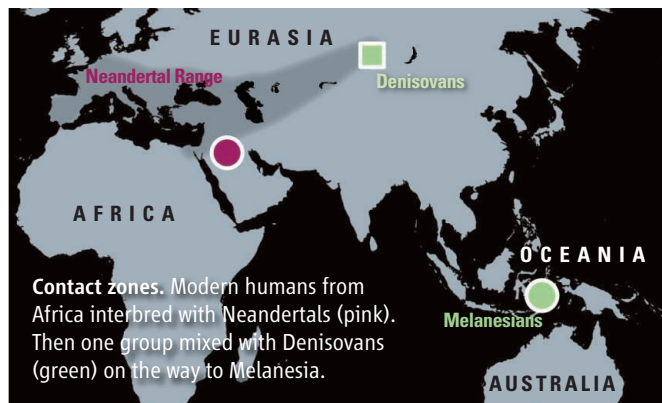
about this,” says Wolpoff, who says that seeing complete replacement falsified twice in 1 year was beyond his wildest expectations. “It was a good year.”

And yet the interbreeding with archaic humans seems limited—from 1% to 8% of some living people’s genomes. Stringer and many others don’t consider it full-scale multi-regional continuity. “I think interbreeding was at a low level,” says Slatkin, who says that if there had been a great deal of admixture, the genetic data would have revealed it already. Low levels of interbreeding suggest that either archaic people mated with moderns only rarely—or their hybrid offspring had low fitness and so produced few viable offspring, says population geneticist Laurent Excoffier of the University of Bern in Switzerland.

In any case, Reich notes that at least 90% of our genomes are inherited from Afri-

can ancestors who replaced the archaic people on other continents but hybridized with them around the margins. And that scenario most closely backs the assimilation models proposed by Smith and Brauer.

Of course, it’s possible that future data will overturn today’s “leaky replacement” model. Slatkin says he cannot rule out an alternative explanation for the data: The “archaic” DNA thought to have come from mating with Neandertals could instead stem from a very ancient ancestor that we shared with Neandertals. Most modern humans retained those archaic sequences, but Africans lost them. But



Slatkin says this “doesn’t seem very plausible,” because it requires modern human populations with the archaic DNA and those without it to have been partially isolated from each other in Africa for hundreds of thousands of years. And it seems even less probable that Melanesians and Denisovans are the only groups that retained a second set of archaic DNA motifs from a common ancestor shared by all modern humans, Neandertals and Denisovans. If those explanations do prove true, replacement would not be falsified.

In the wake of the big genome studies, other researchers such as Hammer are scrutinizing DNA from more living humans to further test the model. Researchers are also trying to pinpoint when admixture happened, which has significant consequences. At just what point did we evolve from archaic humans to become “modern” humans? “There are still archaic [genetic] features floating around until amazingly recently, until 40,000 years ago,” says Hammer. He wonders whether the process of becoming modern took longer and was more complex than once thought. “There’s no line you can draw and say everything after this is modern. That’s the elephant in the room.”

Meanwhile, paleoanthropologists are searching for fossils in Asia that might belong to the enigmatic Denisovan population—and might yield more ancient DNA. Paleoanthropologist Russell Ciochon of the University of Iowa in Iowa City and Wolpoff say there are several known, ambiguous fossils in Asia that might be candidates for early Denisovans. “I believe things were going on in Asia that we just don’t know about,” says Ciochon. “Before this paper on the Denisovans, we didn’t have any insight into this. Now, with this nuclear genome, I find myself talking about ‘the Denisovans.’ It’s already had an impact.”

As for Stringer and Wolpoff, both now in their 60s, their battle has mellowed. Their views, while still distinct, have converged somewhat, and they shared a beer at a Neandertal meeting last year. “The reason we get on well now,” says Stringer, “is we both think we’ve been proved right.” —ANN GIBBONS

The Species Problem

Our ancestors had sex with at least two kinds of archaic humans at two different times and places—and those liaisons produced surviving children, according to the latest ancient DNA research (see main text, p. 392). But were the participants in these prehistoric encounters members of separate species? Doesn’t a species, by definition, breed only with others of that species?

These are the questions paleogeneticist Svante Pääbo dodged twice last year. His team published two papers proposing that both Neandertals and mysterious humans from Denisova Cave in Siberia interbred with ancient modern humans. But the researchers avoided the thorny question of species designation and simply referred to Neandertals, Denisovans, and modern humans as “populations.” “I think discussion of what is a species and what is a subspecies is a sterile academic endeavor,” says Pääbo, who works at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany.

The question of how to define a species has divided researchers for centuries. Darwin’s words in *On the Origin of Species* still hold: “No one definition has satisfied all naturalists.” However, many scientists use the biological species concept proposed by Ernst Mayr: “groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups.”

The draft versions of the Neandertal and Denisovan nuclear genomes show low levels of interbreeding between each of them and modern humans. Apply Mayr’s definition strictly, and all three must be considered *Homo sapiens*. “They mated with each other. We’ll call them the same species,” says molecular anthropologist John Hawks of the University of Wisconsin, Madison.

But that’s a minority view among paleoanthropologists. Many consider Neandertals a species separate from modern humans because the anatomical and developmental differences are “an order of magnitude higher than anything we can observe between extant human populations,” says Jean-Jacques Hublin, a co-author of Pääbo’s at Max Planck. In the real world, he says, Mayr’s concept doesn’t hold up: “There are about 330 closely related species of mammals that interbreed, and at least a third of them can produce fertile hybrids.”

There’s also no agreed-upon yardstick for how much morphologic or genetic difference separates species. That’s why Pääbo’s team avoided the species question a second time with respect to the Denisovans. These hominins are known only from a scrap of bone, a single tooth, and their DNA. They are genetically closest to Neandertals. The genetic distance between Denisovans and Neandertals, in fact, is only 9% larger than that between a living Frenchman and a living San Bushman in Africa, both of whom belong to *H. sapiens*. But so far Neandertals seem to have low genetic diversity, based on the DNA of six Neandertals from Russia to Spain. To Pääbo’s team, that makes the difference from the Denisovans significant.

Also, the Denisovan tooth doesn’t look much like that of a Neandertal. So the team considers them a distinct population but declined to name a new species. “Why take a stand on it when it will only lead to discussions and no one will have the final word?” asks Pääbo.

—A.G.