

# the multiregional evolution of humans

By Alan G. Thorne and Milford H. Wolpoff

Both fossil and genetic evidence argues that ancient ancestors of various human groups lived where they are found today

Three decades ago the paleoanthropological community was locked in a debate about the origin of the earliest humans. The disagreement centered on whether the fossil *Ramapithecus* was an early human ancestor or ancestral to both human and ape lineages. Molecular biologists entered that discussion and supported the minority position held by one of us (Wolpoff) and his students that *Ramapithecus* was not a fossil human, as was then commonly believed. Their evidence, however, depended on a date for the chimpanzee-human divergence that was based on a flawed “molecular clock.” We therefore had to reject their support.

Paleoanthropologists are again engaged in a debate, this time about how, when and where modern humans originated. On one side stand some researchers, such as ourselves, who maintain there is no single home for modern

humanity—the idea that humans originated in Africa and then developed their modern forms in every area of the Old World. On the other side are researchers who claim that Africa alone gave birth to a new species of modern humans within the past 200,000 years. Once again the molecular geneticists have entered the fray, attempting to resolve it in favor of the African hypothesis with a molecular clock. Once again their help must be rejected because their reasoning is flawed.

Genetic research has undeniably provided one of the great insights of 20th-century biology: that all living people are extremely closely related. Our DNA similarities are far greater than the disparate anatomical variations of humanity might suggest. Studies of the DNA carried by the cell organelles called mitochondria, which are inherited exclusively from one’s mother and are markers for maternal lineages, now play a role in the development of theories about the origin

of modern humans across the globe.

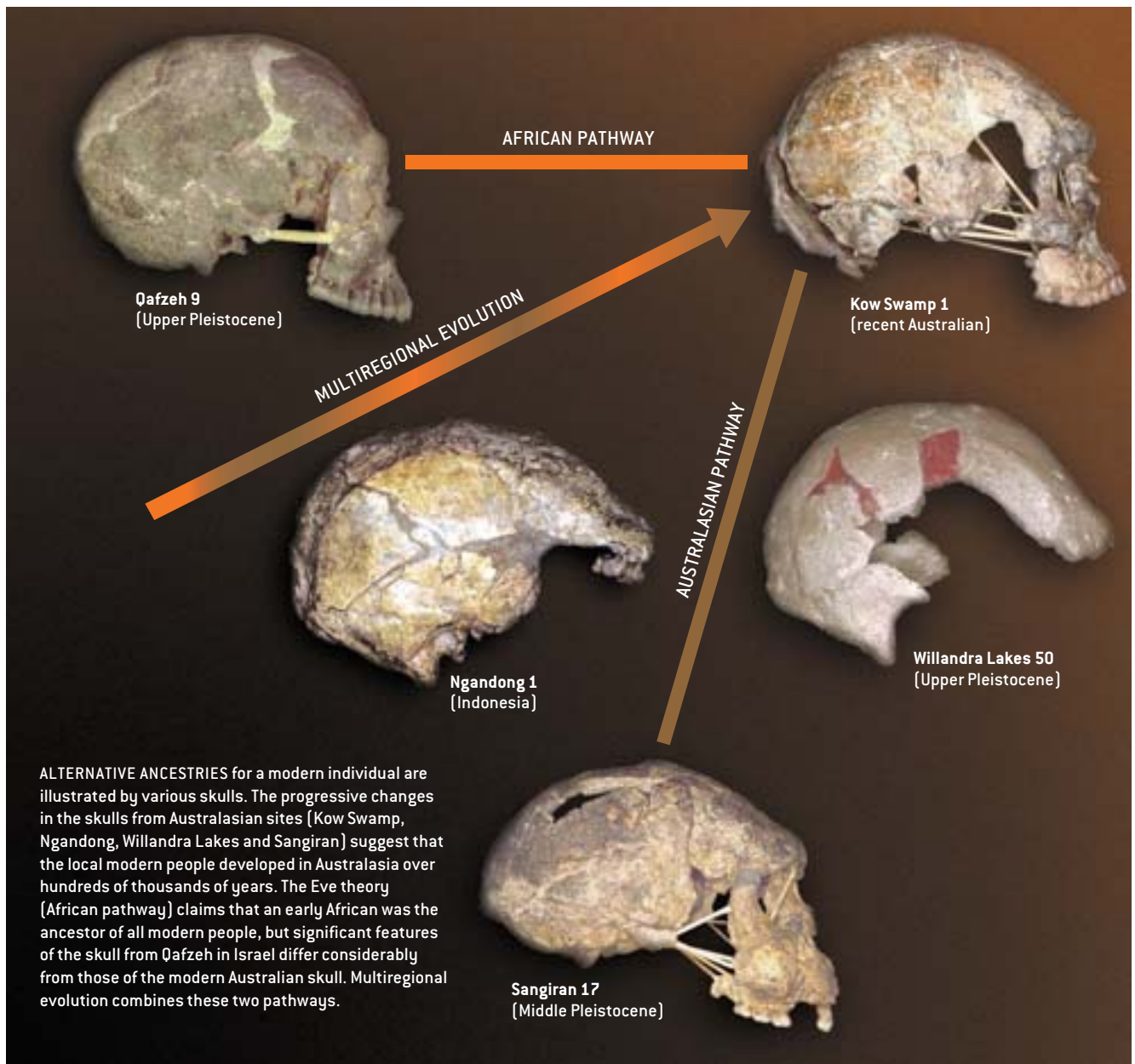
Nevertheless, mitochondrial DNA is not the only source of information we have on the subject. Fossil remains and artifacts also represent a monumental body of evidence—and, we maintain, a considerably more reliable one. The singular importance of the DNA studies is that they show that one of the origin theories discussed by paleontologists must be incorrect.

With Wu Xinzhi of the Institute of Vertebrate Paleontology and Paleoanthropology in Beijing, we developed an explanation for the pattern of human evolution that we described as multiregional evolution. We learned that some of the features that distinguish major human groups, such as Asians, Australian Aborigines and Europeans, evolved over a long period, roughly where these peoples are found today, whereas others spread throughout the human species because they were adaptive.

Multiregional evolution traces all modern populations back to when humans first left Africa almost two million

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**POINT-COUNTERPOINT:** For an opposing view of how humankind arose around the globe, see “The Recent African Genesis of Humans,” on page 54.



years ago, through an interconnected web of ancient lineages in which the genetic contributions to all living peoples varied regionally and temporally. Today distinctive populations maintain their physical differences despite interbreeding and population movements; this situation has existed ever since humans first colonized Europe and Asia. Modern humanity originated within these widespread populations, and the modernization of our ancestors has been an ongoing process.

An alternative theory, developed by paleontologist William W. Howells of

Harvard University as the “Noah’s ark” model, posited that modern people arose recently in a single place and that they subsequently spread around the world, replacing other human groups. That replacement, recent proponents of the theory believe, must have been complete. From their genetic analyses, Allan C. Wilson and his colleagues at the University of California at Berkeley concluded that the evolutionary record of mitochondrial DNA could be traced back to a single female, dubbed “Eve” in one of Wilson’s first publications on the subject, who lived

in Africa approximately 200,000 years ago. Only mitochondrial DNA that can be traced to Eve, these theorists claim, is found among living people.

### Padding in a Pool

HOW COULD THIS BE? If Eve’s descendants mixed with other peoples as their population expanded, we would expect to find other mitochondrial DNA lines present today, especially outside Africa, where Eve’s descendants were invaders. The explanation offered for the current absence of other mitochondrial

**SERIES OF CHINESE SKULLS** shows continuity in form without evidence of a replacement by African characteristics. From left to right, the male skulls are from the Zhoukoudian Lower Cave (Middle Pleistocene period), Dali site (early Upper Pleistocene period) and Zhoukoudian Upper Cave (late Upper Pleistocene).



DNA lineages is that none of the local women mixed with the invading modern men from Africa—which means that Eve founded a new species. Wilson’s reconstruction of the past demands that over a period of no more than 150,000 years there was a complete replacement of all the preexisting hunter-gatherers in Africa and the rest of the then inhabited world; later, the original African features of the invading human species presumably gave way to the modern populational features we see in other regions.

An analogy can highlight the difference between our multiregional evolution theory and Wilson’s Eve theory. According to multiregional evolution, the pattern of modern human origins is like several individuals paddling in separate corners of a pool; over time, they influence one another with the spreading ripples they raise (which are the equivalent of genes flowing between populations). In contrast, the total replacement requirement of the Eve theory dictates that a new swimmer must jump into the pool with such a splash that it drowns all the other swimmers. One of these two views of our origin must be incorrect.

Mitochondrial DNA is useful for guiding the development of theories, but only fossils provide the basis for refuting one idea or the other. At best, the genetic information explains how modern humans might have originated if the assumptions used in interpreting the genes are correct, but those conditions are only hypothetical, and one theory cannot be used to test another. The fossil record is the real evidence for human evolution, and it is rich in both human remains and archaeological sites stretching back for two million years. Unlike the genetic data, fossils can be matched to the predictions of theories about the past without relying on a long list of assumptions.

The Eve theory makes five predictions that the fossil evidence should corroborate. The first and major premise is that modern humans from Africa must have completely replaced all other human

groups. Second, implicit within this idea is that the earliest modern humans appeared in Africa. Third, it also follows that the earliest modern humans in other areas should have African features. Fourth, modern humans and the people that they replaced should never have mixed or interbred. Fifth, outside of Africa an anatomical discontinuity should be evident between the human fossils before and after the replacement.

### No Trace of Invasion

WE ARE SURPRISED by the allegation that beginning about 200,000 years ago one group of hunter-gatherers totally replaced all others worldwide. Although it is not uncommon for one animal species to replace another locally in a fairly short time, the claim that a replacement could occur rapidly in every climate and environment is unprecedented.

We would expect native populations to have an adaptive and demographic advantage over newcomers. Yet according to the Eve theory, it was the newcomers who had the upper hand. To use a modern analogy, however, despite the overwhelming forces of destructive technologies and infectious diseases, most American and Australian indigenous populations and their genes have continued to persist through adaptation and interbreeding.

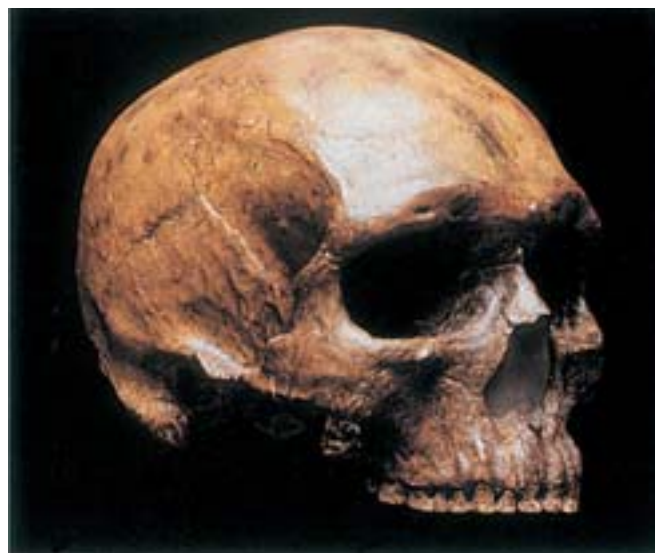
If a worldwide invasion and complete replacement of all native peoples by Eve’s descendants actually took place, we would expect to find at least some archaeological traces of the behaviors that made them successful. Yet examining the archaeology of Asia, we can find none. For instance, whereas the hand ax was a very common artifact in Africa, the technologies of eastern Asia did not include that tool either before or after the Eve period. There is no evi-

dence for the introduction of a novel technology.

Geoffrey G. Pope of William Paterson University has pointed out that six decades of research on the Asian Paleolithic record have failed to unearth any indication of intrusive cultures or technologies. Types of artifacts found in the earliest Asian Paleolithic assemblages continue to appear into the very late Pleistocene. If invading Africans replaced the local Asian populations, they must have adopted the cultures and technologies of the people they replaced and allowed their own to vanish without a trace.

Archaeological evidence for an invasion is also lacking in western Asia, where Christopher B. Stringer of the Natural History Museum in London and a few other researchers believe the earliest modern humans outside of Africa can be found at the Skhūl and Qafzeh sites in Israel. The superb record at Qafzeh shows, however, that these “modern” people had a culture identical to that of their local Neandertal contemporaries: they made the same types of stone tools with the same technologies and at the same frequencies; they had the same stylized burial customs, hunted the same game and even used the same butchering procedures. Moreover, no evidence from the time when Eve’s descendants are supposed to have left Africa suggests that any new African technology emerged or spread to other continents. All in all, as we understand them, the Asian data re-





fute the archaeological predictions implied by the Eve theory.

Perhaps that refutation explains why Wilson turned to a different advantage, asserting that the invasion was successful because Eve's descendants carried a mitochondrial gene that conferred language ability. This proposal is yet to be widely accepted. Not only does it conflict with paleoneurology about the language abilities of archaic humans, but if it were true, it would violate the assumption required of Wilson's clock that mitochondrial mutations are neutral.

The remaining predictions of the Eve theory relate to abrupt anatomical changes and whether the earliest recognizably modern humans resembled earlier regional populations or Africans. With the fossil evidence known at this time, these questions can be resolved in at least two and possibly three regions of the world. The most convincing data are from southern and northern Asia.

The hominid fossils from Australasia (Indonesia, New Guinea and Australia) show an anatomical sequence during the Pleistocene that is uninterrupted by a new African species at any time. The distinguishing features of the earliest of these Javan remains, dated to more than one million years ago, show that they had developed when the region was first inhabited.

Compared with human fossils from other areas, the Javan people have thick skull bones, with strong continuous

browridges forming an almost straight bar of bone across their eye sockets and a second well-developed shelf of bone at the back of the skull for the neck muscles. Above and behind the brows, the forehead is flat and retreating. These early Indonesians also have large projecting faces with massive rounded cheekbones. Their teeth are the largest known in archaic humans from that time.

A series of small but important features can be found on the most complete face and on other facial fragments that are preserved. These include such things as a rolled ridge on the lower edge of the eye sockets, a distinctive ridge on the cheekbone and a nasal floor that blends smoothly into the face.

Most of this unique morphology was retained for at least 700,000 years while other modern characteristics continued to evolve in the Javan people. For example, the large fossil series from Ngandong, which evidence suggests is as old as 200,000 years, offers striking proof that the Javans of that time had brain sizes similar to modern Australian popu-

lations but were otherwise remarkably similar to much earlier individuals in the region.

## Australians and Eve

THE FIRST INHABITANTS of Australia arrived more than 60,000 years ago, and their behavior and anatomy were clearly those of modern human beings. Some of their skeletons show the Javan complex of features, along with further braincase expansions and other modernizations. Several dozen well-preserved fossils from the late Pleistocene and early Holocene demonstrate that the same combination of features that distinguished those Indonesian people from their contemporaries distinguishes some ancestors of indigenous Australians from other living peoples.

If the earliest Australians were all descendants of Africans, as the Eve theory requires, the continuity of fossil features would have to be no more than apparent. All the features of the early Javans would need to have evolved a second time in the population of invaders. The repeated evo-

### THE AUTHORS

ALAN G. THORNE and MILFORD H. WOLPOFF have extensively studied the original fossil material on the origins of *Homo sapiens*. Thorne is adjunct fellow in the department of archaeology and natural history at the Australian National University. He graduated from the University of Sydney in 1963 and later taught human anatomy at the medical school there. Thorne's excavations at Kow Swamp and Lake Mungo produced most of the Pleistocene human remains in Australia. Wolpoff is professor of anthropology at the University of Michigan at Ann Arbor, where he directs the paleoanthropology laboratory. He received his Ph.D. in 1969 from the University of Illinois at Urbana-Champaign. Wolpoff would like to thank lecturer Rachel Caspari of the University of Michigan for her help in drafting the epilogue.

lution of an individual feature would be conceivable but rare; the duplication of an entire set of unrelated features would be unprecedentedly improbable.

Northern Asia also harbors evidence linking its modern and ancient inhabitants. Moreover, because the similarities involve features that are different from those significant in Australasia, they compound the improbability of the Eve theory by requiring that a second complete set of features was duplicated in another population.

The very earliest Chinese fossils, about one million years old, differ from their Javan counterparts in many ways that parallel the differences between north Asians and Australians today. Our research with Wu Xinzhi and independent research by Pope demonstrated that the Chinese fossils are less robust, have smaller and more delicately built flat faces, smaller teeth and rounder foreheads separated from their arched brows. Their noses are less prominent and more flattened at the top. Perhaps the most telling indication of morphological continuity concerns a peculiarity of tooth shapes. Prominently “shoveled” maxillary incisors, which curl inward along their internal edges, are found with unusually high frequency in living east Asians and in all the earlier human remains from that area. Studies by Tracey L. Crummett of San José State University show that the form of

prehistoric and living Asian incisors is unique to the region.

This combination of traits is also exhibited at the Zhoukoudian Cave area in northern China, where fully a quarter of all known human remains from the Middle Pleistocene have been found. As Wu Rukang and Zhang Yinyun of the Chinese Academy of Sciences have pointed out, even within the 150,000 or more years spanned by the Zhoukoudian individuals, evolutionary changes in the modern direction, including increases in brain size and decreases in tooth size, can be seen. Our examinations of the Chinese specimens found no anatomical evidence that typically African features ever replaced those of the ancient Chinese in these regions. Instead there is a smooth transformation of the ancient populations into the living peoples of east Asia and the Americas.

Paleontologists have long thought Europe would be the best source of evidence for the replacement of one group, Neandertals, by more modern humans. Even there, however, the fossil record shows that any influx of new people was neither complete nor without mixture. The most recent known Neandertal skull, from Saint-Césaire in France, apparently had the behavioral characteristics of the people who succeeded the Neandertals in Europe. The earliest post-Neandertal Europeans did not have a pattern of either modern or archaic African features, and

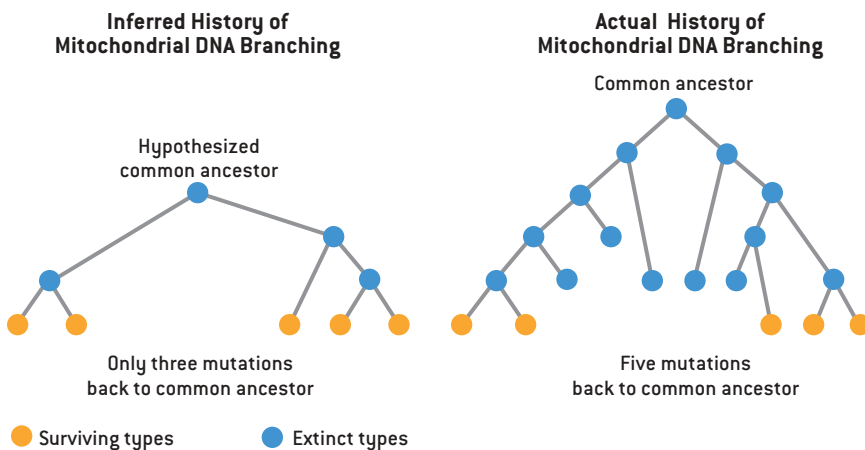
many have been described as mixtures. Clearly, the European Neandertals were not completely replaced by Africans or by people from any other region.

Instead the evidence suggests that Neandertals either evolved into later humans or interbred with them, or both. David W. Frayer of the University of Kansas and Fred H. Smith, now at Loyola University of Chicago, have discovered that many allegedly unique Neandertal features are found in the Europeans who followed the Neandertals—the Upper Paleolithic, Mesolithic and later peoples. In fact, only a few Neandertal features completely disappear from the later European skeletal record.

Features that persist range from highly visible structures, such as the prominent shape and size of the nose of Neandertals and later Europeans, to much more minute traits, such as the form of the back of the skull and the details of its surface. A good example is the shape of the opening in the mandibular nerve canal, a spot on the inside of the lower jaw where dentists often give a pain-blocking injection. The upper part of the opening is covered by a broad bony bridge in many Neandertals, but in others the bridge is absent. In European fossils, 53 percent of the known Neandertals have the bridged form; 44 percent of their earliest Upper Paleolithic successors do, too, but in later Upper Paleolithic, Mesolithic and recent groups, the incidence drops to less than 6 percent.

In contrast, the bridged form is seen rarely in fossil or modern people from Asia and Australia. In Africa the few jaws that date from the suggested Eve period do not have it. This mandibular trait and others like it on the skull and the skeleton must have evolved twice in Europe for the Eve theory to be correct.

In sum, the evolutionary patterns of three different regions—Australasia, China and Europe—show that their earliest modern inhabitants do not have the complex of features that characterize Africans. There is no evidence that Africans completely replaced local groups. Contrary to the Eve theory predictions, the evidence points indisputably toward the continuity of various skeletal features between



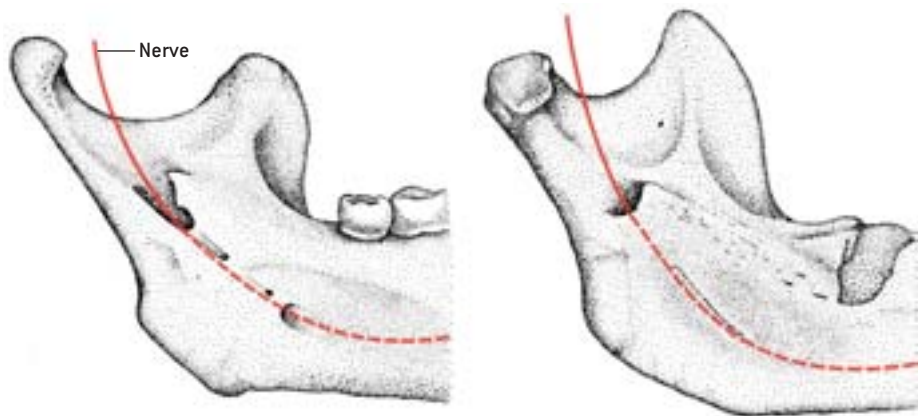
MATERNAL LINEAGE RECONSTRUCTIONS based solely on the mitochondrial DNA types found today are inherently flawed. A hypothetical tree inferred from only five surviving types (left) leaves out the branches and mutational histories of extinct lines (right). Consequently, it sets the date for a common ancestor much too recently by presenting evidence of too few mutations.

the earliest human populations and living peoples in different regions. Like genetic variation, human anatomical variation reflects significant differences in occurrence for characteristics found in all populations.

### Focus on Features

IF AFRICA REALLY WAS the “Garden of Eden” from which all living people emerged, one would expect to find evidence for the transition from archaic to modern forms there—and only there. Following the lead of German researcher Reiner Protsch von Zieten of Goethe University in Frankfurt, Germany, some paleontologists did argue that modern *Homo sapiens* originated in Africa because they believed the earliest modern-looking humans were found there and that modern African features can be seen in these fossils. But the African evidence is similar to other regions in that modern *features* and not modern *populations* appear gradually and at about the same time as they appear elsewhere.

The African record differs from other regions in that the earlier, archaic populations are more variable and have no specifically African features. Modern-appearing humans and technologies first arise during the time between the last two glaciations. The technologies seem regional and impermanent, not continent-wide, but anatomical features are more widespread. We believe the main reason that Africa differs from the rest of the world at this time is that it is much more heavily populated—many, if not most, people lived there—and more population movement is outward than inward. The key specimens addressing modernity span the continent, from Omo Kibish in Ethiopia to Klasies River Mouth Cave in South Africa. The three Omo Kibish crania date roughly to between 100,000 and 200,000 years ago and are similar to other African remains from this time in combining ancient and modern features. Omo 2 is the more archaic, with a lower skull and a much broader and more angled cranial rear, resembling those of Laetoli 18 from Tanzania. Its browridge, however, is smaller than Omo 1’s, which generally appears more



**JAW MORPHOLOGY** distinguishes many Neandertal skeletons. In most living people and in fossils, the rim around the mandibular nerve canal opening is grooved (*left*), but in a number of Neandertals, it was surrounded by a bony bridge (*right*). Some later Europeans also had this Neandertal feature, although it was less common.

modern in its higher skull and more rounded cranial rear. An associated mandible has a definite chin. Like the Levant remains of similar age from Qafzeh and Skhül, even this small Omo sample combines a mix of archaic- and modern-appearing individuals.

The best excavated remains are from Klasies River and are securely dated to between 80,000 and 100,000 years ago. Some of the skull fragments are small and delicate and are said to “prove” that modern humans were present. Yet a comparative analysis of the entire sample by Rachel Caspari of the University of Michigan at Ann Arbor showed that others are not modern-looking at all. Two of the four lower jaws do not have chins, so thorough proof of a modern jaw is lacking. The single cheekbone from the site is not only larger than those of living Africans but also larger and more robust than those of both the earlier transitional humans and the archaic humans found in Africa. The claim that this sample contains modern Africans is highly dubious and does not justify the proposal that the earliest modern humans arose in Africa.

### DNA Reanalyzed

WITH THE DISPROOF of the unique African ancestry theory for the living people of most areas and the lack of evidence showing that modern people first appeared in Africa, we conclude that the predictions of the Eve theory cannot be substantiated. We must wonder why the

analysis of mitochondrial DNA suggested a theory so contrary to the facts. Perhaps the mitochondrial DNA has been misinterpreted.

The basic difficulty with using mitochondrial DNA to interpret recent evolutionary history stems from the very source of its other advantages: in reproduction, the mitochondrial DNA clones itself instead of recombining. Because mitochondrial DNA is transmitted only through the maternal line, the potential for genetic drift—the accidental loss of lines—is great: some mitochondrial DNA disappears every time a generation has no daughters.

The problem is analogous to the way in which family surnames are lost whenever there is a generation without sons. Imagine an immigrant neighborhood in a large city where all the families share a surname. An observer might assume that all these families were descended from a single successful immigrant family that completely replaced its neighbors. An alternative explanation is that many families immigrated to the neighborhood and intermarried; over time, all the surnames but one were randomly eliminated through the occasional appearance of families that had no sons to carry on their names. The surviving family name would have come from a single immigrant, but all the immigrants would have contributed to the genes of the modern population. In the same way, generations without daughters could have extinguished some lines of mitochondrial

DNA from Eve's descendants and her contemporaries.

Any interpretation of the surviving mitochondrial DNA mutations in populations consequently depends on a knowledge of how the size of the populations has changed over time and how many maternal lines may have vanished. Random losses from genetic drift alter a reconstruction of the tree of human mitochondrial DNA branching by pruning off signs of past divergences. Each uncounted branch is a mutation never taken into account when determining how long ago Eve lived.

Changes in population sizes have been dramatic. In parts of the Northern

Hemisphere, some human populations shrank because of climate fluctuations during the ice ages. Archaeological evidence from both Africa and Australia suggests that similar population reductions may have taken place there as well. These reductions could have exacerbated genetic drift and the loss of mitochondrial DNA types.

At the end of the ice ages, along with the first domestication of animals and plants, some populations expanded explosively throughout a wide band of territory from the Mediterranean to the Pacific coast of Asia. Although the number of people expanded, the number of surviving mitochondrial DNA lines

could not—those lost were gone forever.

Human populations with dissimilar demographic histories can therefore be expected to preserve different numbers of mutations since their last common mitochondrial DNA ancestor. They cannot be used together in a model that assumes the lengths of mitochondrial lineages reflect the age of their divergence. One cannot assume that all the variation in a population's mitochondrial DNA stems solely from mutations: the history of the population is also important.

### No Molecular Clock

A MAJOR PROBLEM with the Eve theory, therefore, is that it depends on an accurate molecular clock. Its accuracy must be based on mutation rates at many different loci, or gene positions. Yet genes in the mitochondrial DNA cannot recombine as genes in the nucleus do. All the mitochondrial DNA genes are the equivalent of a single locus. The molecular clock based on mitochondrial DNA is consequently unreliable.

Mitochondrial DNA may not be neutral enough to serve as the basis for a molecular clock, because some data suggest that it plays a role in several diseases. Because of random loss and natural selection, some vertebrate groups have rates of mitochondrial DNA evolution that are dramatically slower than Wilson and his colleagues have claimed for humans. A number of molecular geneticists disagree with Wilson's interpretation of the mitochondrial genetic data.

The molecular clock has, we believe, major problems: its rate of ticking has probably been overestimated in some cases and underestimated in others. Rebecca L. Cann of the University of Hawaii at Manoa and Mark Stoneking of Pennsylvania State University, two of Wilson's students, have acknowledged that their clock was able to date Eve to only between 50,000 and 500,000 years ago. Because of the uncertainty, we believe that for the past half a million years or more of human evolution, for all intents and purposes, there is no molecular clock.

Putting aside the idea of a clock, one can interpret the genetic data in a much more reasonable way: Eve carried the

|                    |        | EUROPE AND LEVANT                                     | AFRICA   | EAST ASIA                                      | AUSTRALASIA                                  |
|--------------------|--------|---|--|--|--|
| UPPER PLEISTOCENE  | LATE   | Lagar Velho<br>Predmostí<br>Mladeč                    | Afalou<br>Lukenyá                                      | Shandong<br>Ziyang<br>Liujiang                 | Kow Swamp<br>Keilor<br>Willandra<br>Lakes 50 |
|                    | MIDDLE | Vindija<br>Kebara<br>La Ferrassie<br>La Chapelle      | Dar es Soltan  | Maba   | Lake Mungo 1, 3                              |
|                    | EARLY  | Qafzeh<br>Krapina                                     | Klasies<br>Omo Kibish                                  | Dingcun<br>Xujiayao                            |  |
| MIDDLE PLEISTOCENE | LATE   | Ehringsdorf<br>Biache<br>Zuttiyeh                     | Ngaloba<br>Florisbad                                   | Dali<br>Jinniushan                             | Sambungmachan<br>1, 3<br>Ngandong            |
|                    | MIDDLE | Sima de los Huesos<br>Petralona<br>Arago<br>Steinheim | Kabwe<br>Ndotu   | Zhoukoudian H<br>Hexian<br>Nanjing             |  |
|                    | EARLY  | Gran Dolina   | Bodo<br>Ternifine<br>Olduvai 12                        | Zhoukoudian<br>D, E, L<br>Chenjiawo<br>Yunxian | Sangiran 2, 10,<br>12, 17<br>Trinil          |
| LOWER PLEISTOCENE  | LATE   |   | Buia, Bouri<br>Olduvai 9                               | Gongwangling<br>Yuanmou                        |  |
|                    | MIDDLE |   | Konso Gardula<br>Lake Turkana<br>(east) 992            |  | Sangiran<br>4, 27, 31                        |
|                    | EARLY  | Dmanisi   | Lake Turkana<br>(east) 730, 3883, 3733<br>(west) 15000 |  | Mojokerto                                    |

WELL-DATED FOSSILS point to the continuous, linked evolution of modern humans at sites around the world. Modern human groups in different regions developed distinct anatomical identities. Nevertheless, gene flow between the groups through interbreeding spread important changes throughout and was sufficient to maintain humans as a single species.



most recent common ancestor of all existing human mitochondria, but she is not the most recent common ancestor of all living people. Mitochondrial history is not population history, just as the history of names mentioned earlier is not the same as the history of populations. Such an interpretation can fully reconcile the fossil record with the genetic data. We propose that future research might more productively focus on attempts to disprove this hypothesis than on attempts to recalibrate a clock that does not work.

The dramatic genetic similarities across the entire human race show the consequences of linkages between people that extend to when our ancestors first populated the Old World. They are the results of an ancient history of population connections and mate exchanges that has characterized the human race since its inception. Human evolution happened everywhere because every area was always part of the whole.

Neither anatomical nor genetic analyses provide a basis for the Eve theory. Instead the fossil record and the interpretation of mitochondrial DNA variation can be synthesized to form a view of human origins that does fit all the currently known data. This synthetic view combines the best sources of evidence about human evolution by making sense of the archaeological and fossil record and the information locked up in the genetic variation of living people all over the world. The richness of human diversity, which contrasts with the closeness of human genetic relationships, is a direct consequence of evolution. We are literally most alike where it matters—under the skin.

## Epilogue

IN THE DECADE since this article originally appeared in *Scientific American*, significant discoveries and analyses have changed the nature of the debate about the pattern of human evolution. The finding of a 25,000-year-old Portuguese child from Lagar Velho who has a combination of Neandertal and “modern European” characteristics suggests that Neandertals mixed with other populations and therefore were the same species. A million-year-old Ethiopian skull found in Bouri that is

similar to Asian *Homo erectus* remains, and is anatomically intermediate between earlier and later Africans, suggests that the evolving *Homo* lineage in the early and middle Pleistocene was a single species, not a mix of different species evolving in different places. Early specimens of “moderns” are also instructive. In the Australian case, significant ancestry in the Ngandong fossils from Indonesia could not be excluded. In the European case, a 50 percent contribution by Neandertals for the earliest moderns could not be excluded. These anatomical studies support the idea of multiregional evolution.

Meanwhile genetic research has become more definitive. The rate of change of mitochondrial DNA (mtDNA) was first estimated over millions of years from comparisons with chimpanzees, but with modern intergenerational studies the rates have been found to be many times as fast. The effects of accidental loss of mtDNA variation were greatly underestimated. Then came the realization that because mtDNA is a single molecule, it cannot recombine or have crossover, so selection on any part of it is selection on the whole. Natural selection has repeatedly reduced its variation; the same has been found in the nonrecombining parts of the nuclear chromosomes. If selection and not population history accounts for mtDNA variation, it does not address the Eve theory.

MtDNA has also been recovered from Neandertals and from ancient Australians, and some of it is unlike the modern form. This evidence addresses the issues of how, and how quickly, mtDNA changes, but it does not help resolve the pattern of evolution. Also less than helpful is the possibility that all the Neandertal mtDNA recovered so far may have been altered by contamination or DNA breakdown. This is suspected because the most recent Neandertal

mtDNA is most like that of living humans, whereas the oldest is least alike—the opposite of what we would expect from unaltered Neandertal mtDNA evolving in a separate genetic line.

More recently, researchers have obtained sequences of nuclear DNA, and they provide a different picture. Most fundamentally, nuclear genes prove to be older than the mitochondrial gene, in some cases by millions of years. If the origin of today’s mtDNA was also the origin of a new species, all the older nuclear variations should have been eliminated, and most genes should be the approximate age of the species or younger. This is the most significant disproof of the Eve theory. Nuclear genes are much older than Eve and preserve evidence of past migrations, mostly out of Africa but also from some other regions, followed by population mixtures that preserve past variation. This genetic evidence significantly supports multiregional evolution.

A greater focus on epistemology also has made it clear that the original debate over modern human origin was indeed a debate about the *pattern* of human evolution. The multiregional model is an intraspecific, network model, fundamentally different from the tree-based Eve theory. This was important because an assumption that tree (branching) attributes describe population histories underlies the acceptance of gene trees as population trees. The increasing molecular and anatomical evidence against recent speciation underscores the appropriateness of such a network model. Molecular and anatomical variation reflect something different than the time since the separation of populations. They include the complexities of gene flow between groups, different histories of selection, and different population structures across space and over time. SA

### MORE TO EXPLORE

**Race and Human Evolution.** Milford Wolpoff and Rachel Caspari. Simon & Schuster, 1997.

**Modern Human Ancestry at the Peripheries: A Test of the Replacement Theory.** Milford H. Wolpoff, John Hawks, David W. Frayer and Keith Huntley in *Science*, Vol. 291, pages 293–297; 2001.

**Mitochondrial DNA Sequences in Ancient Australians: Implications for Modern Human Origins.** Gregory J. Adcock et al. in *Proceedings of the National Academy of Sciences USA*, Vol. 98, No. 2, pages 537–542; January 16, 2001.

**Number of Ancestral Human Species: A Molecular Perspective.** D. Curnoe and A. Thorne in *Homo: Journal of Comparative Human Biology*, Vol. 53, Issue 3, pages 201–224; March 2003.