The case against Eve.

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FOR much of this century anthropologists have been locked in debate over one of evolution's best kept secrets: where exactly did modern humans, Homo sapiens, originate? Until recently the argument centred almost exclusively on evidence from fossils. But in the mid-1980s molecular biologists entered the fray, brandishing new evidence from human genetics. The result? The publication in 1987 of what, on the face of it, seemed like a fantastic claim: that all family trees lead back to a single African woman. "Eve", as she became known, was suddenly a newspaper celebrity.

Since then Eve may have slipped from the headlines but she continues to enthral anthropologists. Her name has become inextricably linked with the most controversial theory about human origins ever proposed. This theory, the brainchild of Allan Wilson, a biochemist at the University of California at Berkeley, holds that modern humans are a completely new species that arose in Africa, and Africa alone, between 100 000 and 200 000 years ago. By implication, the descendants of Eve must have spread out from Africa, replacing ancient, indigenous humans all around the world--probably in an abrupt and violent manner. Wilson and other supporters of Eve maintain that this single, all-embracing takeover has left its mark on our DNA (see Box 1).

Four years on, anthropologists remain divided over the theory. Some consider a migration of conquering humans from Africa to be at odds with the fossil record. They feel that the evidence of "molecular anthropology", as the genetic approach is dubbed, has been wrongly interpreted, and argue that fossils are a better guide to human evolution than DNA.

So who is right? Did Eve really exist, or is she an illusion, the result of reading too much into genes perhaps? For the past 12 years we have been working on the problem of human origins with colleagues in the United States, Australia and China. Recently we have uncovered new fossil evidence which challenges the existence of Eve. We have discovered some important similarities between the skulls of ancient humans and their modern counterparts, similarities that are hard to square with a theory based on African migration and mass replacement. We back a completely different theory: that Homo sapiens evolved from ancient humans gradually in many parts of the world.

Before the advent of the "Eve" hypothesis, there were two general schools of thought about about human origins. One was that modern humans evolved in many different parts of the world at different times; the other that they evolved in just one place and then spread out, mixing with indigenous archaic populations. There was no consensus on the place of origin, however: some anthropologists favoured Africa, others Asia, and still others Europe. What made the Eve theory revolutionary was not so much the idea of a single place of origin, but that modern humans (wherever they evolved) replaced, rather than mixed with, indigenous archaic humans.

Although some of Eve's supporters cite evidence from the fossil record, the impetus for the theory comes from studies of the DNA inside present-day human mitochondria, the tiny structures that provde cells with energy ("The Asian Connection", New Scientist, 17 November 1990 and "All about Eve", New Scientist 14 May 1987). Like other brands of DNA, mitochondrial DNA is made up of a series of nucleotides arranged in a certain sequence. As human populations have split and gone their separate evolutionary ways, their mitochondria have acquired distinctive DNA sequences.

Woman at the end of the line

By studying mitochondrial DNA from around the world, Wilson and his colleagues constructed an evolutionary tree for the human species. The tree uses the variations that exist in the mitochondrial DNA sequences of different human populations as a measure of "evolutionary distance". As people inherit their mitochondria solely from their mothers--via the cytoplasm of the egg--the evolutionary tree depicts only the female line. Wilson's team contend that this line can be traced back to a single woman, the putative Eve.

The Eve theory makes a number of predictions, which biologists can test by consulting the fossil record. According to the theory, Eve must have lived in Africa at the beginning of the Upper Pleistocene, between 100 000 and 200 000 years ago. If all modern humans stem from her offspring, then they should carry clear signs of their pedigree. The population of a given area should resemble archaic African stock rather than the people who lived in the area prior to Eve's day. Crucially, there should be no continuity over time in the anatomical characteristics of humans living in any one region. By stark contrast, if modern people evolved locally in many different places, then each population ought to resemble its own antecedents. In this case regional continuity in the features of human fossils should be the norm.

Our research, with James Spuhler of the Los Alamos Radiation Laboratory, Fred Smith of Northern Illinois



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University, Geoffrey Pope of the University of Illinois and David Frayer of the University of Kansas, supports the second pattern. Using six measurements that reflect the shape of the skull, we compared living people from different regions with two sets of fossils: archaic African specimens and local fossils from each region. The African specimens came from Broken Hill, a famous site in Zambia that was first excavated in 1921.

In conflict with the Eve theory, our measurements show that modern Chinese, Australasians and Europeans each resemble their local predecessors much more than they resemble archaic Africans. But that is not all. In each region of the world, we have uncovered links that tie living populations to their own local antecedents, whose remains are preserved in the fossil record for the area. The most convincing evidence comes from Asia.

For example, the fossils of Indonesia can be arranged in an anatomical sequence which shows no signs of interruption by African migrants at any time. The sequence starts around one million years ago, with the remains of Java Man--a representative of the hominid species Homo erectus discovered in 1891--and ends with the remains of Australians dated at around 10 000 years ago. Java Man bears certain distinguishing features, notably a robust cranium and a distinctively shaped face. Compared with Homo erectus from elsewhere, the Javan skulls have thick bone, pronounced ridges above the eyes and a well-developed shelf of bone at the back of the skull for anchoring the neck muscles.

These early Indonesians have large projecting faces, with massive rounded cheek bones and large teeth. The face bears a number of small but important features: a "rolled edge" on the lower margin of the eye socket, a distinctive ridge on the cheek bone and a nasal floor that "flows out" smoothly onto the face. These and other traits combine to create a special Indonesian variation on the Homo erectus theme.

The next set of fossils in the sequence come from Ngandong in Java and are dated at around 100 000 years ago. These skulls carry the same special combination of features, although they have bigger brains. Our research also shows that these hominids were not confined to Java, but probably migrated to Australia. For the earliest known Australian hominids, which are less than 50 000 years old, share the Javan features, along with even larger brains and other signs of modernisation.

Some anthropologists question the significance of the Indonesian sequence, saying it is based on too little fossil information to be reliable and that it is unclear whether the Australian fossils represent one or more populations. Yet no other ancient population has the special combination of features found in the Indonesians and Australians. And if Africans rather than Indonesians were the ancestors of Australian people, why do neither modern Australians nor their ancestors have African features? In reality, the traits distinguishing modern Australoids from other living human populations are precisely those that distinguish their regional predecessors from their own contemporaries in East Asia, Africa and Europe. Such continuity would be impossible if the modern populations were invaders descended from a species of Africans with another set of regional features.

The fossils of northern Asia tell a similar story, but with a different set of distinctive features. The very earliest Chinese fossils, which are at least 750 000 years old, differ from their Javan counterparts in ways that parallel the differences between northern and southern Asians today. These folk tend to have smaller faces and teeth, flatter cheeks and rounder foreheads. Their noses are less prominent and are flattened at the top.

The combination is also evident in fossils from the Zhoukoudian Cave, the site where the celebrated Peking Man was discovered. Researchers have uncovered specimens there with large brain and other features confirming that the ancient population of China was evolving in a modern direction. Again, various details, such as the shape and orientation of the lower border of the cheek bone, link these fossils with the modern people of the region.

In the early 1980s, two particularly important Chinese skulls came to light in Dali and Jinnui Shan. Even though they date from about 200 000 years ago--the beginning of Eve's era--their features are consistent with regional modernisation rather than mass replacement by invading Africans. Later Chinese fossils also point to a smooth transition from ancient to modern forms.

In Europe, long thought to be the best source of evidence for replacement, the fossil record offers equally little comfort to Eve's supporters. The evidence points to much mixing between the invaders and the native Neanderthals. According to our own analysis, many features once thought unique to Neanderthals lingered on among later Europeans. Only a few Neanderthal features disappear completely from the fossil record with the demise of the group as a whole.

These persistent features range from highly visible traits, such as the shape and size of the nose, to tiny details on the skull. A good example from the second group is the shape of the opening to the mandibular nerve canal, a spot on the inside of the lower jaw where dentists give



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pain-blocking injections. The shape of the opening varied among the Neanderthals. Some individuals, 53 per cent in Europe, had the opening partially covered by a broad, bony bridge. The bridge was still common in later populations: for instance, 44 per cent of the more modern people of the early Upper Palaeolithic had it, although later on its incidence dropped to below 6 per cent.

This tiny structure is far more important than its size suggests. It is rare in both fossils and modern people from Asia and Australia, and absent from the few African jaws that date from Eve's day. The implications are clear. If Eve's descendants replaced earlier humans in Europe, then the trait must have evolved twice--once among Neanderthals and then again in the European branch of Eve's family tree. A less tortuous explanation is that the Neanderthals bred with other forms and so made a genetic contribution to later European populations. This of course runs counter to the Eve theory.

Evidence from Africa also casts doubt on the theory. Researchers who see Africa as the Garden of Eden for all living people argue that it is the only place where evidence of a transition from archaic to modern humans can be found. They maintain that the earliest modern-looking humans are African. Yet the African fossil evidence is sparse, fragmentary and for the most part poorly dated. It also contains materials that are hard to square with the theory of an African Eve.

The most significant of these African fossils come from three sites: Omo in Ethiopia, and Klasies River and border Cave, both of which are in South Africa and attracted widespread attention only in the 1980s. Some of the individuals at Omo and Border Cave resemble modern humans. They have high rounded cranial vaults, with small brow ridges and steep foreheads. The facial fragments also have a modern look. Yet both sites pose problems for supporters of Eve.

The Omo remains were found on the surface. Their age of 130 000 years is based on a technique that is widely considered unreliable. Some of the bones at Border Cave, including the distinctive cranium, were dug out by workmen looking for fertiliser and their age is unknown. And others, found at a level corresponding to 90 000 years ago, may have been buried there in more recent times; the original excavation was not performed with enough care for researchers now to be able to date the remains with confidence.

The best excavated remains are from Klasies River. Their age of between 80 000 and 100 000 years is not in dispute, yet their true significance is difficult to gauge. Some of the skull fragments are small and delicate but

others do not look at all modern. The single cheekbone from the site is not only larger that those of living Africans, but larger and more robust than those of archaic African forms. The claim that this sample is modern African is highly dubious.

Not so modern Eve?

If the analysis of mitochondrial DNA has produced a theory that jars with the fossil record, has the testimony of mitochondria been misinterpreted? Proponents of the Eve theory argue that the mitochondrial DNA of non-African people shows no signs of local ancestry, only the telltale signs of Eve and her descendants. They interpret this as the result of replacement of those ancient populations by Eve's descendants. But we believe this evidence could also reflect the very first expansions of humankind (archaic rather than modern) from Africa, over a million years ago. It all depends on the date calculated for Eve, and for this we must rely on DNA, whose reliability as a molecular clock has yet to be proven.

Also, any attempt to base a genealogy on mitochondria runs into a fundamental problem: mitochondria are inherited only through the female line, so if a woman has no daughters, her mitochondria are at an evolutionary dead end. Consider the following analogy. Imagine trying to reconstruct family histories in a population whose women take their husband's name when they marry. (Families without sons are now the losers, but the principle is the same.) If anthropologists encountered a migrant neighbourhood in a large city and found that many of the families shared just a few surnames, they might assume that a small number of highly successful families had replaced their less successful neighbours. But another explanation is that many families came to the city and mixed with their neighbours, and that over the years, names were increasingly lost to families who had only daughters--until just a few names were left. Those names can be traced back to just a few of the founding families, but each individual carries a selection of genes from many families.

So, even taking the mitochondrial sequences at face value, we may be seeing only a part of the picture. The mitochondrial DNA of living humans could easily reflect an unknown (and unknowable) number of losses in lineages without daughters, rather than a process of replacement without mixing. On top of that, however, we dispute even the basic notion that all of today's mitochondrial sequences lead back to one person in one African population. Our own DNA analyses reveal sequence variations among 10 non-African populations which cannot be explained in this way. The variations indicate that the populations are at least 100 000 years old, stretching back

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to the time of Eve or perhaps even earlier. This seriously undermines the idea of mass replacement, the linchpin of the Eve theory.

So, if not in Africa, where did we originate? The fossils point to several places rather than just one. The era of the modern human began with a smooth transition rather than an abrupt invasion. Humans may be unique, but the signs are that we are not a new species.

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