A little over four years ago, in January 1987, the late Allan C. Wilson and his colleagues Rebecca Cann and Mark Stoneking published a paper in *Nature*, titled "Mitochondrial DNA and Human Evolution." In the paper the three University of California at Berkeley biochemists presented certain genetic data from 147 human subjects from around the world and suggested that a long-standing anthropological problem might at last have been solved. That problem concerned the origin of anatomically modern humans, *Homo sapiens sapiens*: where and when they evolved. An integral element of this argument was the question of the fate of the Neanderthal: Were they the direct ancestors of modern humans, or were they a side branch of human history that became extinct without issue?

The new genetic data, noted Wilson and his colleagues, supported the notion that the transformation of archaic to modern forms of *Homo sapiens* occurred first in Africa, about 140,000 to 100,000 years ago, and that all present-day humans are descendants of that African population. The corollary of this is that the Neanderthal were not ancestors of *Homo sapiens sapiens* but were close evolutionary cousins, now extinct. In a commentary on the paper, published in the same issue of *Nature*, Jim Wainscoat of the Radcliffe Infirmary in Oxford, England, described the Berkeley study as providing "the strongest molecular evidence so far in favour of the African population." The corollary of this is that the Neanderthal were not ancestors of *Homo sapiens sapiens* but were close evolutionary cousins, now extinct. In a commentary on the paper, published in the same issue of *Nature*, Jim Wainscoat of the Radcliffe Infirmary in Oxford, England, described the Berkeley study as providing "the strongest molecular evidence so far in favour of the African population."

In the short time since the Berkeley team published its paper, the origin of modern humans has become the undisputed hot issue of physical anthropology. No anthropological gathering has been complete without its own symposium on the topic, and a stream of books, both scholarly and popular, is coming off the presses. The genetic evidence is not the only factor fueling this interest, however. New fossil data have contributed too, producing a critical mass of academic attention. Without doubt, this most recent event in human evolutionary history has grabbed the headlines from the more usual high-profile reports of "the oldest" this or "the first" that.

**Beyond dissonance**

Those who hoped that scholarly consensus might emerge from all this activity, however, have been disappointed. The differences of anthropological opinion that marked out this piece of intellectual territory four years ago are just about as disparate as they ever were. And the genetic evidence that did so much to enliven discussion has become highly controversial, the target of sharp criticism from anthropologists and molecular biologists alike. Wilson, meanwhile, was openly exasperated by the current ruckus. He considered the problem to be "essentially solved" and charged that the critics "either don't understand the data or don't take the trouble to look at it carefully."

There is no doubt that the elements of the ruckus are many and complex, extending beyond a residual antagonism between molecular and anatomical approaches to solving issues of phylogeny, or evolutionary relationships. Some question Wilson's technique itself, while others raise questions relating to population biology and population genetics theory. Recently, linguistics has insinuated itself into the fray in a most unexpected manner. Archeological evidence has a bearing too. (See "Archaeology and Eve" accompanying this article.) The result: multiple possibilities for disagreement, many of which have already been realized.

Wilson was no stranger to controversy, particularly in connection with human origins research. In the late 1960s and throughout the 1970s, he and his Berkeley colleague Vincent Sarich struggled to convince anthropologists...
Genetic and archaeological data both are fueling a debate that in four years has become the hottest in anthropology.
that the first members of the human family, the hominids, evolved close to 5 million years ago, not the 15 million to 20 million previously inferred from fossil evidence. Wilson and Sarich based their claim on what today look like crude tools of molecular biology, simple immunological measures of differences among blood proteins. Eventually the biochemists prevailed, but only after a decade and a half of controversy and much bad feeling on both sides. (See articles in Mosaic Volume 10 Number 2 March/April 1979, Volume 11 Number 3 May/June 1980, and Volume 14 Number 6 November/December 1983.)

As the science of molecular biology advanced over recent years, giving ever closer access to species' genetic material, Wilson assiduously exploited the new opportunities for tracking evolutionary information at the molecular level. One such path led him to analyze mitochondrial DNA in humans. The reason for this analysis was twofold.

First, although most cellular genetic material cells is packaged inside nuclei, a very small amount is located inside mitochondria, organelles responsible for energy metabolism. A mammalian sperm does contain mitochondria, but they are excluded when the nucleus enters the ovum. Each new offspring inherits nuclear DNA in equal parts from both its mother and father, but inherits mitochondria—and the mitochondrial DNA they contain—from its mother only. Because mitochondrial DNA is maternally inherited—traced back through mother to grandmother to great-grandmother, and so on—it offers a potentially clean-cut method for reconstructing phylogenetic development. By contrast, the mixing of maternal and paternal genes that occurs in the nucleus tends to blur the image through time.

Second, mitochondrial DNA appears to offer a more sensitive molecular clock by which to measure the genetic distance between individuals. Molecular biologists often determine the degree of genetic relatedness between individuals by the number of mutations that separate them. Because mitochondrial DNA accumulates mutations five to ten times as fast as happens in nuclear DNA, it provides a record of the passage of shorter periods of evolutionary time. An important assumption here, of course, is that, on average, mutations accumulate at a constant rate; specific amounts of accumulated mutations can then be related to the passage of specific periods of time.

Because the origin of modern humans had been generally considered to be a rather recent event, perhaps as recent as 50,000 years ago, the mitochondrial DNA molecular clock seemed to be perfectly suited to establishing the date of the event more precisely. It was this application that Wilson and his colleagues reported in their 1987 Nature paper.

The clock and the quarrel

The Berkeley team had collected mitochondrial DNA from 147 individuals from five geographical regions (although they used Black Americans for most of their African sample). The different DNA samples were then exposed to a battery of restriction enzymes, a procedure that cuts DNA at specific sites, producing a particular pattern of fragments of various lengths for each DNA. Differences in sequence between different individuals' DNA are revealed when enzyme-cutting sites or the lengths of sequences between them have been altered by mutation so that a different pattern of fragment lengths is produced. The method effectively surveyed about 9 percent of the 16,569 nucleotide sequence that constitutes human mitochondrial DNA.

The enormous amount of data that emerges from such an experiment is analyzed in two ways. First, the different fragment patterns, or types of mitochondrial DNA, are identified and compared, allowing an evolutionary tree to be reconstructed. Second, the amount of sequence variation—accumulated mutations—among the patterns is measured. From this, the amount of evolutionary time that separates different patterns can be calculated.

Reconstruction of the simplest possible version of the evolutionary tree produced the now-famous horseshoe-
shaped diagram containing two distinct branches: one that consists of only African types and a second that is a mixture of all types. "We infer from the tree of minimum length that Africa is the likely source of the human mitochondrial gene pool," noted Wilson and his colleagues. In other words, the reconstructed evolutionary tree looks as if it is "rooted" in Africa, with later branches spreading out into the rest of the Old World.

This conclusion is supported by the amount of accumulated variation in the different types of mitochondrial DNA: the African types have more variation than European or Asian types. If the rate of accumulation of mutations is similar in all parts of the world, this implies that African types have been around longest. In other words, they evolved first. The question is, when did they evolve?

"Assuming a rate of 2% to 4% per million years, this implies that the common ancestor of all surviving mitochondrial DNA types existed 140,000 to 290,000 years ago," concluded the Berkeley researchers. The "2% to 4% per million years" refers to the estimated mutation rate in diverging lineages: that is, two to four nucleotide bases in every 100 will mutate every million years. Wilson had derived his figures from data on apes, monkeys, horses, rhinoceroses, mice, rats, birds, fishes, and humans. This appears to be well based and unequivocal, but the single sentence cited above has been the focus of much of the criticism leveled at Wilson's work. The calculated divergence rate has been viewed as far too high, and the attempt to identify a common ancestor at the root of the tree has also been attacked.

"Right from the beginning, there was confusion over what we were saying," said Wilson. "And this wasn't confined to the popular press. Some of our scientific colleagues were responsible too."

The common ancestor referred to is a single female who lived somewhere in Africa, sometime between 140,000 and 290,000 years ago. All living humans derive their mitochondria from this single female. "One lucky mother" is how Wilson often characterized her. Perhaps inevitably, once the Berkeley team's conclusions became known, the single female came to be called Eve, mother of us all. "It was an obvious and sometimes convenient term," acknowledged Wilson, "but it caused us a lot of problems."

Leaving aside these problems for a moment, it should be noted that, in spite of the way events have been widely perceived, the Berkeley laboratory was not the first to tackle the problem of modern human origins using mitochondrial DNA as a tool. In the late 1970s, Douglas Wallace, then at Stanford University but now at Emory University, began a similar program of investigation. By 1983 Wallace and his colleagues had demonstrated that human mitochondrial DNA roots were shallow, that certain variants correlated with geographic and ethnic origins, and that, overall, Old World populations divided into two groups, African and non-African, with a larger amount of variation having accumulated in African
mitochondrial DNA.

There were two ways of interpreting the data, depending on assumptions. "If we assumed a constant molecular clock, then we would conclude that Africa was the origin, because more variation had accumulated there," says Wallace. "On the other hand, if we used parsimony analysis, we would conclude Asia was the origin, because one type of mitochondrial DNA, type 8, was most closely related to other primates and was at highest frequency among Asians." Of the two possibilities, Wallace and his colleagues in their 1983 publication favored the second. They explained the greater variation in African mitochondrial DNA as the result of a higher mutation rate. Now, however, Wallace considers that the weight of data from various laboratories persuasively indicates Africa was the region of origin.

**Two opposing models**

At this point, the mitochondrial DNA results should be set in the anthropological context they were meant to address. For the past half century, anthropologists have had two opposing models for the origin of modern humans.

In the first model, it is envisioned that modern *Homo sapiens* evolved more or less independently in many different parts of the world, from populations of *Homo erectus* that had spread out of Africa about a million years ago. There would have been some gene flow among the different geographical populations, but each is envisioned as making the transition distinct in time and place from the others. The transitions are suggested to have occurred over a relatively long period of time, the last being rather recent, say 50,000 years ago. Each geographical population would have had very deep genetic roots, essentially going back as far as a million years, to the local founding populations of *Homo erectus*. This scenario is known as the multiregional, or candelabra, model.

The second model, which William Howells of Harvard University once called the Noah’s Ark hypothesis, is very different. In this model, the origin of modern *Homo sapiens* is seen as a recent, discrete speciation event: the evolution of the modern human species from a geographically limited population of archaic sapiens. Populations of modern humans would migrate from this point of origin to the rest of the world, replacing existing populations of archaic *Homo sapiens* as they went. In this case, modern populations would have had very shallow genetic roots that could be traced back to the region of origin.

Some anthropologists—notably Milford Wolpoff, Alan Thorne of the Australian National University, Canberra, and Wu Xinzhi of the Institute of Vertebrate Paleontology and Palaeoanthropology, Peking—argue that the fossil evidence supports the predictions of the multiregional model. That is, local geographical populations have anatomical characteristics that can be traced far back into the fossil record of that region. Others contend that no such regional continuity can be demonstrated in the fossils. Instead, these anthropologists say, the fossil evidence indicates evolution of modern humans first in Africa, with a subsequent spread throughout the Old World, and replacement by various degrees of local populations.

According to the multiregional model, the genetic roots of *Homo sapiens* should be deep, reaching as far back as a million years. The Noah’s Ark model predicts much shallower roots. As presented in Wilson’s 1987 Nature paper, the genetic evidence in the form of mitochondrial DNA appears unequivocally to support the Noah’s Ark model.

Perhaps predictably, the most promi-
nent proponent of the Noah’s Ark model, Christopher Stringer of the British Museum (Natural History), has become a keen supporter of the mitochondrial DNA evidence. “As has proved to be the case in the study of hominin origins, paleoanthropologists who ignore the increasing wealth of genetic data on human population relationships will do so at their peril,” wrote Stringer and his coauthor Peter Andrews, also of the British Museum, in Science magazine in March 1988. Equally predictable is that the multiregional model’s most ardent advocate, Milford Wolpoff of the University of Michigan, is the most vocal critic of the conclusions Wilson drew from the mitochondrial DNA data. “Completely misguided” is how he characterizes it. And, with various like-minded colleagues, Wolpoff penned this riposte to Stringer and Andrews, also in Science: “It is appropriate to conclude that paleoanthropologists who ignore the increasing wealth of paleontological data will do so at their peril.” If nothing else, this exchange gives a sense of the somewhat combative nature of the current debate.

Problems with bottlenecks

Back to Eve herself, mitochondrial mother of us all: What does her existence reveal about the origin of modern humans? “You have to realize that, in tracing the mitochondrial DNA lineage, we are almost certainly going back to before the origin of modern humans,” Wilson later explained. “Mitochondrial Eve was probably a member of an archaic sapiens population.”

In addition, he said, the pattern of maternal inheritance of mitochondrial DNA means that it gives only part of the genetic picture. “She wasn’t the literal mother of us all, just the female from whom all our mitochondrial DNA derives.” Other females will have contributed nuclear genes to the pool, just as males did.

The potential for confusion was considerable and was compounded by a sentence at the end of Wilson’s Nature paper: “By comparing the nuclear and mitochondrial DNA diversities, it may be possible to find out whether a transient or prolonged bottleneck in population size accompanied the origin of our species,” wrote the Berkeley researchers. “Then a fuller interaction between paleoanthropology, archeology, and molecular biology will allow a deeper analysis of how our species arose.”

A population bottleneck occurs when population numbers crash to low levels, which occurs in nature from time to time and which some evolutionary biologists suggest may occasionally be associated with the origin of new species. The ultimate population bottleneck, of course, is a single mating couple: Eve and her consort. The idea of a bottleneck at the origin of Homo sapiens was strengthened by Jim Wainscoat: “It is tempting to relate the occurrence of the ancestral mitochondrial DNA type to a severe constriction in population size (bottleneck).” Eve, it seemed, might well have been, if not half of a single couple, then just one of a small population of females that expanded, resulting in the worldwide spread of a single mitochondrial DNA type.

“The idea of bottlenecks was very much in the air when we published our Nature paper,” recalled Wilson. “It was unfortunate.” In fact, the notion had been raised almost seven years earlier, by Wesley Brown, now of the University of Michigan but then a member of Wilson’s Berkeley laboratory. In June 1980, Brown published one of the first studies that related human mitochondrial DNA to the origin of modern humans. “The result indicates that the human species may have passed through a severe population constriction (‘bottleneck’) relatively recently,” he concluded. (Brown now says that he had written several qualifying sentences in the article, offering alternative population models to explain the results, but they were lost in the editing process.) The bottleneck idea was therefore firmly planted.

And just a year before the Wilson lab produced its Mitochondrial Eve Nature paper, Wainscoat and his Oxford colleagues published data on part of the beta-globin gene cluster from eight diverse human populations. Their conclusions were several and included the suggestion that modern humans had arisen recently from a founder population in Africa, spreading from there to the rest of the Old World. “The founder population was small,” they stated. The point was emphasized by an accompanying commentary from Steve Jones and Shahin Rouhani, both of London University, titled: “How small was the bottleneck?” It could have been very small indeed, they said.

It is therefore not surprising that when, during the past several years, new genetic evidence was collected showing that population bottlenecks in human history were extremely unlikely, many people believed the Mitochondrial Eve hypothesis was in deep trouble. The new data, principally the work of Jan Klein and his associates at the Max-Planck-Institut für Biologie in Tübingen, concerns genes of the major histocompatibility complex (MHC), referred to in humans as the HLA complex.

Klein and his colleagues showed that variants of these genes—and there are many—are shared widely between humans and chimpanzees, indicating that population bottlenecks were unlikely to have occurred at any point in human history. One effect of a bottleneck is to reduce the amount of genetic variation that survives through the event. Klein’s data appear to indicate that the range of HLA variants that existed in the population that was the common ancestor of apes and hominid has survived to the present day, thus ruling out a severe population constriction at any point.

“The notion of there being a single Eve who was the first ‘lucky’ mother of us all 200,000 years ago can therefore be discarded,” he wrote in January 1990. Klein’s data had first become widely known a year earlier, at the UCLA Symposium on Molecular Evolution, orga-
organized by Steve O'Brien and Michael Clegg. "The consensus was that the Eve hypothesis was dead," remembers O'Brien. According to Klein's data, the human population has never dropped below a figure of about 10,000, which was a finding that prompted Craig Packer of the University of Minnesota to quip: "The garden of Eden, it turns out, was fairly crowded."

The business of calculating population size to allow certain proportions of genetic variation to survive through time is not easy and rests squarely on the assumptions made. For instance, Naoyuki Takahata of the National Institute of Genetics in Mishima, Japan, considers Klein to have been far too cautious. He calculates that a figure of 100 would be too small, but that something in the region of 1,000—much less than Klein's estimate of 10,000—might well have been possible. A population of 1,000 individuals is small, to the point of being endangered.

**Mitochondrial extinction**

Although many critics of the Mitochondrial Eve hypothesis claim that the unlikelihood of the occurrence of a population bottleneck disproves the hypothesis, bottlenecks are in fact unnecessary. It is possible that a population of large size with a great diversity of mitochondrial DNA types arrived, after a period of time, with a descendant population carrying essentially just one type—all variants of one of the originals. John Avise of the University of Georgia demonstrated this point in a paper published in 1983. "I was prompted to think about the problem when I saw Wes Brown's 1980 paper on human mitochondrial DNA," recalls Avise, who has been studying mitochondrial biology since the mid-1970s. "I felt a population bottleneck was unnecessary. The solution is conceptually simple and has to do with the stochastic loss of mitochondrial lineages through time. "It is easiest to think of in terms of family names, an idea Michael Clegg suggested to me."

For instance, starting with ten couples, each with a different family name and each producing two offspring per generation, a pattern quickly develops.

In the first generation, on average, one quarter of such couples are expected to have two boys, who will carry the family name to the next generation; one half will have a boy and a girl, the family name being carried by the single male child; and one quarter will have two girls, the family name therefore becoming extinct. The same process continues through the generations, so that after...
about 20 generations (twice the number of females in the first generation) only one family name remains. "There need be nothing special or superior about the name that prevails," says Avise. "It is simply a stochastic process. The same holds for mitochondria, except that transmission is through the female line."

Given the logic of lineage extinction, which predicts that a diversity of mitochondrial DNA types in an ancestral population will eventually be replaced by a series of descendants from just one of those types, what is to be said about the pattern as it is seen in humans today? If the multiregional model of modern human origins is correct, then ancient mitochondrial DNA should be present somewhere in today's population, reflecting deep genetic roots. Ancient DNA would show variants that could be traced far back into the past, perhaps as far back as a million years. By shortly before his death in July 1991, Wilson and his colleagues had sampled more than 2,000 non-African individuals without having detected ancient DNA. "Perhaps we've been unlucky," Wilson explained, "but I don't think so. By now [late 1990] I'm pretty sure that we haven't found any because none exists. Archaic populations were completely replaced by modern humans."

Not so, argues Wolpoff. There are two—one technical, the other biological—ways in which the mitochondrial DNA in today's human populations is artificially young, he suggests.

At the annual meeting of the American Association for the Advancement of Science in February 1990, Wolpoff argued that Wilson and his colleagues had miscalculated the rate of accumulation of mutations in mitochondrial DNA. The rate was too high, he said, by perhaps as much as a factor of four. He cited a figure of 0.715 percent, the product of calculations of Masatoshi Nei of Pennsylvania State University. "That would make Eve about 800,000 years old, which is just fine by me." In fact, the comparison between Wilson's 3 percent and Nei's 0.715 percent is inappropriate, an error that has been made by several critics of Mitochondrial Eve. The 3 percent rate reflects the divergence between two lineages, and so counts mutations in both lineages. Nei's figure of 0.715 percent takes into account a substitution rate in one lineage. The proper comparison is therefore between 3 percent (Wilson and colleagues) and 1.43 percent (Nei). There is still a gap, of course, with Nei's Eve being some 400,000 years old as compared with Wilson's at 200,000. But 400,000 years ago. Here, Neanderthal and modern human populations appear to have manufactured the most characteristic of Middle Paleolithic technology, known as Mousterian. There is no sign of the typical Upper Paleolithic assemblages with these early moderns. Similarly, in South Africa, the earliest specimens of anatomically modern humans, such as at Klasies River Mouth, are found with Middle Stone Age technology. "Clearly, there is no necessary correlation between physical type and artifacts," observes Klein. "Equally, a major change in physical type may precede a major change in artifacts."

These caveats aside, the archaeological evidence is the most direct link with our ancestors' behavior and cannot be ignored in searching for the origin of modern humans. For instance, some archaeologists do point to a change in the Middle Stone Age record in Africa about 90,000 to 100,000 years ago that might signal the arrival of modern humans. "I can identify an increase in complexity at this point, associated among other things with a greater production of blades," says Brooks. "But I don't think it is possible to trace this as a subsequent movement into Europe. And you certainly don't see a pace of change in Africa that you eventually see in Europe." She notes, however, that the European record itself is somewhat biased, with its emphasis on events in France and northern Spain. Elsewhere in Europe, the rapid innovation that characterizes the classic Upper Paleolithic is much less evident.

However, viewing the African and European records overall, Brooks is unequivocal: "There is no evidence in the archaeological record for a rapid and total replacement by a wave of people moving out of Africa. There is too much continuity in Europe to indicate total replacement." Geoffrey Pope of the University of Illinois has similar conclusions for Asia. "If invading anatomically modern humans brought with them new technological innovations, then they left no trace of it in the archaeological record of the region which they colonized," he said recently. "The picture that has emerged in Asia is one of a stable lithic technology in which most of the earliest stone tool assemblages are usually qualitatively inseparable from the recent assemblages."

Overall, the picture is at best blurred, with no clear archaeological signal in support of one model of the origin of modern humans over the other. Blade technologies do appear to have originated first in Africa, and there is good indication of an east-to-west flow of modern technology through Europe. There is even evidence of contact between Neanderthals and modern humans in Western Europe, in the form of an apparently mixed technology, the Chatelperronian. But tremendous local variation and an absence of clear-cut predicted patterns make firm conclusions difficult to reach.

Milford Wolpoff of the University of Michigan, who is an ardent proponent of gene flow with respect to anatomical continuity among emerging modern humans, prefers in this confusing context to consider the movement of ideas. "Archaeology gives you dates for the movement of ideas," he says. "It is the movement of ideas that is critical to the origin of modern humans, more so than the movement of genes."

For Klein, the mismatch between morphology and archaeology may indicate that anatomically modern humans, as they are first identified in the fossil record, may not yet be mentally modern. "Important neurological changes may have occurred later, giving rise to behavioral patterns we identify as those of modern humans," he suggests. "It will be very difficult to reconcile all the different forms of evidence with this problem." • R.L.
still does not take Eve back to the beginning of the *Homo erectus* settlement of the Old World.

The question of what exactly is the correct substitution rate is obviously important. Wilson believed that Nei had been too cautious in his analysis and suggests he hadn’t carefully studied the Berkeley group’s calculations. Nei argues that Wilson had overlooked factors that may artificially increase apparent rate. The two groups have so far failed to resolve their differences. Most researchers, however, are confident that the 2 to 4 percent range is reliable.

Recently, Wolpoff, however, has argued that the issue of rate, as calculated, is irrelevant. “With stochastic loss of mitochondrial lineages, it’s impossible to calculate any rate reliably,” he says.

As has been noted, stochastic loss of mitochondrial lines does occur through time; this is the nature of mitochondrial dynamics. Wolpoff points out that if, in a population, older lineages were lost preferentially, the result would be a population with “young” mitochondrial DNA, an artifact of stochastic loss. “But why should you expect to lose just the older lineages?” questions Mark Stoneking.

**“Stochastic loss is precisely that—stochastic. There’s no more reason to expect older lineages to be preferentially lost than there is to expect younger lineages to be lost. If the loss is stochastic, we can be reasonably comfortable that we are seeing a true reflection of the population’s overall history.”**

Wolpoff’s second argument, the biological one, is that selection might have accelerated the lineage extinction process. “If one mitochondrial type has even a slight advantage, it will be favored and will spread more rapidly through the population,” he says. “This would eliminate other types, and make it look as if the mitochondrial DNA population as a whole were young.” The University of Georgia’s Avise agrees that selection could distort the picture. “A mutant could sweep through the population, it’s true,” he says. “You’d have to have strong contact across the entire population for it to happen, but it’s always a worry in basing phylogeny on mitochondrial DNA analysis.” Avise knows of no examples of such a phenomenon, but, in principle, will not rule it out.

“What you have to do is look at other genes,” Allan Wilson said. “It’s true that the mitochondrial genome effectively is one gene as far as working out phylogeny is concerned, a pretty powerful one. But what you’d like is to have data on a range of nuclear genes too. In the end you should see a pattern of concordance. Overall, they should all tell the same story.”

So far, clear-cut data on other genes, including the potentially useful Y chromosome, simply do not exist, principally because of the phenomenon of mixing—or recombination—that occurs with nuclear DNA. Those nuclear DNA data that are available, however, do give the same overall picture that the Berkeley team infers from its mitochondrial evidence.

For instance, Luigi Luca Cavalli-Sforza of Stanford University has for many years been collecting information on a wide range of nuclear genes. For some time he believed that the data indicated that *Homo sapiens* originated in Asia, but recently he became convinced that instead the data points to Africa. Similarly, Pennsylvania State University’s Nei has data on more than 150 genetic loci in the nucleus, the overall pattern of which is “consistent with the hypothesis of an African origin,” he says. He is also able to estimate a date for that origin: about 100,000 years ago.

Even though the resulting pattern coincides closely with Wilson’s inferences from mitochondrial DNA, Nei is critical of the Berkeley conclusions. “While this conclusion is probably right, the amount of mitochondrial DNA variation itself has little to do with the place of origin of a species,” he cautions. “The phylogenetic tree [from mitochondrial DNA] is sub-
ject to large stochastic errors." In other words, chance events may intervene in the origin of modern humans. Here, the genetic picture.

In addition to tangible data, geneticists have also addressed theoretical aspects of the two models to determine the origin of modern humans. Here, the multiregional model finds no support at all. The main problem is that the model calls for extensive genetic continuity over very large geographical areas, too large, it seems, for the required level of gene flow to be feasible.

"The multiregional model of human evolution is theoretically implausible," concludes Shahin Rouhani. "Even under ecologically identical conditions, which is rarely the case in nature, geographically isolated populations will diverge away from each other and eventually become reproductively isolated. . . . It is highly improbable that evolution would take identical paths in this multidimensional landscape."

Rouhani calculates that even under the most favorable conditions, the spread of an advantageous mutation might take almost half a million years to travel from South Africa to the coast of China. Under more realistic conditions, which include cultural and geographical barriers, the rate of spread would be much reduced, essentially ruling out the high degree of genetic continuity demanded by the multiregional model.

"Propponents of the multiregional model simply do not understand population genetics," he states. "They use a model that requires continuous exchange of genes, but it requires enormous amounts of time to reach equilibrium. There has been insufficient time in human history to reach that equilibrium."

Wilson was reluctant to respond directly to his critics, preferring instead to allow the force of the data to be his advocate. "That's the tradition of molecular biology," he declared. Meanwhile, he and his colleagues focused ever more closely on details of the overall picture, exploiting the power of polymerase chain reaction (PCR) and DNA sequencing. With his colleague, Anna Di Rienzo, Wilson most recently produced from a population of some 117 Caucasians sequence data on a fast-evolving section of the mitochondrial genome. A very striking pattern emerges from the data, in which a burst of mitochondrial DNA variations becomes established in this population, beginning some 60,000 years ago. "One explanation is that we are seeing the consequences of rapid population expansion that followed the migration out of Africa," suggests Di Rienzo.

If population dynamics of this sort had truly occurred, as predicted by the Noah's Ark model, then various eventualities might have impressed themselves on the prehistoric record. Many of these would involve aspects of material culture, but one concerns the spread of language. If the multiregional model were correct, then languages in different parts of the Old World would have extremely ancient and disparate roots. The likelihood of relating patterns among them and their local populations would be very small. If, however, the Noah's Ark model were correct, then it is possible that a single language would have been associated with the founding population of modern sapiens, and this would spread out with migrating populations, evolving locally as it went, just as do genes.

Although it had not been his intention to address this issue when he began amassing genetic information on human populations more than a decade ago, Stanford University's Cavalli-Sforza recently realized he would be able to test it. Encouraged by Stanford linguists Joseph Greenberg and Merrit Ruhlen, Cavalli-Sforza and his colleagues essentially matched a genetic map of the Old World with a map of related language families. "Linguistic superfamilies show remarkable correspondence with the two major clusters [in the genetic pattern], indicating considerable parallelism between genetic and linguistic evolution," they concluded.

Although some aspects of the Stanford work are controversial, the pattern inferred from it is consistent with the notion that one of the last elements in the evolution of modern humans included an advance in language capacity. The pattern is also consistent with the Noah's Ark hypothesis.

David Frayer of the University of Kansas said a year ago: "Fossils are the real evidence of human evolution." While it is true that fossils may be the most tangible element of the human record, the genes that living humans carry around in their nuclei and mitochondria are a direct product of that record. Read correctly, the genetic information encrypted in those genes can help reveal that record. For many in the anthropological community, significant questions remain over how correctly our genetic heritage is being interpreted. •