# Pleistocene Population Explosions

## A controversial method of reconstructing prehistorical populations indicates that separate modern human groups—and not a single group from Africa—suddenly expanded about 50,000 years ago

Picture a frigid, overcast dawn, 65,000 years ago. A small band of human ancestors is leaving its campsite in Africa in search of food, scavenging their arid valley for fresh carcasses or small animals they can ambush. But times are tough, perhaps because the bone-chilling cold of the last Pleistocene Ice Age has made it difficult to find food and shelter. Whatever the reason, these early humans are suffering. While there may have initially been 100,000 of them, only 10,000 survive—making them an endangered species. "Our ancestors survived an episode where they were as endangered as pygmy chimpanzees or mountain gorillas are today," says Pennsylvania State University anthropologist Henry Harpending.

But unlike the great apes of the 20th century, the offspring of these ancestors of modern humans made a dramatic comeback, argues Harpending, who is doing research on this pivotal moment in the evolution of modern humans. Their descendants fanned out over Africa, Europe, and Asia, settling in isolated, far-flung regions where their populations grew—slowly at first, but by 50,000 years ago they had adapted so well that they were multiplying by the hundreds and thousands. This created a dramatic series of separate "population explosions" around the world and set the stage for the emergence of fully modern humans.

Harpending bases this scenario not on bones or stones but on the genes of modern human beings, which he argues "preserve a record of population expansions and separations in the remote past." In the current issue of *Current Anthropology*, he and his colleagues present a record of the hypothesized bottleneck and the subsequent explosions through a new statistical method of analyzing mitochondrial DNA in modern humans. If the new method proves solid, and others are hurrying to test it, it would give anthropologists and population geneticists a new window into the past. It would also knock down the hotly debated notion that modern humans emerged in one population—probably as a new species in Africa—then fanned out around the globe, replacing other, more archaic humans, such as the Neandertals in Europe. "The big take home message for me," says Harpending "is that it suggests that modern humans evolved from very isolated precursor populations."

The paper has caused quite a stir in the anthropology community. "People are fascinated by this," says Christopher Stringer, a paleoanthropologist at the Natural History Museum in London. "We're hoping this is a reliable, new way of looking at the mitochondrial data." Part of the stir is that some population geneticists question Harpending's method, saying that certain genetic changes, not connected to population shifts, could have produced the same "signature" in the mitochondrial DNA as a bottleneck and later expansions. "There are still other possible explanations for the same distribution they get [in their models]," says Ranajit Chakraborty, a population geneticist at the University of Texas Health Science Center.


CRAIG CHESNER

**Big bang?** The same volcano that made this lake—Mt. Toba in Sumatra—may have triggered a climate change that made life tough for early humans about 70,000 years ago.

Harpending, though, thinks he's on solid ground. For the past 5 years, he has been working with his former student, University of Utah anthropologist Alan Rogers, to devise a statistical method of reconstructing the demographic prehistory of *Homo sapiens* through genetics. Unlike ancestral trees built around mitochondrial DNA, this method doesn't try to trace the genetic lineage of modern humans to a specific place and time, as was done—erroneously—for an African Mitochondrial Eve (*Science*, 14 August 1992, p. 873). Instead, they look at the genetic variation within a modern population and use it to ask other questions—such as how large the population was in the past, and how rapidly it grew.

Their work was purely theoretical until Penn State anthropologists Mark Stoneking and Linda Vigilant, who did some of the original work on the Eve hypothesis, told Harpending about a graph of some of their mitochondrial data over dinner one night. "I just about fell out of my chair when Linda and Mark showed me one graph they had," recalls Harpending.

That graph showed matches of the mitochondrial DNA between individuals within populations around the world—something known as a pairwise comparison, because the method starts by comparing the DNA of two individuals within a population and finding out how closely it matches (see box on p. 28). Those data were distributed on a histogram, with a horizontal axis showing the number of DNA sequence differences between each pair and the vertical axis showing what fraction of the pairs of people had those differences. What stunned Harpending was that the graph showed the same shape—a sharp mountain peak—that Harpending and Rogers had seen in their models of theoretical populations. That shape, they thought, was the signature of a small population that had gone through a rapid expansion. And now they wondered if it was something more than theory.

The idea that modern humans came from a small founder population is not new: Population geneticists have been suggesting it since the 1970s—and, in a paper in *Nature* in 1990, John Maynard Smith of the University of Sussex used mitochondrial data to calculate that the human ancestral population was once reduced to about 5000 females.

Harpending and Rogers went further to see what happened after the bottleneck. They showed for the first time that the population rebounded in a series of separate, rapid expansions on different continents. Working with Stoneking and graduate student Stephen Sherry, they used three different sets of data from a rapidly mutating region of noncoding mitochondrial DNA—a region that accumulates variation rapidly enough to show differences between individuals or populations. Each mtDNA set came from several populations around the world—in-

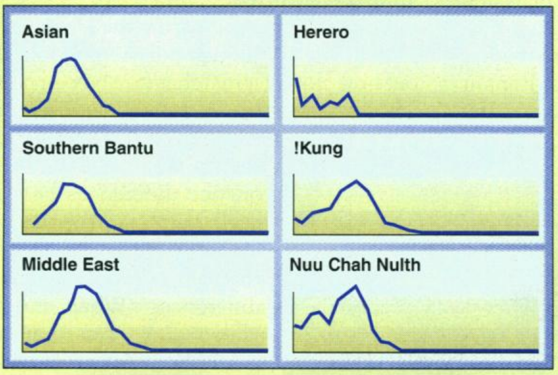
## Graphing Population History

Henry Harpending and Alan Rogers use the mitochondrial genes of modern humans as a time machine to look into the history of a population. They begin by taking the mtDNA sequences of two individuals within a population and comparing how closely the sequences of a region of the mtDNA match. The better the fit, the more likely the two individuals shared a recent, common ancestor for that DNA. If the two individuals share all but five sites in a 360-base pair stretch of mtDNA, for example, then the "mismatch" between them is 5—and that number is plotted on the horizontal axis of a simple histogram. The vertical axis is the number of people with that type of mismatch.

Then, the researchers look at another pair of individuals. If they have 6 mismatches, that's plotted just to the right of the previous pair, so as you move from left to right, the amount of genetic variation increases. Another pair, with 5 mismatches, would go on top of the first pair. After plotting all the differences among at least 20 individuals in a population, the tallest vertical columns represent the amount of variation most common in the population.

Once they draw a line through the top of those columns, they get a shape on the histogram that is a clue to the past history of that population. If the shape is of a mountain peak, with the right side tapering off steeply, then it means that the population expanded recently (because there hasn't been enough time to accumulate a wide range of variation). Harpending and Rogers saw this shape in all but one of the populations they studied. "The method, such as it is, is nothing more than looking at a graph," says Harpending.

**–A.G.**



SOURCE: H. HARPENDING, A. ROGERS

cluding Africans, Asians, Europeans, and Middle Easterners. Through statistical analysis the scientists were able to relate the distribution of genetic variations in each group to the size of that group in the past and learned that each group had started small but rapidly expanded.

But when did these expansions occur? MtDNA accumulates mutations at a steady rate, most scientists believe, making it a molecular clock. The more variations that have accumulated, the more time has passed—in general. By examining the number of mutations in each population, Rogers calculated that the expansions in several different populations took place between 80,000 and 30,000 years ago—with Africans expanding about 80,000 years ago and Europeans about 40,000 years ago. In a dozen populations, all the bursts of expansions seemed centered around 50,000 years ago.

Several population geneticists who have seen the paper think that the method is solid, and they say Harpending and Rogers have good reputations as careful, thorough researchers. "There's nothing wrong with the method," says Joe Felsenstein, a population geneticist at the University of Washington who specializes in statistical methods for analyzing DNA data and building phylogenetic trees. He noted that Harpending and Rogers have run simulated data sets of other types of populations—one that's growing steadily, for example—through their model to see if such data would also create the telltale peak; it didn't. "It's nice they've done a bunch of simulations to try to see which hypotheses don't fit the pattern," Felsenstein says.

Another population geneticist, Richard Hudson at the University of California, Irvine, does have a concern: He wants Rogers to make sure they rule out other factors that could create the same kind of distribution in the data—such as "hot spots" in the mitochondrial DNA that evolve at faster rates. "The signal of the bottleneck and the expansions might be generated by other factors," says Hudson. Chakraborty agrees: "It's a good method that needs further development."

Rogers responds that he has addressed that concern—in a paper published last year in *Molecular Biology and Evolution*. He figured that if there were hot spots, they would cause only a small error in his and Harpending's calculations—and would not change the major conclusion that the populations expanded after a bottleneck. Meanwhile, Harpending is also testing the model in rodents —taking mtDNA from rats with a known population history—to see if it accurately reconstructs what happened to the animals.

As population geneticists decide whether the method is credible, anthropologists are already thinking about its implications. If Harpending's model and interpretation are correct, his results would falsify the so-called strong Garden of Eden or out-of-Africa model. This model proposes that anatomically modern humans arose in a single place as a population very different from their immediate ancestors—perhaps as a genuine new species in Africa about 100,000 years ago. Then, this new species fanned out around the Old World, completely replacing other species of early humans, such as Neandertals in Europe and the descendants of *Homo erectus* in Asia and Indonesia. If that were the case, the histograms would show a different pattern—one where modern populations would all have exactly the same expansion peak, at precisely the same time. But they don't.

Instead, the histograms have peaks at different locations—indicating that the expansions occurred at different times. This data gives more weight to the "weak" Garden of Eden hypothesis, which says that modern humans appeared first in a subpopulation (not a separate species) that survived the bottleneck, then spread slowly over the Old World over tens of thousands of years, perhaps mating at a low rate with the other early humans. Then, these modern humans gained some unknown adaptive advantage—perhaps better tool use or brain reorganization —that spread erratically through these separate, relatively isolated daughter populations, producing irregularly timed expansions.

What would have caused the population shifts? Several anthropologists propose that the coming of the last Pleistocene Ice Age might have been deadly for humans, who evolved during warmer times. The miserable climate may have been even worse for a short while 73,500 years ago, when a gigantic volcano, Toba, erupted on Sumatra. It was the second largest known volcano in history, prompting University of Illinois paleoanthropologist Stanley Ambrose to propose that the dust from Toba may have decreased the temperature by as much as 5 degrees Celsius.

The cause of the subsequent population explosions could have been as simple as the easing of the big chill. Or it could have been that human ancestors suddenly got smarter. Archeologists have found a remarkable shift in the sophistication of tools at about 40,000 years ago—at about the same time Harpending sees population expansions, says Stanford University anthropologist Richard Klein.

Whatever the reason, the new analysis of the mitochondrial data is adding one more critical clue to those from the archeological record in solving the mystery of modern human origins. And so far, "it all holds together very nicely," says Klein.

**–Ann Gibbons**