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Recent advances in the study of human origins have increased our understanding of our ancestors. There have been new, major fossil finds. WT 17000, a 2.5 million-year-old robust *Australopithecus* found in Kenya (Walker et al. 1986), led to a revision of early hominid phylogeny (Delson 1986; 1987). Existing fossil materials have been reassessed. For example, Tattersall (1986) maintains that at least two unrecognized hominid species (*Homo neanderthalensis, H. heidelbergensis* and possibly *H. steinheimensis*) existed between the times of *H. erectus* and fully modern *H. sapiens*.

An exciting development is the application of molecular techniques to the study of human evolution. Molecular biology and evolutionary biology are drawing from and contributing to each other to their mutual benefit. An important, but controversial, result is the assertion by Cann et al. (1987) that some 200,000 years ago an "Eve" existed—one woman from whom all humanity descended.

Cann et al. (1987) also claim the woman probably lived in Africa, thus supporting a single point of origin for modern *H. sapiens* as opposed to several pre-*H. sapiens* populations evolving simultaneously into *H. sapiens*. This claim implies, for example, that modern Chinese did not evolve from Chinese *H. erectus* ("Peking Man"). Instead, the Chinese—like all human groups—originated rather recently in Africa.

The precise claim is that we can all trace the ancestry of our mitochondrial DNA (mtDNA) back to a single woman, a "mitochondrial DNA Eve," who lived in Africa between 140,000 and 290,000 years ago. The specific date depends upon the speed of mtDNA evolution (Cann et al. 1987).

Mitochondrial DNA

Most of our DNA is carried in the nucleus, but mitochondria (and the chloroplasts of plants) contain genes necessary for their functioning. Mitochondrial DNA and chloroplast DNA exist because both organelles are apparently descended from procaryotic organisms which became symbiotic within a proto-eucaryotic cell some 1 to 2 billion years ago (Margulis 1982). These organelles possess their own ribosomes and, in some cases, mitochondria have minor genetic code differences (Grivell 1986).

Mitochondrial DNA is often studied for evolutionary relationships among living organisms because it is a small molecule (15,000 to 18,000 base pairs long) and easily isolated (Avise et al. 1979). Isolated mtDNA is cut into fragments by restriction enzymes which cleave at specific DNA base sequences, called restriction sites (Figure 1). Different restriction enzymes recognize different restriction sites. The lengths of the resultant fragments can be determined by electrophoresis.

A mutation at a restriction site changes that sequence so it will no longer be recognized by the restriction enzyme (a previously unrecognized site may also mutate to a recognized site). Cutting will result in a long piece of DNA instead of two short pieces (or vice versa) (Figure 1). By using a series of different restriction enzymes, many mutated sites can be identified, giving an estimate of the total number of mutations that occurred at these sites since the species (or groups) diverged.

Evolutionary Information from Mitochondrial DNA

Mitochondrial DNA differences between groups (or differences in other macromolecules such as proteins or nuclear DNA) are used in two related ways: to make inferences regarding the relatedness of groups of organisms (to infer the branching pattern of the phylogenetic tree) and to estimate when the branchings occurred. Except for detailed and costly

DNA sequencing, restriction enzymes provide the only method sufficiently sensitive to study the relationships between populations of the same species (Avise et al. 1979). Mitochondrial DNA is particularly useful, since it evolves in animals 5 to 10 times faster than nuclear DNA (Brown et al. 1979).

An underlying assumption of the technique is that restriction site changes occur at a constant rate. The rate need not be metronomic like a clock but can be stochastically constant like radioactive decay. Constancy would result if the changes were neutral, i.e., if the original mtDNA molecule and the new mutant form were equally useful to the organism (were selectively equivalent).

Should the changes be neutral, the rate of change would be proportional to the mutation rate. Assuming a constant mutation rate gives a constant rate of change. Consequently, the more differences there are between groups, the more distant their relationship.

Calibrating this rate of change allows development of a molecular clock by which unknown divergence times can be estimated. Calibration is achieved by comparing the differences between two living groups and the estimated time of their divergence, as derived from the fossil record. The calibration step is critical: if the calibration is incorrect then all divergence times derived from the calibration will be incorrect.

It is possible for molecular evolution to have occurred at a constant rate even if the changes were not neutral, provided selection coefficients averaged out over numerous generations (Lewontin 1974). Here, the molecular information would be useful to make inferences over long periods of time, but not for a short period when an average is inaccurate.

The analysis of human mtDNA genotypes (Whittam et al. 1986) shows much of the diversity (71 percent) to be consistent with neutrality, with some inconsistencies implicating selection. In contrast, Latorre et al. (1986) argue no clear evidence exists that mtDNA evolves like a molecular clock. The accuracy of many mtDNA study conclusions rests on the validity of the assumption of a constant rate of mtDNA evolution.

Until recently molecular dating and the construction of phylogenies were based primarily upon proteins and nuclear DNA. The mtDNA work has largely been similar to nuclear DNA work although the two DNA's are inherited very differently; mtDNA, unlike nuclear DNA, is inherited maternally.

Maternal Inheritance of Mitochondrial DNA

In higher animals, both males and females receive all their mitochondria from their mother and essentially none from their father (Avise & Lansman 1983) (Figure 2). Only the sperm head containing the nucleus enters the egg during fertilization; the sperm neck, containing the mitochondria, does not.

A mother's entire mtDNA genome is passed to her offspring. In contrast, nuclear genes are inherited equally from both parents, and offspring receive half of each parent's genes. Consequently, mtDNA is in-

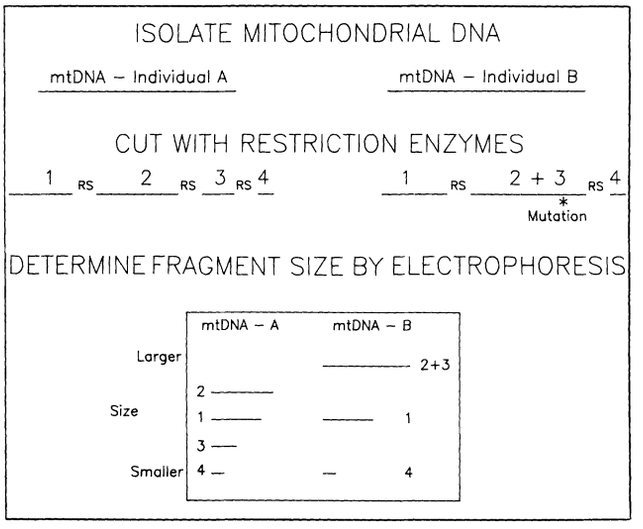

Figure 1. Restriction site analysis. A small portion of the circular mtDNA molecule is shown. Individuals A and B differ by a mutation at the central restriction site (RS). This difference and the sizes of the fragments are determined by electrophoresis. The size of fragment 2 + 3 (individual B) is equal to the sum of the sizes of fragments 2 and 3 (individual A).

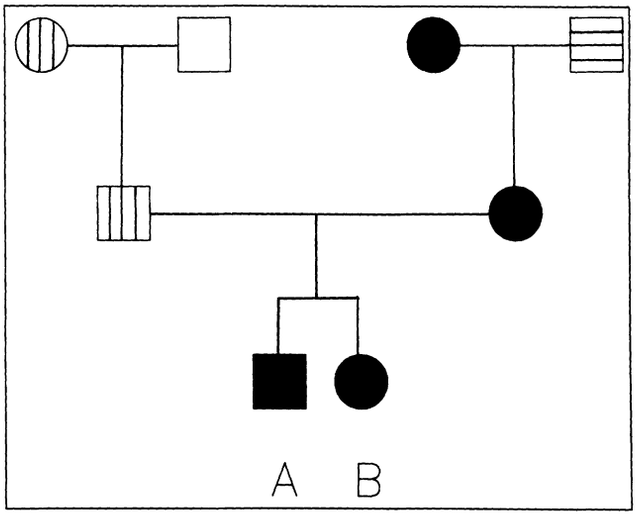

Figure 2. Nuclear DNA and mitochondrial DNA inheritance patterns. Circles indicate females and squares males. Different shadings indicate different mtDNA genotypes. Individuals A and B received all their mtDNA from a single grandparent but received nuclear DNA from all four grandparents. "A" cannot pass his mtDNA genotype to his children; all of "B" 's children will have her mtDNA genotype.

herited clonally and, unlike nuclear genes, the evolutionary history of a particular mtDNA genotype is not obscured by recombination with mtDNA from the other parent. Our mtDNA came from our maternal grandmother, while all four grandparents contributed equally to our nuclear gene complement (Figure 2). An analogous situation is the paternal inheritance of male surnames in societies in which a wife takes her husband's last name. All children will have the surname of their paternal grandfather, but all four grandparents will have contributed equally to the grandchildren's nuclear genomes.

Tracing our heritage back for generations makes it clear that we have received nuclear genetic material from an extremely large number of individuals. Going back 20 generations yields approximately a million ancestors (2^{20}); for 100 generations the number approaches 10^{30} individuals. Clearly these numbers are overestimates; they quickly become much larger than any possible human population size. The overestimate is due to many of the "different" individuals being the same people. We are all somewhat inbred.

The contrast between nuclear and mitochondrial DNA inheritance is emphasized by these calculations. Assuming a generation time of 25 years for humans, 8,000 generations have passed since "Eve" was hypothesized to have existed. While we have received nuclear genetic material from numerous individuals since then, we each have received our mtDNA (altered by mutation) from a single ancestral woman who lived at that time. That woman would have contributed little to our nuclear genome (Wainscoat 1987); she contributed everything to our mtDNA genome.

The assertion of a "mtDNA Eve" is that this single ancestral woman is the same woman for all of us. In light of the differences between the inheritance of mtDNA and nuclear DNA outlined above, this is clearly quite different from the assertion that we have all descended from a single woman who was the only woman that existed at that time, from a true Eve.

"Eve"

Cann and coworkers (1987) examined the mtDNA of 147 people from five geographic populations. They reached two major conclusions. First, all mtDNA genotypes could be traced back to a single, ancestral, mtDNA genotype ("Eve") and second, this woman lived in Africa about 200,000 years ago. The second conclusion is quite profound and implies that all humans have a very recent, common ancestry. As Stephen Gould (1984: 26) succinctly concludes from other data, "human equality is a contingent fact of history."

That all mtDNA lineages appear to converge to a single point does not necessarily imply that this point was a single female ("Eve"). If there were little mtDNA diversity in early human populations, many women (many "Eves") could have had the same mtDNA genotype (Latorre et al. 1986). Which scenario is correct hinges on the (unknown) extent of mtDNA diversity in early human populations. In modern human populations, mtDNA diversity is very high, supporting the single female hypothesis (Cann et al. 1987). Only seven of the 133 distinct types of human mtDNA identified were present in more than one individual. Other species are quite different. Only two mtDNA genotypes were found in New World *Drosophila subobscura* populations (Latorre et al. 1986).

The maternal inheritance pattern of mtDNA complicates the situation. A mtDNA lineage will become extinct if, in any generation, a woman has only male offspring. In contrast, the woman's nuclear genes are passed on in her sons (Figure 2). Avise et al. (1984) showed the stochastic extinction of maternal mtDNA lineages can be quite rapid. We could all have mtDNA descended from a single female living relatively recently but, because of the potentially rapid extinction of mtDNA lineages, "Eve" could have belonged to a population of many thousands or tens of thousands of females polymorphic for mtDNA (Avise et al. 1984).

Out of Africa

It is generally accepted that the first members of the human lineage were the Australopithicines, and that they evolved in Africa. The second conclusion of Cann et al. (1987) is that modern humans also originated in Africa. An African origin is not a new idea. Wainscoat et al. (1986) proposed it based on their studies of the B-globin gene cluster in humans. Europe, Asia, or the Americas have also been proposed as the modern human birthplace (Jones & Rouhani 1986a), although only Asia and Africa are presently considered possible.

Cann et al. (1987) used two findings to support their conclusions. First, the most parsimonious evolutionary tree derived from the mtDNA data has its roots in Africa. The tree has two main branches: one contains only Africans, the other some Africans plus all members of the other populations sampled. Second, the African population shows the most overall mtDNA diversity. Since older populations will have accumulated more mutations and genetic diversity than younger ones, the African population should be the oldest and hence the original.

Fossil data, disputed by some, are consistent with anatomically modern humans having originated in Africa by 100,000 years ago and having become wide-

spread in Africa 50,000 years ago (Delson 1988; Jones & Rouhani 1986a; Lewin 1988; Stringer & Andrews 1988). If true, then "Eve" lived before the origin of modern *H. sapiens* (Lewin 1987).

"Archaic modern humans" or "Proto-Cro-Magnons" were apparently present in southwest Asia (Israel) as early as 92,000 years ago (Valladas et al. 1988). This best supports an African origin but does not disprove the origin of modern humans in southwest Asia. *H. sapiens* may have been divided into southern African and northern African/southwest Asian populations 92,000 years ago (Stringer 1988). "Proto-Cro-Magnons" preceded Neanderthals in southwest Asia (Valladas et al. 1988), precluding the possibility of modern humans evolving from Neanderthals. Rak (1986; Rak & Arensburg 1987) gives

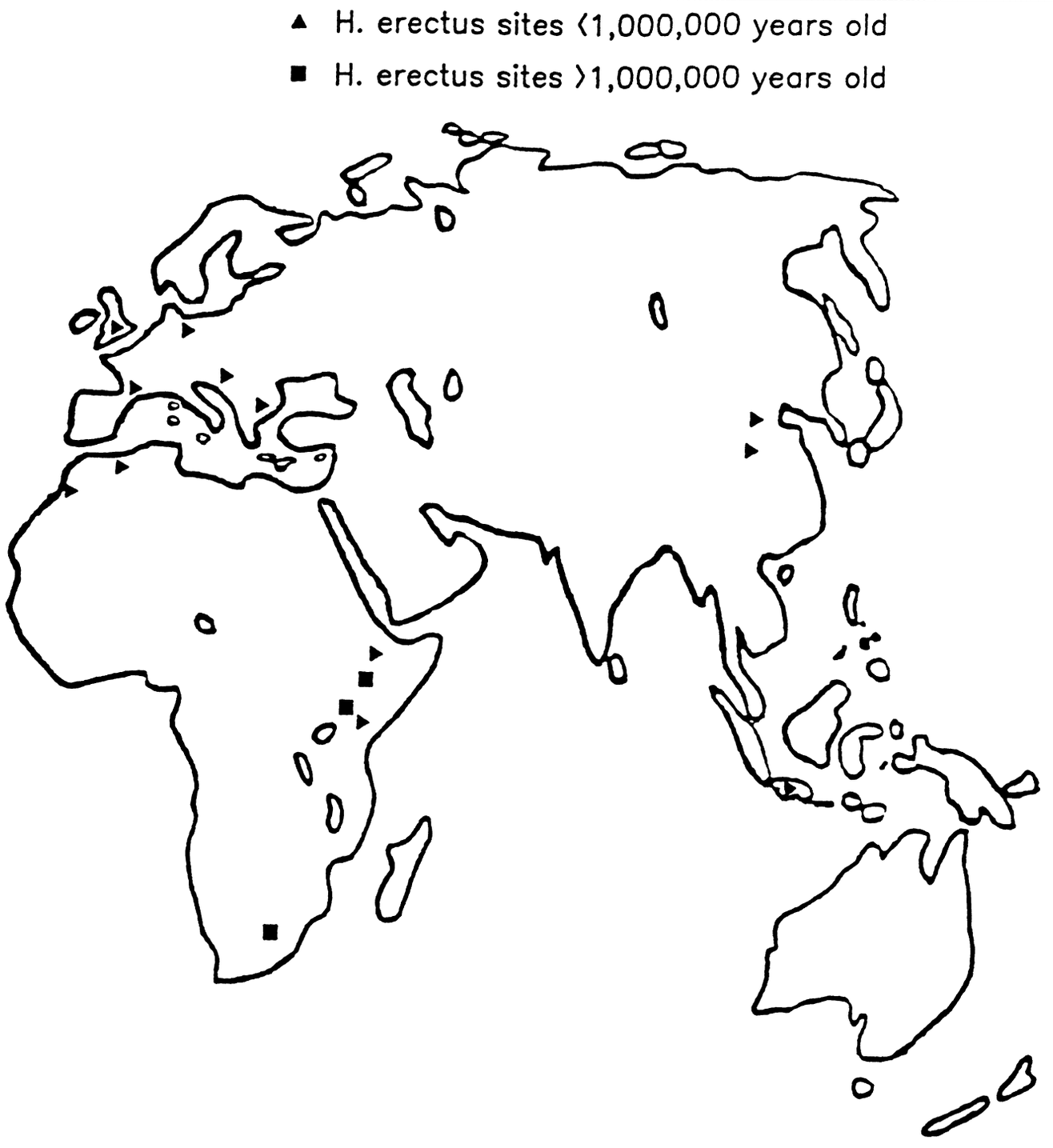

Figure 3. *Homo erectus* sites (from Lewin 1984). The expansion of *H. erectus* from Africa occurred about 1 million years ago. Non African *H. erectus* populations apparently went extinct without descendants. Modern humans evolved from *H. erectus* in Africa and expanded from Africa about 100,000 years ago.

anatomical reasons for excluding Neanderthals from our direct ancestry.

The African single point of origin hypothesis has been questioned (Giles & Ambrose 1986; Van Valen 1986; Darlu & Tassy 1987; Eckhardt 1987). The competing multiple origins hypothesis proposes the more or less simultaneous evolution of widespread *H. erectus* populations into *H. sapiens* (Van Valen 1986). The single point of origin hypothesis, whether in Africa or in nearby southwest Asia, is more consistent with current population genetics and speciation models (Jones & Rouhani 1986b). A single point of origin implies that all other hominid populations, including European Neanderthals and *H. erectus* from all non-African areas (Figure 3), became extinct without contributing genetic material to modern humans.

If modern humans evolved in Africa about 100,000 years ago, they spread very quickly because widely separated populations of modern humans appear contemporaneously in the fossil record. This supports the multiple origins hypothesis but is also consistent with a single point of origin. Human population records are replete with rapid expansions. Once humans entered the New World only 1,000 years may have passed until the southern tip of the continent was reached (Jones & Rouhani 1986a).

The evidence is most consistent with a relatively recent origin of *H. sapiens* in Africa and with all living people being able to trace their mitochondrial DNA ancestry back to a woman (or women) who lived in Africa about 200,000 years ago. Current evidence supports two separate expansions of hominids from Africa. First, about 1 million years ago, *H. erectus* became very widespread (e.g. Peking man, Java man; Figure 3). The *H. erectus* populations differentiated; some evolved into European Neanderthals and other species (Tattersall 1986). All the non-African hominid populations became extinct. In Africa, *H. erectus* evolved into anatomically modern humans, which reemerged from Africa and populated the world.

The above scenario is tentative. Molecular biology has contributed significantly to our understanding of human origins, but since the relationship between the molecular and the anatomical (or between genotype and phenotype) is complex and poorly understood (Marks 1986), inferences drawn from the two data sets may conflict. A case in point is the relationship of humans to the apes. Anatomically, chimpanzees and gorillas seem more closely related to each other than either is to humans (Marks 1986). In contrast, some of the molecular evidence suggests that humans and chimpanzees are more closely related to each other than either is to gorillas (Homquist et al. 1988; Hayasaka et al. 1988). Despite such potential conflicts, the marriage between molecular biology and human evolution promises to be a very fruitful union indeed.

Teaching Aids

NOVA program
The Children of Eve

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Acknowledgments

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