# The Multiregional Evolution of Humans

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# The Multiregional Evolution of Humans

*Both fossil and genetic evidence argues that various human groups arose where they are found today*

by Alan G. Thorne and Milford H. Wolpoff

Two decades ago paleoanthropologists were 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.

Today the paleoanthropological community is 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—humans originated in Africa and then slowly developed their modern forms in every area of the Old World. On the other side are workers who claim that Africa alone gave birth to 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 anatomic 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 human races.

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 much more reliable one. The singular importance of the mitochondrial DNA studies is that they show 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.

Multiregional evolution traces all modern populations back to when humans first left Africa at least a million 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 was an ongoing process.

An alternative theory, developed by the 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, the late 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 his first publications on the issue, 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.

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 most credible explanation for the current absence of other mitochondrial 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 racial 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; although they maintain their individuality 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.

ALAN G. THORNE and MILFORD H. WOLPOFF have extensively studied the original fossil material on the origins of *Homo sapiens*. Thorne is head of the department of prehistory in the Institute of Advanced Studies at the Australian National University. He graduated in anthropology and zoology 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. Among his documentaries is the television series *Man on the Rim*. 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 has written widely on paleoanthropology, including an introductory textbook.

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 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 a 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 power of a theory is measured by how much it can explain; the scientific method requires that we try to incorporate all sources of data in an explanatory theory. Our goal is to describe a theory that synthesizes everything known about modern human fossils, archaeology and genes. The Eve theory cannot do so.

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 they replaced should never have mixed or interbred. Fifth, an anatomic discontinuity should be evident between the human fossils before and after the replacement.

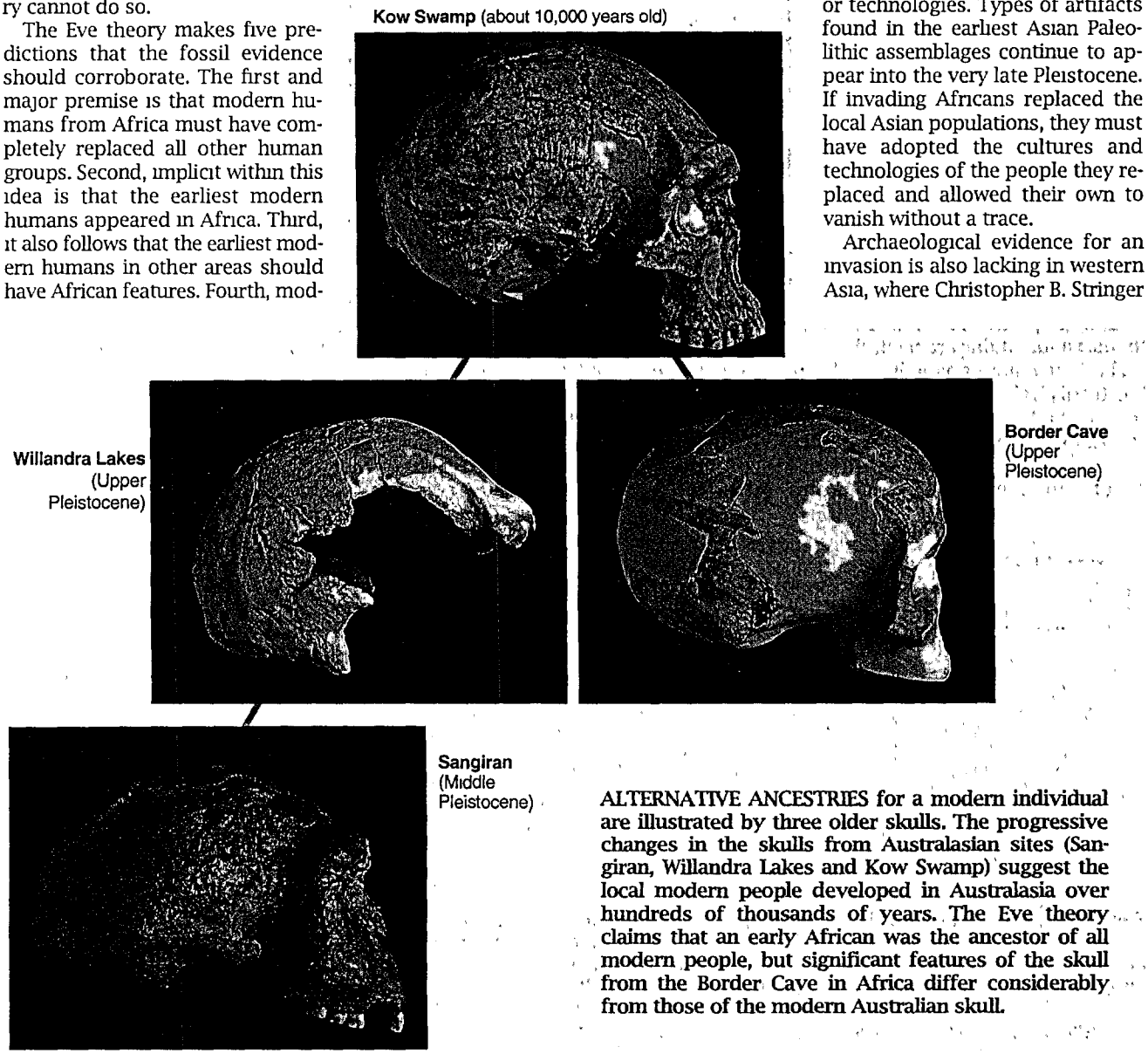
We are troubled by the allegations that beginning about 200,000 years ago one group of hunter-gatherers totally replaced all others worldwide. Although it is not uncommon for one animal species to replace another locally in a fairly short time, the claim that a replacement could occur rapidly in every 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. How much of an advantage is necessary for replacement can be measured by the survival of many hunter-gatherer groups in Australia and the Americas; they have persisted despite invasions by Europeans, who during the past 500 years arrived in large numbers with vastly more complex and destructive technologies.

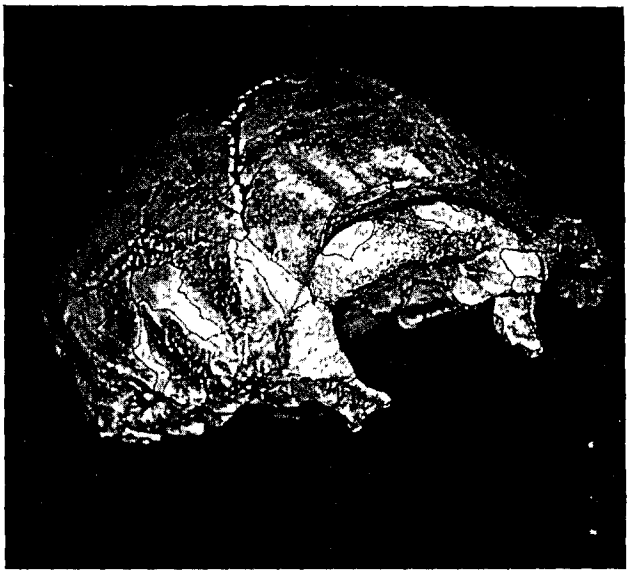
If a worldwide invasion and complete replacement of all native peoples by Eve's descendants actually took place, we would expect to find at least some archaeological traces of the behaviors that made them successful. Yet examining the archaeology of Asia, we can find none. For instance, whereas the hand 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 evidence for the introduction of a novel technology.

Geoffrey G. Pope of the University of Illinois 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




**ALTERNATIVE ANCESTRIES for a modern individual are illustrated by three older skulls. The progressive changes in the skulls from Australasian sites (Sangiran, Willandra Lakes and Kow Swamp) suggest the local modern people developed in Australasia over hundreds of thousands of years. The Eve theory claims that an early African was the ancestor of all modern people, but significant features of the skull from the Border Cave in Africa differ considerably from those of the modern Australian skull.**



SERIES OF CHINESE SKULLS shows continuity in form without evidence of an influx of 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).

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 Neanderthal 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 refute 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 of Wilson's clock that mitochondrial mutations are neutral.

The remaining predictions of the Eve theory relate to abrupt anatomic 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 unambiguously 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 a continuous anatomic sequence during the Pleistocene that is uninterrupted by African migrants at any time. The distinguishing features of the earliest of these Javan remains, dated to about one million years ago, show 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.

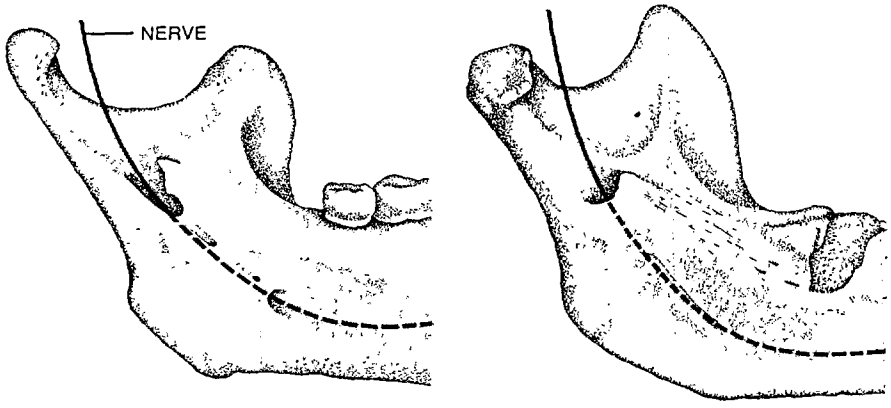
A series of small but important features can be found on the most complete face and on other facial fragments that are preserved. These include such things as a rolled ridge on the lower edge of the eye sockets, a distinctive ridge on the cheekbone and a nasal floor that blends smoothly into the face.

This unique morphology was stable 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 recent evidence suggests may be about 100,000 years old, offers striking proof that the Javans of that time had brain sizes in the modern range but were otherwise remarkably similar to much earlier individuals in the region.

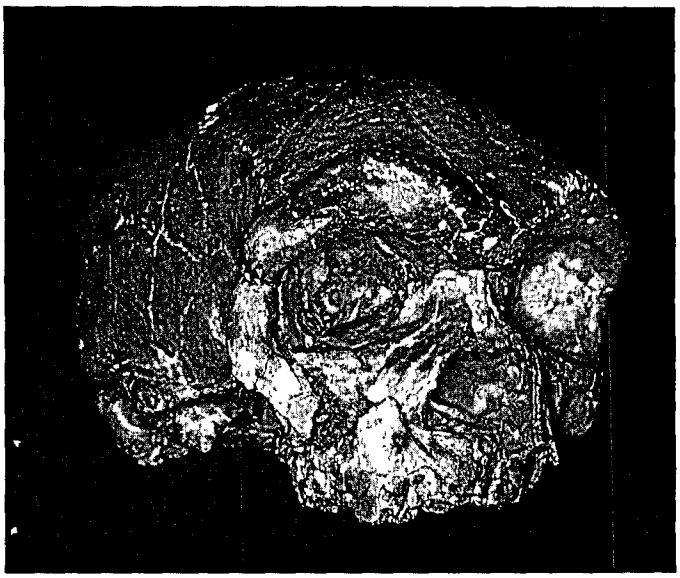
The first inhabitants of Australia arrived more than 60,000 years ago, and their behavior and anatomy were clearly those of modern human beings. Their skeletons show the Javan complex of features, along with further braincase expansions and other modernizations. Several dozen well-preserved fossils from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

If the earliest Australians were 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 evolution 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 different from those significant in Australasia, they compound the improbability of the Eve




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



theory by requiring that a second complete set of features was duplicated in a different 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 browridges 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 the University of Michigan show that the form of prehistoric and living Asian incisors is unique.

This combination of traits is also exhibited at the Zhoukoudian cave area in northern China, where fully a third of all known human remains from the Middle Pleistocene have been found. As Wu Rukang of the Chinese Academy of Sciences has 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, can be seen Our examinations of the Chinese specimens found no anatomic 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.

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

Instead the evidence suggests that Neanderthals either evolved into later humans or interbred with them, or both. David W. Frayer of the University of Kansas and Fred H. Smith of Northern Illinois University have discovered that many allegedly unique Neanderthal features are found in the Europeans who followed the Neanderthals—the Upper Paleolithic, Mesolithic and later peoples. In fact, only a few Neanderthal 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 Neanderthals 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 Neanderthals, but in others the bridge is absent. In European fossils, 53 percent of the known Neanderthals 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 only 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 a number of others like it on the skull and the rest of the skeleton must have evolved twice in Europe for the Eve theory to be correct.

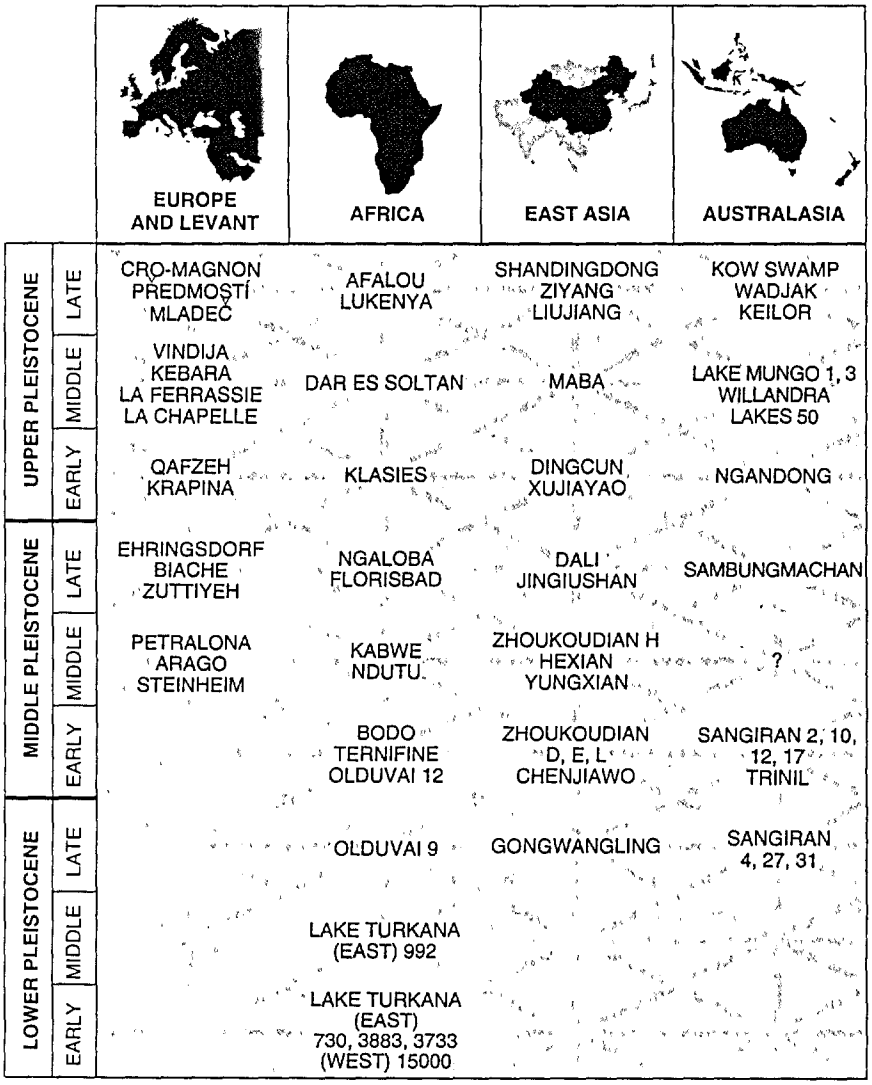
In sum, the evolutionary patterns of three different regions—Australasia, China and Europe—show that their earliest modern inhabitants do not have the complex of features that characterize Africans. There is no evidence that Africans completely replaced local groups. Contrary to the Eve theory predictions,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

If Africa really were 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 the German worker Reiner Protsch of Goethe University in Frankfurt, 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 racial features can be seen in these fossils. But the African evidence is sparse, fragmentary and for the most part poorly dated; it includes materials that do not seem to fit the Eve theory.

Early human remains from Africa, such as the Kabwe skull from Zambia, are extremely rare and are presumed to be at least 150,000 years old. Later transitional fossils from Morocco, Ethiopia, Kenya and South Africa confirm the expectation that local modernization occurred in Africa, as it did everywhere else. No pattern in the fossils, however, indicates the previous emergence of skeletal features that uniquely characterize modern humans generally or even modern Africans in particular.

The evidence for a great antiquity of modern-looking people is based primarily on the interpretation of bones from three sites: the Omo site in Ethiopia and the Klasies River and Border Cave sites in South Africa. Some of the Omo and Border Cave individuals resemble modern humans, but all the remains are fragmentary. Most of the Omo remains were found on the surface, not in datable strata. The estimate of their age, which is based on inappropriate dating techniques, is widely considered to be unreliable. Some of the Border Cave bones, including the most complete cranium, were dug out by local workmen looking for fertilizer and are of unknown antiquity. Other human bones found at a 90,000-year-old level are chemically different from animal bones found there. They may actually be more recent burials dug into the cave.

The best excavated remains are from the Klasies River Mouth Cave 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 Albion College 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.




**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 anatomic identities. Nevertheless, gene flow between the groups through interbreeding was sufficient to maintain humans as a single species.**

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 fails to have 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 (just as Eve's descendants are supposed to have replaced all other humans). 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.

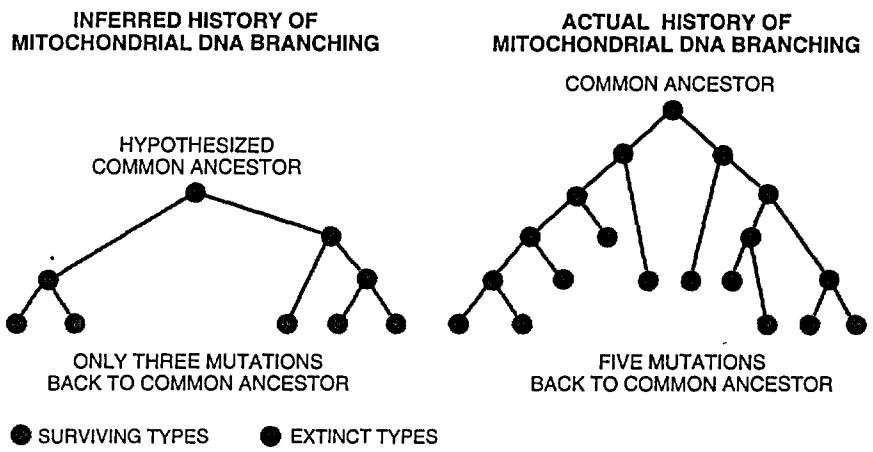
Changes in population sizes have been dramatic. In parts of the Northern Hemisphere, some human populations shrank because of climate fluctuations during the Ice Ages. Archaeological evidence from both Africa and Australia suggests that similar population reductions may have taken place there as well. 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, as Wilson does, that all the variation in a population's mitochondrial DNA stems solely from mutations: the history of the population is also important.

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 —cichlid fish in Lake Victoria in Africa, American eels, hardhead catfish and redwing blackbirds, for example—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.




**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 molecular clock of Wilson and his colleagues 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, admitted recently that their clock was able to date Eve only to 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, the ultimate mitochondrial ancestor of all living humans, lived before the first human migrations from Africa at least one million years ago. The spread of mitochondria would then mark the migration of some early human ancestors into Eurasia when it contained no other hominids. 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 clearly does not work.

The dramatic genetic similarities across the entire human race do not reflect a recent common ancestry for all living people. They show the consequences of linkages between people that extend to when our ancestors first populated the Old World, more than a million years ago. 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 anatomic 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.


FURTHER READING

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