Evidence from Nuclear DNA for the Origin of Modern Humans

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Becky Godkin

ABSTRACT

Recent genetic studies suggest that all living humans can be traced back to a common ancestor who lived about 200,000 years ago, probably in Africa. Early genetic evidence supporting this position was based on mitochondrial (nonnuclear) DNA (mtDNA), which is inherited maternally. However, the assumptions underlying mtDNA studies have recently been challenged and the implications of nuclear DNA (nDNA) analyses have added significantly to genetic reconstructions of the evolution of anatomically modern Homo sapiens. In this review, the evidence from nDNA polymorphisms for the origin of modern humans will be explored and the importance of genetic research in the study of human evolution will be examined.

INTRODUCTION

The 1970's saw the beginning of a quiet revolution in human paleontology concerning the emergence of anatomically modern Homo sapiens. As archaeological interests heightened, increasing attention was given to the biological and behavioural changes that led to the evolution and spread of modern humans. Accordingly, several theories were put forth to explain the origin of anatomically modern H. sapiens and the cultural significance of their subsequent distribution. Scientists were principally concerned with whether our relatively flat, retracted face and our lightly built skeleton were principally concerned with whether our relatively flat, retracted face and our lightly built skeleton developed under unique circumstances in a localized ancestral population or resulted from regionally continuous evolution from H. erectus that led to the appearance of modern humans throughout the world. Genetic studies advanced this controversy and provided researchers with additional tools to interpret the evolutionary significance of human genetic diversity.

The first DNA polymorphisms examined in humans for evolutionary purposes were from mitochondrial DNA1 (mtDNA). Analyses of mtDNA have shown low variation between geographically distant populations, suggesting that intrapopulation genetic divergence in modern humans is greater than interpopulation variation. Moreover, genetic comparisons using mtDNA have convinced many molecular geneticists that "all humans today can be traced along maternal lines of descent to a woman who lived about 200,000 years ago, probably in Africa" (Wilson & Cann 1992: 101). Although this single origin or 'Eve' hypothesis is consistent with some interpretations of genetic and archaeological data, recent reevaluations of the techniques and conclusions of genetic evidence have complicated the study of anatomically modern H. sapiens. The assumptions underlying mtDNA studies have been questioned and the implications of nuclear DNA (nDNA) analyses have added significantly to our understanding of the origin of modern humans. By exploring the evidence from nDNA polymorphisms, hypotheses regarding the origin of anatomically modern humans will be surveyed and the implications of genetic research in human evolution will be examined.

The evolutionary history of hominids is inscribed in the genetic code of living species and molecular geneticists can infer this history from the data of DNA. This branch of science, often termed molecular phylogenetics, has contributed significantly to the study of the origins of anatomically modern H. sapiens and has provided researchers with a set of genetic tools for discerning the evolutionary relationships of modern human populations. Initial applications of genetic data were directed towards the interpretation of two opposing models for the origin of modern humans2. These competing theories of recent human evolution include the 'Out of Africa' or 'Eve' hypothesis and the 'Multiregional Evolution' model.

The Multiregional Evolution Model

The multiregional evolution model assumes morphological continuity from the Middle Pleistocene to modern hominid populations in Africa, Europe, and Asia, with modern regional characters appearing early of the mtDNA of a variety of species, it has been shown that only in mammals is the genetic information so concisely organized.

1 Although there are more than two competing theories for the origin of modern humans, the 'Out of Africa' theory or 'Eve Hypothesis' and the 'Multiregional Evolution' model are the two principal hypotheses currently involved in the origins controversy.
in all three areas. According to this hypothesis, some regional variation is considered to have preceded the appearance of the Homo sapiens morphology and to have been carried over from local Homo erectus ancestors (Stringer & Andrews 1988). In the late 1970's, Richard Leakey described the multiregional model with the following analogy:

Take a handful of pebbles and fling them into a pool of water. Each pebble generates outward-spreading ripples that sooner or later meet the oncoming ripples set in motion by other pebbles. The pool represents the Old World with its basic sapiens population; the place where each pebble lands is a point of transition to Homo sapiens sapiens; and the outward-spreading ripples are the migrations of truly modern humans (Leakey & Lewin 1992: 212).

When Leakey first presented this metaphor for modern hominin evolution he was a strong advocate of the multiregional model, relying heavily on his father's notion that, through culture, humans effectively domesticated themselves. Accordingly, Richard Leakey suggested that, since domestication leads to rapid evolutionary change, the evolution toward fully modern humans would have occurred 'wherever the evolutionary momentum had established itself—in other words, multiregional evolution' (1992: 213).

The 'Out of Africa' or 'Eve' hypothesis

Leakey's original promotion of the multiregional model eventually waned, largely as a result of new dates and fossils which forced him to examine the alternative interpretation that anatomically modern H. sapiens originated as a single evolutionary event in a geographically distinct population. Support of this hypothesis by genetic evidence has convinced other multiregionalists to rethink their position on the origins debate and consider the 'Out of Africa' theory as a viable postulate for the origin of modern humans. This 'Replacement Model' suggests a relatively recent African origin for anatomically modern H. sapiens and contends that this stock spread throughout the world and replaced the more primitive hominid populations they encountered. This theory, propounded by a group of geneticists led by the late Allan Wilson, intimates that archaic lineages mixed little or not at all with early modern humans, but were replaced by them (Stringer 1990). Consequently, transitional fossils from archaic to modern H. sapiens should only be found in Africa and the earliest record of H. sapiens fossils should occur in the African area of origin.

The Controversy

The predictions of these two principal models for the origin of modern humans have established the foundation for much of the current controversy over the implications of genetic research in resolving the origins debate. Mitochondrial DNA studies, which were the first genetic analyses to be directly applied to this controversy, have traditionally supported the African origin hypothesis and contested theories of multiregional evolution based on lack of genetic evidence to support regional continuity in the evolution of modern humans. The most influential research in this area began in the late 1980's with the work of Cann et al (1987) on mitochondrial and cytoplasmic DNA samples from five different ethnic regions. The 147 subjects involved in their initial study possessed 133 different types of mtDNA, all of which were assumed to originate from a single (maternal) ancestral type through a series of genetic mutations. Based on data suggesting a constant rate of mtDNA mutation, Cann and her colleagues computed an evolutionary tree with two main branches: one including only those of African origin and the other of everyone else. They concluded that the most parsimonious root linking the two main branches was in Africa, indicating that the mtDNA of all modern humans stems from a woman who lived in Africa between 140,000 and 290,000 years ago. However, these findings do not indicate that the nuclear DNA of anatomically modern H. sapiens came from a single female ancestor: "some females may have produced only sons or had no offspring, in which case their particular mtDNA would have been lost" (Relethford 1994: 390). Concerns with the consistency of their experimental design and with the narrow potential application of their results led many researchers to question the findings of Cann et al and to extend genetic research in this area. Nuclear DNA studies provided one means of advancing the genetic analysis of evolutionary relationships and calculating the pattern and time of origin of modern humans.

RECONSTRUCTING MODERN HUMAN EVOLUTION: EVIDENCE FROM NDNA

Although archaeological data provides the most direct evolutionary evidence, there is ambiguity in placing fossilized organisms within a phylogenetic tree¹. Particularly in the study of the evolution of H. sapiens...
sapiens, anthropocentric bias in interpreting fossil evidence seems to have prevailed (Hasegawa & Kishino 1991). Morphological phylogeneticists encounter the additional problem of determining whether a particular character state is ancestral or derived. A functional understanding of the character is essential for determining its cladistic value (Klein 1989) and knowledge of phylogenetic relationships is imperative, making the resolution of primitive and derived characters somewhat circular. Conversely, molecular phylogenetics is relatively free from these difficulties and can provide a useful framework for interpreting archaeological data.

In contrast to mtDNA studies, nDNA polymorphisms have been tested on only a limited scale, for only a few populations. Nevertheless, nDNA genetic trees continue to support the hypothesis of an initial African and non-African divergence for modern humans. Comparisons of nDNA polymorphisms with those of ‘classical’ genetic markers and with archaeological and linguistic data have provided additional defense for the ‘Out of Africa’ hypothesis.

Within the past decade, new methods for detecting genetic differences in nDNA have been developed. The two most frequently utilized methods include RFLP analysis and the PCR technique. The first procedure involves the comparison of lengths of DNA fragments. Restriction enzymes are used to partially digest chromosomal DNA producing restriction fragments of nDNA. If phenotypically neutral changes in DNA alter the recognition sites of restriction enzymes, the enzyme will cut one person's DNA but not another's: their DNA restriction fragments would have different lengths. Although traditionally used to isolate the genes for inherited human disorders, RFLP analysis can also detect naturally occurring variation among the nucleotides of normal individuals (Mange & Mange 1988, my italics), thus providing a formula for determining genetic differences among modern humans.

The PCR method is based on the amplification of a DNA segment using DNA polymerase and oligonucleotide primers that hybridize opposite strands of the DNA sequence to be amplified (Klug & Cummings 1991). This process yields large amounts of amplified DNA segments that can be used for determining genetic sequences and genetic distances.

These two techniques provide an enormous and previously untapped source of genetic markers and both of these methods are particularly useful for determining interpopulation variation in nDNA. Nuclear sequence data are difficult to interpret at the intraspecific level because, unlike mtDNA, nDNA undergoes frequent recombination (Mountain et al 1992). Accordingly, nDNA studies are typically applied to comparisons of DNA polymorphisms between several populations.

Among the first comprehensive studies of the evolutionary significance of nDNA is the research by Bowcock et al (1991). The group modelled a reconstruction of modern human differentiation based on 100 DNA polymorphisms tested in five populations from four continents. The populations typed for the DNA markers included: (i) individuals of European origin; (ii) Chinese born in mainland China living in the San Francisco Bay area; (iii) non-Austronesian speaking Melanesians from Bougainville; (iv) one group of African Pygmies from the Central African Republic; and (v) one group of African Pygmies from northeastern Zaire (Bowcock et al 1991). The evolutionary tree based on observed genetic differences confirmed previous postulates that the earliest divergence in modern human evolution separated Africans and non-Africans. The second fission suggested by their genetic data separates Melanesians from Chinese and Europeans. This is consistent with the observation based on classical genetic markers that the second divergence separated Australians, New Guineans, and Southeast Asians from North Eurasians (Bowcock et al 1991: 840; Cavalli-Sforza et al 1988).

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72.7 &\pm 6.4 \\
44.8 &\pm 7.9 \\
20.0 & \\
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\end{align*} \]

\[ \begin{align*}
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\text{PygZ} & \\
\text{Eur} & \\
\text{Chi} & \\
\text{Mel} &
\end{align*} \]

Figure 1a. Evolutionary tree based on observed genetic differences in five human populations (assuming a constant evolutionary rate) (Bowcock et al 1988: 840). The time scale is based on the hypothesis that the divergence between Africans and non-Africans occurred approximately 100,000 years ago.

Nonetheless, there are several significant problems with this tree, which was calculated from a model assuming constant evolutionary rates. If genetic evolution in the different lineages is indeed independent and occurs at equal rates, all distances

stopped at the time the \((n+1)\)th population would be formed (Astolfi, Kidd & Cavalli-Sforza 1981: 156-7).

\(^1\)Classical nuclear (non-DNA) genetic markers include blood group, protein, and HLA polymorphisms (HLA are cell surface proteins involved in the acceptance or rejection of tissue and organ grafts and transplants).
between pairs of populations generated by a specific tree node should be equal (Bowcock et al 1991). In the tree in Figure 1a, the distances between the African populations and the Europeans are significantly smaller than the distances between the African populations and the other non-African groups. Bowcock et al resolved the problem of the short European branch by submitting that Europeans are descendants of a population that arose due to admixture between two ancestral populations. This hypothesis was tested and the data were found to be consistent with admixture between the branch leading to Chinese after their separation from Melanesians and the branch leading to the two African populations (Bowcock et al 1991). Ancestral Europeans were estimated to be an admixture of 65% ancestral Chinese and 35% ancestral Africans.

Ancestral Europeans were estimated to be an admixture of 65% ancestral Chinese and 35% ancestral Africans.

Figure 1b. Evolutionary tree based on observed genetic differences in five human populations (assuming a model of admixture between ancestral Africans and ancestral Asians) (Bowcock et al 1988: 840). Data was found to be more consistent with this tree than Figure 1a. Ancestral Europeans were estimated to be an admixture of 65% ancestral Chinese and 35% ancestral African.

Earlier studies, though not as rigorous as these, also suggested a major division of human populations into African and Eurasian groups. Wainscoat et al (1986) studied the frequency of a group of closely linked nDNA polymorphisms in the fl-globin gene cluster of individuals from eight diverse populations. Five linked polymorphic restriction enzyme sites in the fl-globin gene cluster were examined and the combination of the sites along one chromosome were referred to as the haplotype. Of the 14 different haplotypes, one haplotype (+ - - - -) was the most common in all seven non-African populations and the second most common haplotype (- + + + +) was found in all non-African groups with the exception of the Thai population. A third haplotype (- + - + +) accounted for the majority of the remaining haplotypes found in the non-African populations and the two African groups examined shared a common haplotype (- - - - - +) that was absent in nearly all the non-African populations (Wainscoat et al 1986). Based on this set of data, Wainscoat et al (1986) suggested that, since non of these four common haplotypes can be derived from any of the other three by either a single crossover or by a single-base mutation, these genetic structures have been stable for long periods of time, on the order of 100,000 years. Moreover, their data is consistent with the evolutionary scheme in which a founder populations migrated from Africa and subsequently gave rise to all non-African groups.

As evidence from nDNA polymorphisms for the evolution of modern humans advanced, so too did the methods of genetic analysis. Many researchers extended the scope of their studies to include archaeological evidence and genetic data from non-human primates in an attempt to better discern possible dates for the origin of H. sapiens. Mountain et al (1992) were among the first researchers to introduce this type of comparative approach to the study of the evolution of modern humans. Based on 'classical' nuclear genetic markers (blood group, protein, and HLA polymorphisms), Mountain et al (1992) constructed a genetic tree for 42 aboriginal populations based on frequencies of 120 alleles associated with 44 classical markers. The major separations in this tree were compared to dates of human migrations estimated from archaeological data. Based on migration dates of anatomically modern H. sapiens calculated from archaeological evidence, consistency between the archaeological and 'classical' genetic data "lends support to the hypothesis that the genetic tree corresponds roughly to the evolution of human populations over the last 100ka" (ie. 100,000 years) (Mountain et al 1992: 160).

New Guinean & Australian
Pacific Islander
Southeast Asian
Northeast Asian
Arctic Northeast Asian
Amerindian
European
non-European Caucasoid
African

Figure 2. Genetic tree for 42 aboriginal populations based on frequencies of 120 alleles associated with 44 classical genetic markers (Mountain et al 1992: 160). The first split in this tree occurs between African and non-African, advancing support for the hypothesis that modern humans originated in Africa and then moved out of Africa to Europe and Asia where they replaced other more primitive hominin populations.
Mountain et al (1992) have also broadened their studies to include genetic comparisons with non-human primates. In order to place the human gene frequencies into a broader evolutionary context, they compared 80 nDNA polymorphisms for eight modern human populations with those for chimpanzees, gorillas, and orangutans. For 60 of these 80 polymorphism, they found that chimpanzees share a single allele with humans. "These 60 alleles are assumed to have existed form the time of the separation of ancestral humans and ancestral chimpanzees, and to represent the ancestral alleles at their respective locus" (Mountain et al 1992: 162). The identification of these ancestral alleles has provided preliminary evidence for evolutionary rates in modern humans:

In both the classical marker and DNA marker trees the African populations are found at the end of a very long branch. The length of this branch may indicate either a higher evolutionary rate within African populations, or an African origin for modern humans. The former would have occurred if African populations remained relatively small, or experienced bottlenecks, after separation from other populations. The African populations, however, have higher frequencies of ancestral alleles, indicating that these populations have experienced a relatively low rate of allele frequency change (Mountain et al 1992: 164). Therefore, the identification of ancestral alleles from non-human primate studies seems to strengthen the African origin hypothesis advocated by many evolutionary geneticists.

More recently, Mountain and Cavalli-Sforza (1994) have extended these non-human primate investigations and have incorporated data on ancestral allelic states into a cladistic analysis of nDNA restriction polymorphisms in modern humans. They analyzed 79 human restriction fragment length polymorphisms (RFLPs) tested in eight human populations 1 and examined these same RFLPs in non-human primates and, thereby, identified likely ancestral alleles for 62 of these polymorphisms (Mountain & Cavalli-Sforza 1994). Identification of these ancestral alleles provided a cladistic criterion for the inference of evolutionary trees: "By assuming a roughly constant evolutionary rate, we can infer the position of the root of a tree with greater confidence than without identification of ancestral states" (Mountain & Cavalli-Sforza 1994: 6515). Based on the frequencies of the ancestral alleles and genetic distances (including a virtual ancestral population representing the time of origin of new alleles for all polymorphisms), they concluded that the root of their evolutionary tree clearly separated African and non-African populations. Their cladistic approach strengthened the conclusion that anatomically modern H. sapiens originated in Africa. Additionally, their results suggest that the average time since mutation of the ancestral alleles producing the current set of polymorphisms is approximately 700,000 years (Mountain & Cavalli-Sforza 1994).

The Evolutionary Battlefield: Debate Over the Significance of nDNA Evidence

In the early 1990's, it was generally thought that genetic evidence was sufficient to dismiss the multiregional model for the origin of anatomically modern humans: genetic data clearly pointed to Africa as the area of origin. However, recent reevaluations of the methods and results of genetic studies have cast more than a shadow of doubt on theories for the origin of modern H. sapiens. Several researchers have challenged the significance of genetic data in confirming the Out of Africa hypothesis. One scientist in particular has advocated for the rejection of nDNA data as evidence for the African origin of anatomically modern H. sapiens. Although other researchers have also assumed this position, Alan Templeton's critique and reanalysis of the evolutionary implications of nDNA results provide a representative illustration of the nature of this controversy.

Based on his evaluation of both multilocus and single-locus studies of nDNA, Templeton concludes that "the out-of-Africa replacement hypothesis is incompatible with the overall pattern that emerges from the nuclear DNA data" (1993: 67). Templeton acknowledges that population trees based on multilocus genetic studies clearly show that African groups diverged first. However, he qualifies this affirmation by contending that, since patterns of genetic divergence do not fit a strictly branching evolutionary tree, this reflects long-term restricted gene flow rather than a recent African origin (1993).

Templeton's critique, according to Stoneking (1994), overlooks several important points. Most notably, Stoneking (1994) argues that Templeton fails to note that the lack of fit between genetic distances and a strictly dichotomous evolutionary tree can be attributed to the use of a tree-building method that assumes a constant rate of evolution. "A much better fit is observed when the neighbour-joining method, which does not assume a constant rate of evolution, is used to construct trees from multilocus data" (Stoneking 1994: 135; see also Mountain et al 1992). Furthermore, Stoneking maintains that, although multilocus data are not sufficient to disprove multiregional evolution, Templeton is wrong in asserting that multilocus data are incompatible with the recent African origin hypothesis (1994).

In his analysis of single-locus nDNA studies, Templeton specifies a similar conclusion: "Overall, these various single-locus studies yield a rather diverse set of inferences . . . This overall pattern is not compatible with ... the specific hypothesis of an out-of-Africa replacement" (Templeton 1993:68–9). Templeton's discussion of fl-globin data (Wainscoat et al 1986) centres on his assertion that the study is subject to ambiguities of interpretation. However,
Templeton neglects to point out that this study did find that Africans diverged first, as would be predicted by the Out of Africa hypothesis (Stoneking 1994). More generally, Templeton maintains that inferences from both multi- and single-locus nDNA studies are locus-specific and not population-specific.

Stoneking's extended discussion of nDNA data submits that Templeton's analysis is flawed and illogical. Although Stoneking readily admits that genetic results are, as yet, insufficient to disprove the multiregional evolution of modern humans, he maintains that Templeton is "wrong to conclude that the Out of Africa replacement hypothesis is also incompatible with the overall pattern that emerges from the nuclear DNA data" (1994:137). Templeton's complete rejection of the Replacement Model opposes Stoneking's and others' contention that genetic data are more consistent with the African origin hypothesis than with theories of multiregional evolution (see also Nei & Roychoudhury 1993). Accordingly, Templeton proposes that the basis of the debate remains the different methodological viewpoints of the scientists involved: "Stoneking primarily approaches the problem as one of hypothesis compatibility, whereas I had approached it as one of hypothesis testing" (1994:141). These conflicting analytical frameworks are indeed what shapes much of the controversy over the significance of genetic data in establishing the origin of modern humans.

**CONCLUSION**

Until recently, most reviews of nDNA and other genetic evidence have favoured models of a recent African origin for anatomically modern H. sapiens. Increasing concerns with the systematics of genetic approaches have encouraged persistent debate over the validity of nDNA results. These concerns have typically been directed at the different theoretical models that have been proposed to account for the distribution of genetic variation across human populations. The various models and their individuals dialectical approaches represent fundamentally different conceptual approaches to the analysis of modern human population genetic structure. One challenge for the future will be to determine which models are the most appropriate for specific empirical cases.

Regardless of the controversial nature of genetic interpretations, examinations of molecular data have provided scientists with some general resolutions about the origin of anatomically modern H. sapiens. Analyses of phylogenetic trees involving nuclear polymorphisms tested by electrophoresis or immunological techniques, restriction fragment length polymorphisms of nuclear genes, and mitochondrial DNA all show a somewhat greater difference between Africans and non-Africans than between other human groups (Cavalli-Sforza, Menozzi & Piazza 1994). Additionally, these genetic data offer some information on dates supporting the interpretation that the origin of modern humans was in Africa, from which an expansion to the rest of the world started about 100,000 years ago.

The resolution of the current debate over the origin of anatomically modern H. sapiens will require improved communication between paleoanthropologists and geneticists, allowing the latter to make an increasingly influential contribution to the molecular study of the evolution of modern humans. "As has proved to be the case in the study of hominid origins, paleoanthropologists who ignore the increasing wealth of genetic data on human population relationships will do so at their peril" (Stringer & Andrews 1988: 1268). Conceptual and intellectual cooperation by all scientists involved in the origins controversy will undoubtedly direct future research towards reaching a specific theory on the origin of anatomically modern H. sapiens.
Table 1. Numbers of chromosomes possessing the various haplotypes in each population. Analyses of 601 chromosomes in 10 different human populations by Wainscoat et al (1986) revealed 14 of the 32 (25) possible haplotypes (492). The four most common haplotypes, as mentioned in the text, are indicated by an arrow.

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