A Diffusion Wave out of Africa

The Mechanism of the Modern Human Revolution?[1]

by Vinayak Eswaran

This paper proposes that the worldwide transition to an anatomically modern human form was caused by the diffusive spread from Africa of a genotype—a coadapted combination of novel genes—carrying a complex genetic advantage. It is suggested that the movement out of Africa was not a migration but a "diffusion wave"—a continuous expansion of modern populations by small random movements, hybridization, and natural selection favoring the modern genotype. It is proposed that the modern genotype arose in Africa by a shifting-balance process and spread because it was globally advantageous. It is shown that the genotype could have spread by directionally random demic diffusion, but only under conditions involving a low rate of interdeme admixture ("interbreeding") and strong selection. This mechanism is investigated using a quantitative model that suggests explanations for many puzzling aspects of the genetic, fossil, and archaeological data on modern human origins. The data indicate significant genetic assimilation from archaic human populations into modern ones. A morphological advantage of the modern phenotype— possibly reducing childbirth mortality—is proposed as the cause of the transition. The evidence of this and previous human "revolutions" suggests that the shifting-balance process, proposed by Sewall Wright, was particularly important in human evolution —possibly because human populations had a small-deme social structure with low interbreeding rates that allowed it to operate. This may explain the relative uniqueness of human evolution.

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The century-old problem of modern human origins has remained one of the most fiercely disputed scientific questions of our time. The problem pertains to the means by which earlier humans of "archaic" anatomy—with characteristically out-thrust jaws and faces and receding foreheads—gave way, in the past 100,000 years, to people of essentially modern anatomy who are classed as *Homo sapiens sapiens*. While the evidence exclusively supports neither theory, the current debate has generally focused on two models—recent African origin (Stringer and Andrews 1988) and multiregional evolution (Wolpoff, Wu, and Thorne 1984).

Two vividly contrasting pictures of recent human evolution and its mechanisms are offered by these models. The commonly held view of proponents of a recent African origin is that there was a speciation event in Africa around (or before) 130,000 years ago that resulted in the emergence of anatomically modern humans. This was followed, it is proposed, by a migration of modern humans out of Africa and the subsequent replacement, without genetic admixture, of all non-African archaic people. Another "Out-of-Africa" theory, that of Bräuer (1984), suggests an African emergence and migration of modern humans but with some admixture with the archaics resident in the other continents.

In contrast, the multiregional-evolution model proposes that modern humans evolved from regional populations that were initially created by the ca. 1.5–2.0-million-year-old expansion of *Homo erectus* from Africa. Its proponents hold that humans evolved as a single polytypic species united by a worldwide pattern of gene flow and migration. The "standard" version of the model asserts that "modern humans evolved though the coalescence of a series of modern traits that appeared independently at various areas at different times" (Wolpoff et al. 1994:178). An alternative ("assimilation") version of the multiregional-evolution model, proposed by Smith (1985), accepts an African origin for modern humans but suggests that diffusive gene flow—involving localized population movements ("diffusion"), admixture, and selection—spread the advantageous genes associated with modern humans to other populations and initiated their transition to anatomical modernity. However, few of the hybrid fossils expected in this scenario have been found outside Africa, and this has led to some doubt regarding the model (Aiello 1993).

The testable predictions of the models of Smith (1985) and Bräuer (1984) are difficult to distinguish from each other.[2] That these models are qualitative adds to the difficulty. Many empirical data cannot be explained entirely in qualitative terms, among them the limited evidence of hybridization, the low non-African genetic depths, the apparently low effective population of Pleistocene humanity, the evidence of bottlenecks in human prehistory, and the genetic evidence of "population explosions" in

2. These models are considered to be variants of the multiregional-evolution and the recent-African-origin model, respectively, which shows that the differences between the latter are not as great as they are generally made out to be.

the late Pleistocene. In contrast, a quantitative model would give precise predictions, under assumed conditions, which could then be qualitatively compared with the empirical data.

In this paper I suggest that most of the features associated with anatomical modernity evolved in Africa as a coadapted gene combination (or "genotype") and spread across the world because they *collectively* offered some strong selective advantage. The development of such a genotype can quite plausibly be based on the shifting-balance theory of Sewall Wright (1932). Wright's theory suggests that, in populations subdivided into small semi-isolated demes, evolution can occur in the following three phases: (1) Genetic drift propels different demes along different trajectories, facilitating an exploration of the adaptive landscape available to the species. (2) *Intra*deme selection allows some demes to reach a new and higher adaptive peak. (3) *Inter*deme selection propagates the gene combinations that correspond to these adaptive advances and shifts the entire species to the new peak. For all this to occur, the demes are required to be (*a*) small enough to allow significant genetic drift and (*b*) semi-isolated, to facilitate the formation of complex coadapted gene combinations that would otherwise be broken up by admixture.

Evolutionary biologists are still undecided regarding the viability of Wright's shifting-balance process as a whole. For example, Coyne, Barton, and Turelli (1997) have argued, from a comprehensive survey of both theory and empirical data, that while phases 1 and 2 could occur under certain conditions, major theoretical objections undermine the plausibility of phase 3 of the process. A number of model studies have shown that the spread of advantageous—in particular, multilocus and complex—genotypes is very uncertain and occurs, if at all, under very restrictive conditions.

Thus the immediate, and central, difficulty with the idea that a modern genotype spread out of Africa is the need for a plausible mechanism by which such a genotype could have traveled across the world. This mechanism cannot be just "gene flow"—which is generally taken to mean a combination of movement and admixture such as is suggested by Wobst's (1976) picture of demes fixed in location but genetically linked by mate exchanges. It is unlikely that an advantageous *coadapted* gene combination could have spread in such circumstances: the gene combination would have been repeatedly "broken up" by interdeme mating and would have lost its coadapted advantage upon such a breakup, thus limiting its spread.

However, another possibility exists: that of demic diffusion and admixture.[3] The advantageous genotype could have been carried whole in the demes and been broken up only when admixture ("interbreeding") occurred between members of different demes, one of which did not

carry the genotype. Thus, if the interbreeding rate was low and the genotype advantage was high, there is the possibility that the population of demes carrying the modern genotype would have increased at the expense of the others that did not; the genotype would then have spread out of Africa and across the world. In this paper, I investigate this possibility using a quantitative model.

Although demic diffusion and selection have been suggested as a mechanism of genetic exchange between populations (see, e.g., Smith, Falsetti, and Donnelly 1989), without low interbreeding rates this mechanism is essentially the same as diffusive gene flow and is incapable of spreading complex genotypes. I demonstrate this by means of the quantitative model. Thus the added constraint of a sufficiently low interbreeding rate is crucial for the spread of genotypes.

The favored modern genotype could have, by demic diffusion, entered areas hitherto occupied by archaics and, being aided by natural selection, finally have prevailed in the local population. This process, repeated area by area, would have caused a slow, wavelike spread of modernity—here called a "diffusion wave"—which was akin to the wave of advance of a single advantageous allele. (Fisher 1937) and like the latter would have spread at a constant wave speed under constant conditions.

The diffusion wave of a complex coadapted genotype differs, however, from the gene flow of a single advantageous allele. It can spread only when there is a strong selective advantage for the genotype and a low interbreeding rate between demes. It would also propagate, *uni*directionally and over vast distances, the neutral genes of the original population wherein the genotype first emerged while greatly restricting genetic assimilation from the other populations. All this creates the impression of a migration. However, the diffusion wave is not a migration, for demic diffusion is assumed to be directionally neutral. It is only the added effect of natural selection that causes the inexorable directional advance of the wave into regions populated by archaic humans. The diffusion wave is essentially an expansion—by small random movements, hybridization, and natural selection—of the populations carrying the modern genotype.

My quantitative model simulates the movement of demes that, over generations, relocate in small directionally random steps (i.e., demic diffusion) along with mating between members of different demes (i.e., interbreeding). These two processes are treated as independent and complementary. The demes are taken to be hunter-gatherer groups. The selection for a genotype made up of a number of coadapted genes collectively carrying an advantage is also incorporated into the model.

While the possibility of long-range migrations is specifically disregarded, the model shows that anatomical modernity could have propagated as a diffusion wave at speeds compatible with the known fossil record. The model simulations, computed with partly empirical and partly assumed parameters, also show how African neutral genes could have spread far—which would explain, without invoking a migration, the African-derived ge-

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3. "Demic diffusion" is too often taken to mean a slow migration—which is *not* meant here. By "demic diffusion." I mean the strictly random-directional small movements of demes (say, hunter-gatherer groups) over generations.

netic patterns in global populations today. The model further offers answers to a number of questions relating to the genetic evidence to be elaborated upon later in this paper, chief among which are the following: (1) *the African bottleneck* (why the "migration" out of Africa was apparently so small and only from the edge of the populations with the deepest genetic roots), (2) *Late Pleistocene population explosions* (why mitochondrial DNA [mtDNA] data indicate large population increases in Africa, Asia, and Europe that occurred as much as 50,000 years apart), (3) *the Pleistocene bottleneck* (why some genetic markers indicate low effective populations and coalescence times), (4) *differential bottlenecks* (why other genetic markers show large effective populations and high coalescence times), and (5) *differential genetic depths* (why non-African populations show lower genetic diversity than African populations in recent polymorphisms but comparable genetic diversity in ancient ones). The explanations offered suggest that there must have been significant but not overwhelming *cumulative* genetic assimilation of archaics into modern populations as the diffusion wave progressed far from Africa. The essential features of the fossil and archaeological data also seem to be compatible with the diffusion-wave hypothesis. The theory thus reconciles the diverse data on modern human origins.

It is proposed below that the modern morphology may itself have given the advantage, possibly due to lowered childbirth mortality, that propagated anatomical modernity. The model also suggests explanations for (*a*) the disappearance of Neandertal cultures in Europe and the contrasting cultural evidence from Asia, (*b*) the delay, compared with West Asia, in the modern transition in Europe and East Asia, and (*c*) the fossil and genetic uniqueness of Australo-Melanesia.

The disappearance of archaic humans has been speculatively assigned a variety of causes, some as extreme as genocide by modern humans. The theoretical framework provided by this paper allows it to suggest that, given a selective disadvantage and nonzero interbreeding rates, the archaics would have been progressively hybridized and would have essentially disappeared by hybridization. The model thus provides a compelling mechanism for the "extinction" of archaic humans. Hybridization, however, would have been confined to the relatively narrow "wave front" (where moderns and archaics coexisted), which may also explain why not many hybrid fossils have been found outside Africa.

The picture that emerges from an interpretation of the empirical data in the light of this theory is that the final stages of the evolution of the modern human genotype took place in the east-south corridor of Africa (see "core" region in figure 1), from the Northeast African "edge" of which the genotype spread as diffusion waves to West Africa and West Asia. From West Asia it spread to the Far East by two waves, separated by geographical barriers, through North Asia and South Asia and, after some delay, by a third wave into Europe. In each of these waves, anatomical modernity was spread, the model suggests, exclusively by a small modern subpopulation at the wave front, from which all moderns on the path of that wave were finally descended. Because these wave-front subpopulations were only slowly modified, by assimilation from archaic populations and by genetic drift, the descendant populations would have been very closely related.

This theory thus suggests, in contrast to the recent-African-origin model, that the emergence of modern humans was not a speciation but an intraspecies "character change" (Wright 1982). However, in contrast to the standard multiregional-evolution model, it suggests that the emergence of the modern genotype was largely localized in Africa rather than being the product of a worldwide pattern of gene flow. Yet again, it suggests that the movement out of Africa was not a migration but an expansion characteristic of the third phase of the shifting-balance process. This theory thus reconciles—to the extent that they can be reconciled—the two models within the framework of Wright's shifting-balance theory.

Although broadly multiregional in spirit, the explanation of modern human origins presented here is closer to Smith's (1985) theory than to the standard multiregional-evolution model. However, the shifting-balance process, low interbreeding rates, advantageous gene combinations, and lowered childbirth mortality, all of which are important, even central, to this thesis, do not find significant mention in Smith's model. The theory proposed here also provides a detailed mechanism by which, and the conditions under which, a coadapted genotype could propagate. That these conditions are essentially those required by Wright's shifting-balance theory further suggests that the uniqueness of human evolution may be rooted in Wright's process.

The Out-of-Africa diffusion wave of anatomical modernity may not have been a singular occurrence in human evolution. There are genetic and fossil clues that it had been preceded by a wave from East Asia. There may have been even earlier revolutions that swept through global human populations. Indeed, human evolution in the Pleistocene may have been characterized by multiregional evolution occasionally interrupted by worldwide "revolutions" caused by the rapid diffusive spread of advantageous genotypes created regionally by a shifting-balance process. The multiregional-evolution model too suggests that regional genotypes could have formed by a shifting-balance process. The theory presented here differs in that it further suggests that regionally formed genotypes would have spread globally, when globally advantageous, as diffusion waves—thereby causing relatively sudden transitions in human populations.

Finally, I suggest that human evolution was fundamentally facilitated by a social structure of small demes linked by low interbreeding rates. This is required both for the formation of new genotypes by the shifting-balance process and for the spread of advantageous genotypes by diffusion waves. Such a social structure was possibly created in hominid populations—from even before the appearance of *Homo*—by an adaptive shift to collective hunting and scavenging. The operation of the shifting-balance process could explain the unique evo-
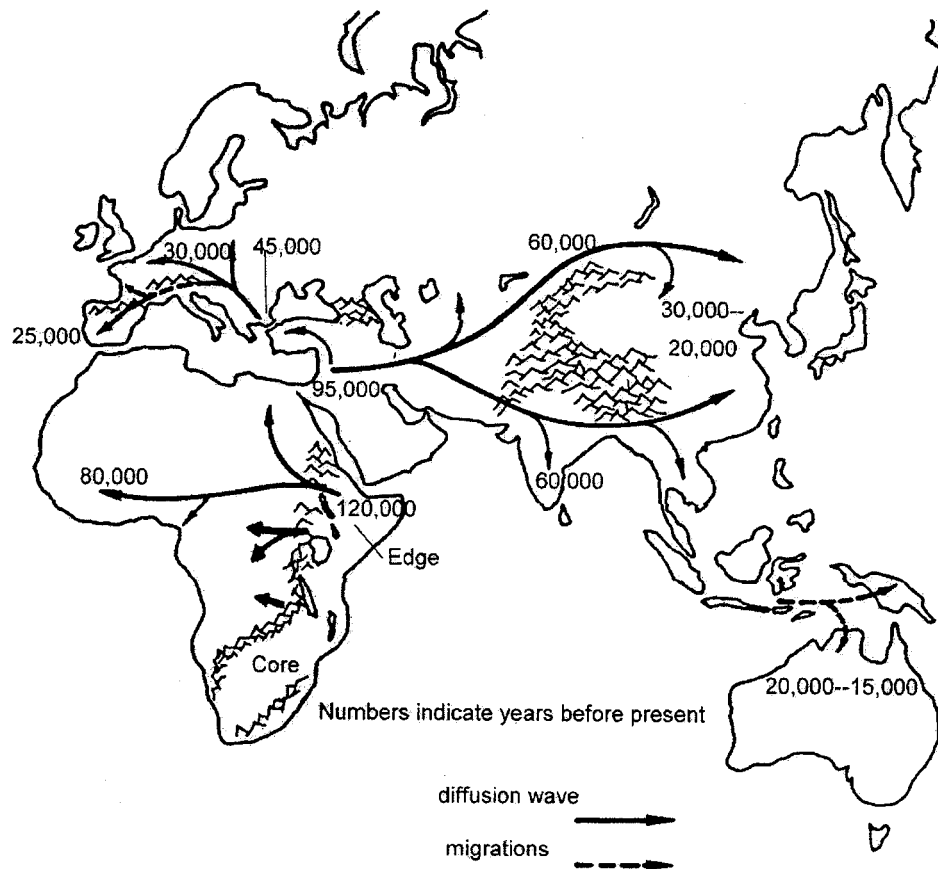
FIG. 1. *The pattern of diffusion waves which, according to this theory, propagated the modern human revolution. The dates are suggested mainly by the empirical evidence and the wave paths by the natural lines of advance from Northeast Africa.*

lution of the human line as compared with that of the anthropoid apes.

The Monte Carlo Model

Fisher (1937) and Kolmogorov, Petrovskii, and Piskunov (1937) had independently proposed an equation to simulate the movement—driven by diffusion (i.e., localized random movement) and natural selection—of an advantageous allele of a single gene through a widespread population. They showed that an advantageous allele, in contrast to a neutral one, would spread spatially at a constant speed, given constant conditions. The Fisher-Kolmogorov equation,

$$\frac{\partial P}{\partial t} = \frac{\sigma^2}{2}\frac{\partial^2 P}{\partial x^2} + \alpha P(1 - P), \qquad (1)$$

simulates the progress in a one-dimensional space of a single additively advantageous allele in a population in which the child-parent variance distance is σ^2(km^2/ gen-

eration). The equation incorporates a logistic growth model for the advantageous allele that has a relative growth rate per generation of α, which is its selective advantage derived from a greater fitness. Here $P(x,t)$ is the normalized frequency of the allele in the local population at (x,t), where x is the spatial distance in kilometers (km) and t is time in generations, both measured from some arbitrary origin.

The present work uses a Monte Carlo model that is an extension of the Fisher-Kolmogorov model to simulate the spread of an advantageous "modern" genotype made up of alleles of several genes in a widespread population of constant density. The model considers the demic diffusion of equal-sized hunter-gatherer group-demes, the interbreeding between them, and selective growth due to the genetic advantage of modernity. The diffusion and growth procedures are essentially Monte Carlo analogues of the corresponding terms in the Fisher-Kolmogorov equation. However, unlike the latter, the model incorporates selection cognizant of the role of a number of genes and explicitly simulates the interbreeding between demes. The quantity α now indicates the

selective advantage of persons carrying the complete modern genotype who appear with a frequency $P(x,t)$ in the local population, while σ^2 quantifies the variance of the distance moved by a deme in a generation.

An "individual" is represented here by an abbreviated "genome" that includes only those $N(= $ "gene number") diploid genes[4] the alleles of which are presumed collectively to give modern humans their coadapted genetic advantage. These genes are assumed to be unlinked and diallelic ("modern" and "archaic"), and the advantage is assumed to accrue only when the genome is fully "modern," that is, when it has $2N$ modern alleles at the loci associated with the modern genotype. A fully archaic genome has all archaic alleles, while a hybrid one has some archaic and some modern alleles. Each fixed-sized deme is represented by a single genome, under the assumption that demes are made up of closely related individuals. It is assumed that no biological barriers to fruitful interbreeding existed between modern and archaic humans but that hybrids had the same relative disadvantage as the archaics until they reached full modernity.

The definition of modernity used here and the meaning of the gene number should not be interpreted too literally, for they are merely intended to mimic the effects of a coadapted advantage accruing from the collective action of a number of genes. The greater the gene number the greater is the degree of coadaptation, thereby implying that a more complex genotype is being simulated.

The Monte Carlo simulations are done on a population in a one-dimensional array of contiguous discrete locations, or *areas*. Simulations using the analogous Fisher-Kolmogorov equation show that one-dimensional estimates give a reasonable approximation of the wave travel times on a two-dimensional representation of the Old World.

In the Monte Carlo model, the demic diffusion process is simulated by a random exchange of demes between adjacent areas, devised so as to maintain a specified variance, σ^2, of the distance moved per generation. The selective growth is simulated by increasing, through replication and at a selective advantage α, the frequency of the advantaged modern demes at the expense of the disfavored archaic/hybrid ones. The interbreeding occurs, between demes in the same area, with a probability that is a prescribed fraction of the random mating probability. This fraction $m_0(\leq 1)$ is hereafter called the *interbreeding rate*; it restricts the interbreeding between demes, lower values of m_0 implying a greater restriction. In cases of interbreeding, a deme-genome is replaced by an "offspring" produced by mating it with another deme-genome from the same area, using Mendelian rules for each gene locus. Otherwise, in cases of *in*breeding, the deme-genome is carried forward into the next generation without modification.

The processes of genetic drift and mutation are not included here.[5] The model merely examines the spread of an already formed genotype. Because of the model assumptions made, the group size and population density are not required to be estimated. The parameters σ^2, α, m_0, and N, of which only the first two appear in the Fisher-Kolmogorov equation, respectively characterize the demic diffusion, selective growth, interbreeding rate, and coadapted recessiveness of the genotype in the present model.[Details of the model may be found in the electronic edition of this issue on the journal's web page.]

Results of Monte Carlo Simulations

The simulations usually start from initial conditions wherein all areas, constituting a one-dimensional spatial array of discrete locations, are populated by fully archaic demes except the left-most area, which is maintained modern throughout to represent "Africa," the source of the wave of modernity. The population is then time-evolved, generation by generation, by the specified processes of diffusion, mating, and selection.

A diagnostic variable, African *parentage*, keeps track of the fraction of each deme's ancestry that is "African." This is assigned an initial value of unity in the African moderns and zero in the non-African archaic populations; thereafter, the parentage of an individual deme-genome is the average of its parents' parentage values. The parentage thus represents the fraction, in the deme, of "African" neutral alleles unassociated (i.e., not linked) with the alleles conferring modernity.[6]

DIFFUSIVE REPLACEMENT

When there is no interbreeding between demes (i.e., $m_0 = 0$), the exact solution for any N is obtained from the Fisher-Kolmogorov equation. The direct numerical solution of the Fisher-Kolmogorov equation is compared with the Monte Carlo solution in figure 2, at 1,000, 2,000, 3,000 and 4,000 generations, for a case with $\alpha = 0.02/$generation and $\sigma^2 = 320$ km^2/generation.[7] The figure shows only the frequency of moderns; however, as the population density is constant, the areas with no moderns are fully populated by archaics.

The wave obtained by the Monte Carlo solution, av-

5. The shifting-balance process is, of course, strongly dependent on genetic drift. However, the quantitative model simulates only the final phase of the process, which need not involve genetic drift. Simulations of variant models show that genetic drift, though likely to be strong in the small wave-front population, would not affect the gross features of the results presented here.
6. The "modern" alleles, of course, are *functional* (i.e., not neutral) genes. Thus the deme-genome could become fully modern without its parentage value's necessarily becoming unity. A parentage value between 0 and 1 indicates a partly hybrid lineage.
7. This value of σ^2, which is one-half (to account for the one-dimensional model) of the estimate of 250 miles^2/generation (= 640 km^2/generation) of Weiss and Maruyama (1976) obtained from present-day ethnographic data, will be used throughout as a representative value for Paleolithic hunter-gatherer groups.
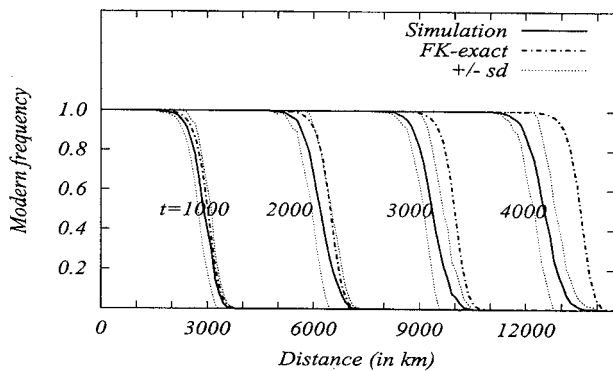
4. The "genes" here are perhaps more akin to linkage groups, for they are taken to mean portions of the DNA that are inherited whole.

FIG. 2. *Monte Carlo simulations and the exact (numerical) solution of the Fisher-Kolmogorov equation for a case with α = 0.02/gen and no interbreeding (m₀ = 0).*

eraged over 20 simulations and shown with the standard deviation, is somewhat slower than the exact solution of the Fisher-Kolmogorov equation. This effect is due to the assumption of a finite population in the Monte Carlo simulations.[8] Figure 2 shows that, for the parameters assumed, a diffusion wave from Ethiopia could reach the far ends of the Old World, 12,000 km away, in 4,000 generations (≃80,000 years).

The transition to modernity occurs essentially at the wave front, the narrow moving region between the fully modern and fully archaic areas. To the left of the wave front the frequency of moderns is unity; this frequency falls to zero across the wave front, since beyond it the transition has yet to occur. However, as the moderns move into archaic areas by demic diffusion and keep increasing because of natural selection, the wave front moves to the right, somewhat like an expanding wave. This wavelike progress of modernity—essentially at constant speed—is what is referred to here as a diffusion wave.

It is important to note that the wavelike progress in figure 2 is due to the effect of natural selection. Figure 3 shows that for neutral diffusion without a selective advantage ($\alpha = 0$), the spread of genes and parentage is not like a constant-speed wave; rather, their penetration distance varies approximately as $\sqrt{t}$ and is barely 2,000–3,000 km in 4,000 and 8,000 generations, respectively. This indicates that neutral traits/genes by themselves would have an inherently local range.

EFFECT OF THE INTERBREEDING RATE ON WAVE
SPEED

The Fisher-Kolmogorov wave speed (theoretically, $V = \sigma\sqrt{2\alpha}$) for the case with interbreeding holds approxi-

8. The Fisher-Kolmogorov solution speed is sensitive to the leading edge of the diffusion wave where P≪1, which the Monte Carlo simulations cannot capture very accurately. However, the latter probably more closely approximate the wave in a finite and discrete population.

mately for an advantageous dominant allele and then is independent of the interbreeding rate involved. However, the progress of advantageous recessive alleles ($N = 1$) and of recessively coadapted genotypes ($N > 1$) is strongly affected by the interbreeding rate. Figures 4 and 5 show the distance traveled in 4,000 generations for $\alpha = 0.04/$ generation and three interbreeding rates—$m_0 = 0.02$, 0.06, and 0.10—for $N = 1$ and 8, respectively. When $\alpha > m_0$, the effect of N is minor, as can be seen in these figures when $m_0 = 0.02$. However, when $\alpha < m_0$, the wave speed decreases more markedly for larger N. Thus, *large genotypes will not propagate unless their selective advantage exceeds the interbreeding rate.* While in the present model m_0 constrains the interbreeding between any two demes, for the modern genotype to propagate it is necessary only that the interbreeding rate between moderns and nonmoderns (i.e., archaics and hybrids who have not reached modernity) be so restricted.[9]

The above rule can be explained thus: Interbreeding causes a loss of the coadapted advantage of modernity in hybrids and results in a decrease in the effective selective advantage. The modern human fraction increases, because of its selective advantage, at a rate of $\alpha P(1-P)$, while hybridization causes a "loss" of moderns at the rate of $m_0 P(1-P)$ per generation; the latter follows directly from the definition of the interbreeding rate. The selective advantage, α, thus may be taken as a measure of the rate of increase of moderns due to natural selection, while the interbreeding rate, m_0, may be taken as a measure of the number of moderns being lost to hybridization. Thus, when the former exceeds the latter (i.e., $\alpha > m_0$), the modern genotype will propagate unambiguously—justifying the "law" above.

A separate factor to be considered is the rate at which hybrids become modern and thus gain the advantage of positive selection. We have seen that hybrids, in this model, obtain the coadapted advantage only when they

9. In models incorporating multiple genomes per deme, to obtain the same result it would seem necessary to introduce *intra*deme mating constraints to prevent nonmodern hybrids from reducing the fitness of otherwise modern demes.
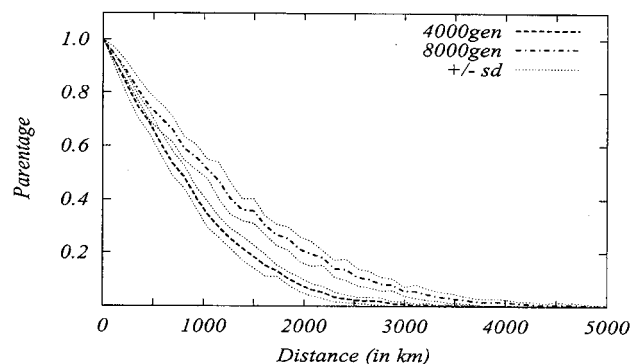

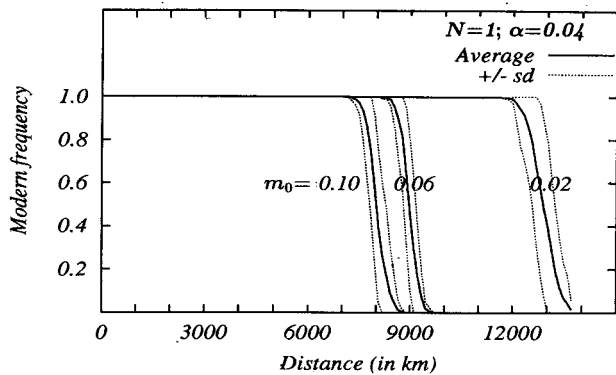FIG. 3. *The African parentage after neutral ($\alpha = 0$) gene diffusion for 4,000 and 8,000 generations.*

FIG. 4. *The progress of a recessive allele* (N = 1) *at 4,000 generations for various interbreeding rates and α = 0.04/gen.*

become "fully" modern, inheriting all $2N$ alleles making for modernity. As Mendelian inheritance is independently random for each locus, the rate at which hybrids become modern is obviously related to the gene number (which models the number and degree of coadaptation of the unlinked loci that influence modernity) of the genotype—the larger N is, the lower is the chance that a hybrid lineage will become modern. Conversely, when the gene number is small, the number of hybrid lineages attaining modernity may be significant. The value of N has a strong inverse effect on the fraction of hybrids that attain full modernity, with fewer doing so for larger N.

The differing effect of N on the diffusion-wave speed for the cases with $\alpha > m_0$ and with $\alpha \leq m_0$ can be explained thus: when $\alpha > m_0$, the genotypes of *all N* are supported by natural selection, as the rate of increase of moderns due to selection exceeds the rate at which they are lost by hybridization. Here, the fact that more hybrids attain modernity for lower N has a minor effect, merely causing a slight increase in the wave speed. In high-gene-number cases, when few hybrids will reach modernity, the effective growth rate of moderns will essentially be $\alpha - m_0$. In these cases, the wave speed can be adequately represented (when $\alpha > m_0$) by a modified Fisher-Kolmogorov formula $V_{\alpha - m_0} = \sigma\sqrt{2}\sqrt{\alpha - m_0}$.

When $\alpha \leq m_0$, the larger genotypes have effectively no selection, as the moderns become totally hybridized and virtually no hybrids become modern. However, for the smaller (i.e., low-N) gene-combinations some hybrids *do* reach modernity, and the wave propagates fundamentally because of this. Thus when N is low the genotype will spread, while when N is high it will not. This effect of N on the wave speed (when $0 < \alpha \leq m_0$) is likely to be even more pronounced in *real* populations, for there is likely to be significant intrademe selection—which the present model does not allow—for small advantageous gene combinations, leading to an even greater rate of their increase.

Nevertheless, model simulations (not shown here) suggest that single dominant and recessive alleles can propagate even under conditions of random mating ($m_0 = 1$). They show that advantageous dominant alleles will travel at the Fisher-Kolmogorov wave speed while recessive alleles ($N = 1$) spread at about one-half of that wave speed for high-interbreeding-rate cases. Recessive alleles with small selective advantages (say, $\alpha = 0.02$/generation) may travel over continental distances (~5,000 km) in 3,000 to 4,000 generations.

AFRICAN PARENTAGE

Ethnographic studies of present-day hunter-gatherers suggest an interbreeding rate of around 0.05 (Weiss and Maruyama 1976). This value of m_0 with an assumed $\alpha = 0.07$/generation would allow a diffusion wave of modernity to spread at a rate compatible with the fossil record—traveling a distance of 11,000 km or so in 4,000 generations. Recall that α is the *relative* growth rate in a *generation* of, say, 20 years. It quantifies a selective advantage. A value of $\alpha = 0.07$ may imply, for example, that if the fertility of archaic women was 7 children per mother, that of modern women was 7.5 children (these are typical values in natural populations), given that all other factors remained the same.

As long as the selective advantage is large enough to compensate for the loss of moderns due to hybridization (i.e., $\alpha > m_0$), the rate of spread of modernity is essentially independent of gene number. However, gene number has a marked effect on the spread of African parentage. Figure 6 shows the parentage of the emergent modern populations at 4,000 generations, after the passage of the wave. Parentage is strongly influenced by gene number: at every location, the higher the gene number, the higher is the African parentage. For $N = 8$, the neutral genes of modern populations even 10,000 km away are more than 50% "African," so to speak. As was argued above, the number of hybrids reaching modernity drastically decreases with increasing N. As all assimilation of archaic genetic material into modern populations occurs
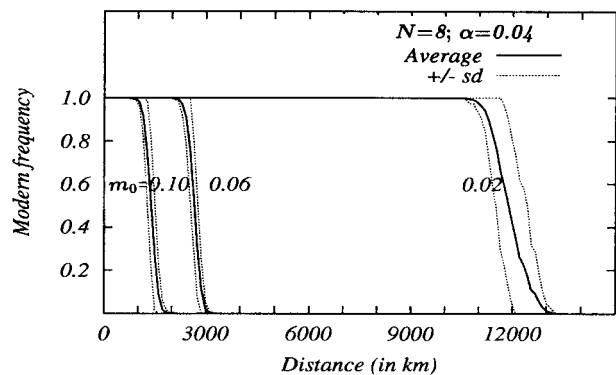

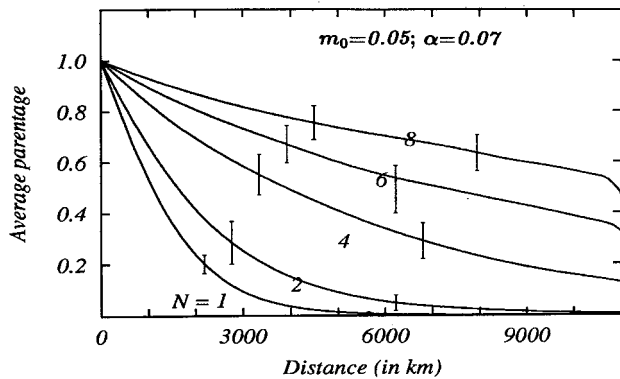FIG. 5. *The progress of a* N = 8 *genotype at 4,000 generations for various interbreeding rates and α = 0.04/gen.*

FIG. 6. *The African parentage of emergent moderns at 4,000 generations for various gene numbers;* $m_0 = 0.05$, $\alpha = 0.07$/gen. *The vertical bars indicate the* $(\pm)$ *standard deviation.*

only through hybrids that reach modernity, such assimilation is monotonically reduced for higher N, leading to a slower rate of decrease of African parentage with distance—to the extent that even "replacement" (parentage $\simeq 1.0$ everywhere) may be obtained with nonzero interbreeding rates. Thus, a larger combination of coadapted *functional* alleles conferring modernity will result in a greater fraction of African *neutral* genes in the non-African modern populations.

These results suggest that a relatively complex modern genotype could explain how all modern humans were closely related, even in the presence of interbreeding and assimilation, to the African subpopulation that initiated the wave of modernity. Yet, for a single recessive allele ($N = 1$; fig. 6) significant African parentage barely spreads 3,000 km, only slightly farther than the distance attained by merely neutral diffusion (fig. 3). Single advantageous dominant alleles will carry along even smaller levels of parentage. In these cases, the advantageous genes spread without carrying along the neutral genes of the initiating population.

REGIONAL EVOLUTION AND GLOBAL CHANGE

With these features of the diffusion process in mind, we may now attempt to explain the development of the modern genotype in Africa and even to suggest a general mechanism for human evolution. This mechanism is essentially the three-phase shifting-balance process of Sewall Wright.

Regional populations may have been subjected, over extended periods, to genetic drift and to minor advantageous changes in single genes (which can spread even when $\alpha < m_0$). These mutations could thus have propagated in local populations and yet not become widespread. Fortuitously, a number of such mutations that cause a series of small developments may have culminated in a coadapted combination of novel alleles that

together conferred a large advantage. If this gene combination finally achieved a selective advantage that exceeded the interbreeding rate, it would have propagated as a diffusion wave and, if globally advantageous, caused a transition in the entire human population. Alternatively, a genotype that was merely regionally advantageous could have created a unique regional type, such as the Neandertals.

Thus, the course of human evolution may have contained phases when regional populations, only weakly linked by gene flow, evolved essentially separately, for neutral gene diffusion would have affected only local populations and single advantageous genes would not have carried unlinked neutral genes or traits very far. However, interspersed between these periods may have been occasions when a regionally evolved advantageous genotype spread as a "revolution" across all populations, homogenizing them. It will later be shown here how a strong homogenization would have occurred with the spread of a high-gene-number genotype.

This proposed scenario is essentially that of Wright's process acting on a worldwide human population. The local development and subsequent fixation of advantageous genotypes would correspond to phases 1 and 2 and the diffusion wave to phase 3 of the shifting-balance process. It is important to recognize that Wright's process can only occur—as, we have seen, the diffusion wave can only propagate—when the interbreeding rate between the demes is low, so that each deme is relatively isolated. Under such conditions, aided by the high genetic drift typical within small subpopulations, coadapted gene combinations can form that may be advantageous only at a late stage of their development. High interbreeding rates would cause the breakup of these combinations before they formed and, as has earlier been seen, would even otherwise prevent their propagation.

EVIDENCE OF HYBRIDIZATION

One interesting aspect of the interaction between modern and archaic humans is that hybridization may have occurred between them. Even proponents of the recent-African-origin model do not deny such hybridization, even if they discount the possibility that it finally led to genetic assimilation. The genetic evidence seems to show few obvious signs of assimilation. That few fossils of clearly hybrid morphology (e.g., Duarte et al. 1999) have been found also suggests that little if any hybridization occurred.

However, this model indicates that the latter inference is not necessarily correct. It shows that it is possible that there was a progressive and complete hybridization of the archaics at the wave front even while there was a low rate of assimilation of archaic neutral genes into the emergent modern population. The model further suggests that, far from being an occasional occurrence of little significance, hybridization, along with natural selection for anatomical modernity, could have been the *principal* reason for the disappearance of the archaic mor-

phology, thus explaining the apparent "extinction" of archaic humans.

The simulations show that African parentage levels full sharply to zero at the wave front, implying that gene flow is associated only with the wave and does not penetrate beyond. So, *if* the advantage of anatomical modernity was fundamentally linked to morphology, all signs of hybridization would have appeared only at the wave front; hybrids that attained full modernity would have shown few signs of hybridization, at least in their primary metrics. The simulations show the wave front to be barely 800 km in width, and the region within which clear signs of hybridization would have appeared could have been as narrow as 300 km. Hybrids ahead of this narrow region were close to archaic, while those behind were essentially modern. Thus if the diffusion wave traveled through 3,000 km of Europe between 45,000 and 25,000 years ago, only 10% of the fossils of that period could be expected to have clearly mixed morphology—which may explain the rarity of obvious hybrids in the fossil record.

Another empirical observation that could be explained by these simulations is the relatively rapid transition that has been recorded to occur at the local level (Mellars 1989). The transition from "progressive" archaic to "essentially" modern could have taken as little as 2,000 to 3,000 years, the time required for the 300-km core of the wave front to pass over a site.

DISAPPEARANCE BY HYBRIDIZATION

The archaics at the wave front would have been progressively hybridized even while the fraction of moderns there increased because of natural selection. An obvious way to demonstrate this hybridization is in terms of the archaic/modern parentage ratio—the ratio of the average African parentage of the local archaics (including not-fully-modern hybrids) to that of moderns in the same area. Because the African parentage of a "pure" archaic is always zero, any nonzero value is due to hybridization. As the maximum African parentage in an area would presumably be found in the moderns, the archaic/modern parentage ratio would normally be less than or equal to unity. The ratio could be used to measure the degree of hybridization in the local archaics, larger values of the ratio indicating a more hybridized population. A ratio of zero would indicate that no hybridization had occurred. A ratio of close to unity would indicate that the local archaics had nearly as many African neutral genes as the local moderns, which could only be due to a complete hybridization of the archaics.

Figure 7 shows, for each location, the archaic/modern parentage ratio for a case (henceforth case A) with $\alpha = 0.07$/generation, $m_0 = 0.05$, $N = 8$, at two distinct times in each area's local transition to modernity: $R_{1/2}$ is the ratio at the point when archaics (including nonmodern hybrids) constitute exactly half of the local population, the other half being modern, and R_0 is the ratio when the archaics are at the point of local "extinction." The figure shows, for the chosen parameters, that even half-
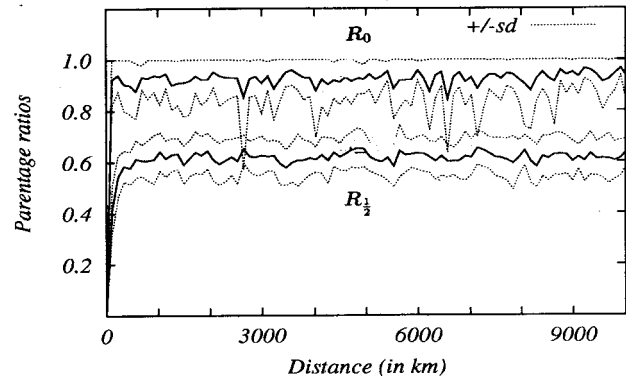

FIG. 7. *The* $R_{1/2}$ *and* R_0 *values for case A, showing the archaic/modern parentage ratio respectively halfway and at the end of the local transition for each location.*

way through the transition the archaics share 60% of the African neutral genes of the local moderns (as $R_{1/2} \simeq 0.6$), indicating that the archaics are substantially hybridized. As the archaics disappear, almost 90% of their neutral genes are finally the same as those of the local moderns (as $R_0 \simeq 0.9$). Therefore, the model indicates that, in addition to being gradually depleted by natural selection, the archaics at the wave front will also be progressively hybridized. Thus, given a coadapted genetic advantage of modernity, archaic humans may have disappeared merely by hybridization and a selective disadvantage.

Here hybridization refers to genetic mixing between moderns and archaics, while assimilation refers to the degree to which archaic genetic material enters into the modern populations that finally emerge. I have already suggested that fewer hybrids attain modernity when the genotype gene number is high. Because assimilation can occur only through hybrids that become fully modern, high-gene-number cases will have low rates of assimilation. Thus, while figure 7 shows that archaics were progressively and completely hybridized, figure 6 shows that low assimilation occurs for the same case ($N = 8$). This underscores the important point that high levels of archaic hybridization may yet be accompanied, when the gene number is high, by low rates of assimilation into modern populations. Thus, genetic studies indicative of low rates of archaic assimilation do not necessarily imply that no hybridization occurred between archaics and modern humans. Indeed, the archaics may have disappeared essentially because of hybridization, becoming partly assimilated into the modern populations.

THE SUB-SAHARAN/OTHER SPLIT

The genetic evidence seems to suggest that although sub-Saharan populations like the Khoisan and the Central African Republic pygmies have the greatest genetic depths, the Out-of-Africa migration was almost exclu-

sively from Northeast Africa. Large sets of nuclear DNA data show a sub-Saharan African/Other split, where sub-Saharan Africans have many genetic polymorphisms uniquely their own but non-African populations seem quite closely related to the North Africans (Nei and Roychoudhury 1982, Cavalli-Sforza, Menozzi, and Piazza 1994).

The model offers an explanation for this feature of the genetic evidence. It has been argued above that the modern human genotype may have evolved by a shifting-balance process in African populations. The intermediate evolution of the genotype possibly took place over a wide region, involving a large number of demes with considerable genetic diversity. Once the critical barrier—the selective advantage's exceeding the interbreeding rate—was passed, the genotype would have propagated out of the core region, carrying with it both modernity and African parentage (i.e., neutral genes). The question now arises: would modernity and neutral genes from the *entire* core region have been so carried outwards? The model shows that the spread would necessarily have been only from the *edge* of the core region wherein modernity first evolved.

Figure 8 shows the simulations for case A where the initial condition has the modern population in some depth—extending from −1,120 km to 0 on the horizontal axis of the figure—of which the "edge" modern populations are taken to be only 225 km wide (from −225 km to 0) while initially all populations beyond 0 are archaic. The figure shows, after the passing of the diffusion wave, the fractional contribution of the edge region as compared with the whole core region to the spread of African parentage. This fraction is obtained by using two separate parentage "tags" to mark the initial edge and core populations and tracking them through the simulations. As the "edge" is a subset of the "core," the fraction can at most be unity. The figure shows that the fraction approaches unity beyond 2,000 km. This indicates that the long-range transmission of modernity and neutral genes is almost exclusively due to the descendants of the modern groups from the edge of the initially modern core region.

THE UNIQUENESS OF THE WAVE FRONT

The above result can readily be explained in terms of the differing processes acting on the wave front and elsewhere. The "edge" region is essentially the initial location of the wave front. At the wave front, where alone both archaic and modern human types are found together, there is natural selection of moderns in preference to archaics, as well as the usual demic diffusion. When the modern populations expand, these expansions are actually confined to the small subpopulation of moderns coexisting at the wave front with archaics and increasing at the latter's expense. The wave-front speed (i.e., wave speed) is determined by this rate of increase, along with the diffusion parameters.

However, behind the wave front only diffusion acts, as there can be no selection—because there is no coex-
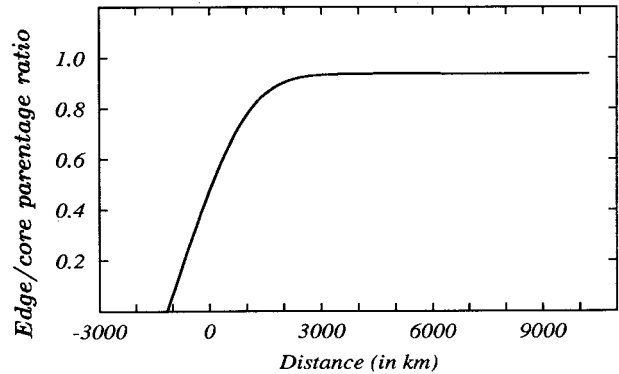

FIG. 8. *The fraction of the African parentage contributed from the "edge" (as compared with the whole of the "core" region) after 4,000 generations for case A.*

istence—between archaics and moderns. The difference is crucial: the wave front moves unidirectionally forward at a constant speed, while the modern groups behind the wave front move by random-directional diffusion. Thus modern groups that are behind the wave front will not catch up with the wave front.[10] Therefore, they will not further participate in the creation of new modern populations, which can occur only at the wave front, and thus will not transmit their genes to these new populations.[11] This is in contrast to the modern subpopulation at the wave front, which continuously creates new modern populations that carry its genetic signature.

This picture is substantiated by simulations that show that almost all the African parentage of the wave-front moderns at *any* time is derived from modern groups within or close to the wave front. Thus, the African neutral genetic inheritance of the wave-front moderns is derived almost exclusively from previous generations of wave-front moderns.

The significance of this is evident, for *all* new modern human populations are created at the wave front; only there do the archaic and modern types coexist, and only there can the modern genotype replace the archaic one. Because the results show that practically no modern groups that were *ever* behind the wave front contribute to this process, we are left with the conclusion that *all moderns created by the diffusion wave are essentially the direct descendants of a perpetual subpopulation of moderns at the wave front.* This has profound implica-

10. The wave front moves at a constant speed approximated by the modified Fisher-Kolmogorov wave-speed formula $V_{\alpha-m_0} \simeq \sigma\sqrt{2}\sqrt{\alpha-m_0}$. In contrast, the average (root-mean-square) distance moved by a group in t generations by diffusion is $\chi = \sigma\sqrt{t}$, which can be cast as an average diffusive "speed," $V_{diff} \equiv \partial\chi/\partial t = 1/2(\sigma/\sqrt{t}) = 1/2(\sigma^2/\chi)$, that can be seen to decline rapidly with distance moved. A simple calculation shows that, for the parameters assumed previously, unless a modern group were actually at or very near the wave front it would be left behind as the wave front surged ahead.
11. Except, perhaps, later by localized diffusion.

tions for the interpretation of the genetic and other data on modern human origins.

It is now assumed that the modern human diffusion wave was of a high-gene-number genotype that allowed limited assimilation at the wave front. It is shown below that the empirical evidence is consistent with this assumption.

The Genetic Evidence

The simulations presented above have demonstrated how, for certain model parameters, a diffusion wave of moderns could have expanded at speeds compatible with the fossil record. The wave of a complex genotype could transmit high fractions of African neutral genes to the emergent modern populations everywhere. The model shows how a low rate of assimilation of archaic human genetic material (resulting in a slow reduction of African parentage, with time and distance, in the emergent modern populations) could nevertheless have been accompanied by a progressively complete hybridization of archaic humans at the wave front. Even if the simulations are valid only as a "first-order" approximation, they support the possibility that the modeled processes of demic diffusion, hybridization, and genotype selection were the primary mechanisms in the modern human revolution.

Most strikingly, the model suggests that, in such a diffusion wave, all non-African modern populations were essentially created by a small wave-front modern population which—although possibly modified later by archaic assimilation and genetic drift—originated at the edge of the region where the modern genotype evolved. This point is now taken further. It is shown below that many of the puzzling features of the genetic evidence can be explained in terms of the present theory.

THE EFFECTIVE POPULATION OF WAVE-FRONT MODERNS

The number of moderns at a wave front of a continental wave about 800 km wide, say, half-filled with moderns, spanning another 800 km across its front, assuming a population density of 0.03 persons/km^2, will be 9,600 ($\simeq \frac{1}{2} \times 800 \times 800 \times 0.03$) individuals. Of this the effective population will be, say, around 2,000 individuals. This is according to the usual factor (of one-fifth) applied by conservation biologists to stable populations. In expanding populations, as in the modern population at the wave front, the effective populations may be a much smaller fraction of the breeding population (see, e.g., Templeton 1998), and the effective population figures here may actually be overestimates.[12]

THE APPARENT BOTTLENECK AT THE WAVE FRONT

Because the wave front spreads faster than the modern groups behind it, the wave-front moderns are essentially isolated, except for such archaic assimilation as may occur. A useful predictor of the genetic effect of isolation is the ratio N_b/t_b, where N_b is the effective size of an isolated population and t_b is its age in generations; if $N_b/t_b < 10$, then there is a significant reduction of genetic diversity—an effective bottleneck—that is correspondingly more severe for smaller ratios (Takahata 1993).

As the wave travel times are long ($\sim$ 4,000 generations) and the effective size of the wave-front modern population small ($\sim$ 2,000 individuals), given sufficiently low archaic assimilation rates there will be a severe reduction of genetic diversity in the wave-front moderns, particularly at mtDNA and Y-chromosome loci, which have effective populations one-fourth that of diploid markers. Thus correspondingly low genetic diversity will be passed on by the wave-front moderns to their descendant populations, which will all seem to have emerged from a bottleneck.[13] This bottleneck will be only *apparent*, as the breeding population—including the moderns behind the wave front and the archaics ahead of it—need never have been small.

THE WAVE FRONT AS A MECHANISM OF HOMOGENIZATION

At low archaic assimilation rates, the genetic profile of the wave-front modern population would have changed slowly. Thus the descendant populations created along the wave path would have been closely related to each other. Even taking into account that there were several continental waves (fig. 1), given that they had the same initiating population in Northeast Africa, a low rate of archaic assimilation, and wave-front bottlenecks, the entire world population would have been homogenized by the modern transition. Further, because populations along the same wave path (say, the European) would have been particularly closely related, with greatly reduced genetic distances, it is possible that the separate diffusion waves created the "races" and "subraces" of present-day humanity.

The wave-front bottlenecks and the consequent homogenization could explain why genetic diversity is low in human populations, as are the apparent coalescence times for some loci (particularly in mtDNA and Y-chromosome studies), and why so small a number as around 10,000 individuals has been estimated by many geneticists as the effective size of the modern human lineage. The diffusion-wave theory thus offers an alternate explanation for these empirical observations that have gen-

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12. All the numbers used in the effective-population estimate are subject to some uncertainty. The population density is within the range proposed by Wobst (1976). An 800-km-wide front would be expected in Western Europe, along the South Asian wave path, and in North Asia between the Altai and Tien Shan Mountains. The ratio of effective/census populations could have been as low as 0.03 (Relethford 1998). The width of the wave front is essentially fixed

by the variance σ^2 and the wave speed, both of which have some empirical backing.

13. If there were a substantial archaic assimilation rate there could be no bottleneck, as the wave-front moderns would not then be sufficiently isolated. Thus, a low assimilation rate—and a high-gene-number modern genotype—is seemingly indicated by the empirical evidence.

erally been interpreted as support for the recent-African-origin replacement model.

THE DIFFUSION WAVE AS AN ENGINE OF "POPULATION GROWTH"

An interpretation of the mtDNA data in terms of effective population sizes has shown that African, Asian, and European populations apparently had large demographic expansions (of factors greater than 100) that were respectively initiated approximately 100,000, 88,000, and 56,000 years ago and were possibly associated with the spread of modern humans (Rogers and Harpending 1992, Harpending et al. 1993, Rogers 1995).

The diffusion wave explains these "population explosions" detected by mismatch analyses of mtDNA data. In the wake of the wave front, the populations descended from the bottlenecked wave-front moderns would initially have had a genetic unity indicative of a small effective size. After the passing of the wave, however, the genetic diversity would again have increased in the emergent modern populations, and the indicated regional effective size would have approached the much larger actual breeding population, giving the impression of a large population increase.

MISMATCH AND INTERMATCH ANALYSES OF mtDNA

Apart from detecting population explosions, mismatch and intermatch analyses of mtDNA data suggest (1) that these demographic expansions in the African, Asian, and European populations and even within these populations occurred as much as many tens of thousands of years apart and (2) that the Asian and European populations seem to have separated from the African around 100,000 years ago, long before their respective expansions (Harpending et al. 1993). Both these observations can readily be explained in terms of the model simulations.

The "population explosions" would, of course, have occurred in a region only after the diffusion wave front had passed over it. Traveling at around 3 km per generation, the diffusion wave would have taken tens of thousands of years to traverse intercontinental distances, which would explain the differing expansion times in the global populations. Further, as has been argued above and checked by the simulations, the modern populations behind the wave front would have ceased to have any effect on the wave-front moderns because of the difference in diffusion speed and wave speed. As the wave front left Africa around 100,000 years ago, the wave-front moderns that finally transmitted modernity and African mtDNA to Asian and European populations would have been isolated from the African thereafter—which explains the empirical observation of the apparently early separation of the Asians and Europeans from Africans. The Asian and European lineages would themselves have split when the wave reached West Asia.

ALLELE LOSS AT THE WAVE FRONT

The genetic diversity of present-day Africans at neutral DNA loci has usually been found to be higher than in all other populations. This is usually seen as support for the recent-African-origin model. However, in the present theory, the same empirical observation is expected from the core region, where the modern genotype first evolved and modern humans have the deepest roots.

Given a sufficiently low archaic assimilation rate and thus a slow rate of reduction of African parentage in the wave front, the latter would have carried many African neutral genes far out of Africa. However, if any African polymorphism had been lost from the wave front it would not have traveled farther, as all long-distance transmission of neutral alleles occurs only by "surfing" on the wave front.

Unique African polymorphisms, carried along for as many as 4,000 generations by an effective population of about 2,000 individuals, would have suffered a severe decrease of genetic diversity because of the wave-front bottleneck. The farther the wave front traveled, the greater would have been the progressive loss of the unique African alleles—leaving "tracks" seemingly indicating a migration out of Africa. Furthermore, because of the bottleneck at the wave front, there would have been steadily decreasing genetic diversity away from Africa, given low assimilation rates. Both patterns have been observed in present-day populations, in single-locus and in multilocus microsatellite studies (e.g., Tishkoff et al. 1996, Harpending and Eller 1999). While such evidence has generally been interpreted as supporting the recent-African-origin model, it can also be explained in terms of the wave-front bottleneck, as proposed here.

DIVERSITY IN HUMAN POPULATIONS

The F_{st}, a measure of the ratio of interpopulation diversity to total diversity, is around 0.10 to 0.15 between continental human populations. This value is larger than would be expected from a recent African origin of modern humans and their subsequent expansion into other regions (Harpending and Rogers 2000). For example, if modern humans split into continental groups of effective size 10,000 individuals around 2,000 generations ago, the expected F_{st} would be barely 0.096, even excluding the unifying effects of more recent gene flow.

However, the present theory suggests that the initial effective populations would have been much smaller, as the separate continental populations would have been created primarily by the wave-front moderns. Even ignoring the possibility of archaic assimilation, genetic drift in these smaller wave-front populations would have been greater and would explain the higher F_{st} empirically obtained. The present theory suggests that the population expansions followed in the wake of the wave front and thus would have had no impact on the genetic drift within the wave-front moderns.

Harpending and Rogers (2000) further propose that, instead of a single population expansion, there may have

been a cascading series of colonization bottlenecks as modern humans spread—which would explain the larger-than-expected F_{st} as well as the steadily decreasing genetic diversity away from Africa. A high-gene-number diffusion wave, because of the bottleneck at the wave front, would very naturally have created conditions akin to the cascading bottlenecks they propose. The present theory would therefore explain the same features of the genetic data.

REPLACEMENT OR ASSIMILATION?

Not all genetic studies show signs of bottlenecks. For example, proteins, blood groups, and alleles of the major histocompatibility complex (MHC) loci show non-Africans having a genetic diversity comparable to and often greater than that of Africans (Takahata 1995). The presence of numerous ancient alleles at the MHC loci has been interpreted as suggesting that no population bottlenecks may *ever* have occurred in human and hominoid evolution (Ayala 1995). Other genetic systems too do not carry the bottleneck-and-expansion signature seen in mtDNA and at some other loci. These contrasting indications from different genetic studies need an explanation, particularly because the presence of bottlenecks has been construed as supporting a replacement scenario for the modern transition. I will now show that the dichotomy in the genetic data strongly suggests that assimilation from archaic populations occurred during the modern transition.

The resolution offered here stems from the observation that, typically, loci with high mutation rates and hence with recent polymorphism show bottlenecks while those with low mutation rates and ancient polymorphism do not. The difference is suggestive because the former would have formed unique regional patterns in hominid populations within a few hundred thousand years, while the latter, in particular the very ancient polymorphisms that predate the genus *Homo*, would possibly be found across the world population of hominids. The contrasting features of the genetic evidence can be explained in terms of the differing effects of the diffusion wave of modernity on polymorphisms that were global and widespread before the wave in comparison with those that were local to particular regions.

It is already been argued above that unique African neutral alleles being carried by the diffusion wave front would have developed the typical symptoms of bottlenecked populations, leading to significant allele loss. However, with ancient and widespread polymorphisms there would also have been the possibility of allele *replenishment* through assimilation from archaic populations, for the same polymorphisms, so to speak, would have been found in both modern and archaic humans. A wave-front population initially identical at these loci to the global archaic populations would have subsequently diverged and shown the effects of bottlenecking only if there were essentially no assimilation at the wave front.

Recall that, according to this theory, (1) all assimilation from archaic humans would have occurred only at the wave front, (2) the wave front would have been isolated from the moderns in its rear, and (3) all new modern populations would have been created at the wave front, and therefore any signs of bottlenecking in the wave-front moderns would also have appeared in the emergent populations. Now consider that without assimilation the wave front would have been completely isolated—from the moderns behind it because of its greater speed and from the archaics ahead by the bar on admixture. Under these conditions *all* neutral polymorphisms, whether local African or widespread, would have been bottlenecked and shown the same symptoms of reduced genetic diversity away from Africa.

However, such a bottleneck would not have allowed many polymorphisms to survive in the wave front as it spread slowly across the Old World. For example, simulations of a wave-front population of 2,000 individuals tracked through time suggest that only around 4 neutral alleles per locus survive the bottleneck for 4,000 generations if the population has no assimilation. However, with an assimilation rate of merely one individual per generation, from archaics identical at these loci to the initial wave-front population, an average of 40 alleles remain in the wave front.[14] Thus a very considerable diversity could have been passed on to non-African populations even with low (but not *zero*) rates of assimilation.

As many loci do show ancient polymorphisms of considerable diversity in non-African populations, this definitely suggests that assimilation *did* occur at the wave front. Otherwise, genetic diversity would have severely decreased farther from Africa. Assimilation explains why proteins, blood groups, MHC loci, etc., show no signs of an Out-of-Africa bottleneck. Thus, the empirical fact of the absence of bottlenecking[15] in ancient polymorphism implies that *assimilation, not replacement, is the best explanation of the genetic data.*

However, given that the genetic evidence also shows a considerable spread of African alleles, which could happen only with a low assimilation rate, the latter was probably not much in excess of the minimum required to prevent bottlenecking in the widespread polymorphisms. To obtain an estimate of the rate of assimilation from archaic populations, we can use Wright's (1931) rule

14. These simulations—which were done without diffusion and selection—track neutral genes in a population of 2,000 wave-front moderns through time, assuming random mating and a prescribed assimilation rate. The computations were initialized with 100 alleles per locus. For assimilation rates of 0.5, 2, and 4 individuals per generation, the average numbers of alleles per locus present in the population after a few thousand generations are respectively around 27, 60, and 80. As the assimilation is random, the particular alleles within the wave front may change over time, with the result that the final spectrum of alleles in the emergent moderns may be even wider than these figures indicate.
15. Loci with alleles that were widespread before the wave would be less likely to show either bottlenecks or expansions. This may explain why evidence of expansions is not always apparent in the genetic data (Harpending and Rogers 2000). The differing effects of the wave on "local" and "widespread" polymorphisms would also explain why mtDNA and some nuclear genes present contrasting pictures of human evolution (Hey 1997).

that one immigrant (meaning here the assimilated genetic equivalent[16] of one archaic individual) every two generations is enough to prevent significant bottlenecking of the ancient polymorphism in the wave-front moderns, who would have transmitted their genes to all emergent modern populations. This, of course, is an estimate of the minimal assimilation required. Even this low rate of assimilation into the wave-front modern population—of, say, 2,000 individuals—would, in 4,000 generations, have resulted in a cumulative 60% assimilation of archaic neutral genes in that population.[17] Therefore, in this view of the genetic data, there must have been substantial non-African archaic assimilation into modern populations farther away from Africa.

FURTHER EVIDENCE OF ASSIMILATION

Other evidence suggests that assimilation did occur. For example, the unique and ancient (> 200,000-year-old) polymorphisms that exist in some Asian populations and the high coalescence time obtained in a Melanesian population (Harding et al. 1997, Fullerton et al. 1994) can most easily be explained by archaic assimilation into modern populations. Similar genetic evidence from another locus determining hair and skin pigmentation has suggested assimilation from Eurasian archaic populations (Harding et al. 2000).

There is also fossil evidence in Asia of morphological continuity across the archaic-modern transition (Pope 1992), reinforced by fossil evidence from across the world (Wolpoff et al. 2001). Assimilation could also explain the long-standing continuity of anatomical features such as shovel-shaped incisors in East Asians. Many such traits were presumably neutral. Simulations of the Monte Carlo model (not shown here) indicate that single *advantageous* alleles would have been even more readily assimilated from archaic populations. Such assimilation from resident archaics could have aided the genetic adaptation of the moderns to local ecological conditions as the wave moved far from Africa.

Fossil and Archaeological Evidence

WAS THE MODERN HUMAN ADVANTAGE MERELY ANATOMICAL?

The interpretation of the genetic evidence offered above supports an assimilation scenario. However, the mor-

phological similarity of early modern humans across the world has generally been interpreted as suggesting population replacement. The evidence of regional continuity is generally seen, if at all, only in the more minor features of the cranial and dental characteristics of regional populations.

That, in the presence of genetic assimilation, identical modern features appeared across the world suggests that the modern anatomical form was *itself* advantageous —probably the very advantage being propagated by the diffusion wave. Thus the modern human advantage may have been purely anatomical. This possibility is interesting because it is usually assumed that some singular development of intellect, culture, or linguistic capability precipitated the modern human transition.

The modern phenotype differs from the archaic primarily in the cranium and the pelvis and in robusticity. The modern features—which include a short, high-domed cranium, thinner cranial walls, the presence of a chin, and reductions in the mid-face projection, in browridges, and in the size of dental structures—all seem to be associated with a decrease of the anterior-posterior diameter of the modern cranium. This dimension is crucially linked to birth difficulty (Rosenberg 1992), which for humans is significantly greater than in closely related species. These changes, along with concomitant modifications of the pelvis, may have reduced birth difficulty and hence childbirth mortality in anatomically modern populations.

Thus, while further study into the root cause of the modern human advantage is undoubtedly required, a reduction in childbirth mortality could have been *the* co-adapted advantage offered by the modern phenotype. An increase in fertility due to this advantage is sufficient to explain the modern transition.[18]

THE CULTURAL EVIDENCE FROM EUROPE

The clear association in Europe of the Middle-to-Upper Paleolithic transition in lithic culture with the morphological transition to anatomical modernity also needs to be explained. This association has often been used to argue the case for a presumed intellectual superiority of modern humans. However, a lithic culture associated with the wave-front moderns would have propagated even if it was an inherited neutral attribute that neither offered an advantage nor was symptomatic of one. The genetic evidence shows, as was argued above, a rate of assimilation of archaic genes possibly as low as the genetic equivalent of one individual every two generations. This low rate of assimilation would not have changed a group attribute, such as culture, of the population of, say, 2,000 wave-front moderns. Therefore the latter's culture

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16. Given the mechanisms at play, it is very unlikely that any archaic individual could enter whole into the modern gene pool. The more probable mode of assimilation would be that of many hybrids, each with a small degree of archaic parentage, reaching full modernity at the wave front.

17. The African parentage, *f*, of an assumed population of 2,000 wave-front moderns assimilating the genetic equivalent of one-half of an archaic human per generation can be modeled by $df/dt = -f/4000$ (with $f[0] = 1$), which has the solution $f = exp(-t/4000)$ and yields a parentage of $e^{-1}(\approx 0.37)$ after 4,000 generations. An assimilation rate of one individual per generation would reduce this figure to $e^{-2}(\approx 0.14)$ and increase the cumulative archaic assimilation to 86%.

18. A linkage between the maternally inherited mtDNA and greater maternal mortality in archaic populations could also explain, given the already low rate of assimilation, how the mtDNA of Neandertals may have been lost (Krings et al. 1997) to modern populations without, however, precluding the possibility that nuclear genes were assimilated.

would have been inherited, along with genes, by the new modern populations all along the wave path.

Thus the Aurignacian culture, which had clear antecedents in West Asia, could have propagated because of the anatomical modern advantage merely because it was the culture of the wave-front moderns when the diffusion wave entered Europe. Language, being usually inherited, would have spread by similar means—by surfing the diffusion wave front. Therefore, the spread of the Aurignacian culture is an indication of the profound cultural and linguistic[19] homogenization that could have been wrought by the diffusion wave of modernity, thus suggesting a context for the subsequent developments in human societies.

THE DELAY IN THE TRANSITION IN EUROPE AND EAST ASIA

Although modern humans had apparently reached West Asia 100,000 years ago, the modern transition took place in Europe after another 60,000 years and in East Asia perhaps even later. One explanation for this delay is possibly that the human populations of West Asia and Europe were separated from each other by the flooded Turkish straits from around 130,000 till around 70,000 years B.P., when the fall of sea levels to approximately 60 m below the present (Rohling et al. 1998) would have created land bridges from Europe to West Asia.[20] This seems to have been followed by a Neandertal movement into West Asia (the later Neandertal sites, at Kebara, Amud, and Shanidar, all date to around or after 70,000 years B.P.). It is possible that a hybridized wave front in West Asia somewhat later and the diffusion wave moved into Europe around 45,000 years ago. In Asia, there probably was no "delay"; the wave may have kept moving into Asia after reaching West Asia 100,000 years ago. It could have taken the diffusion wave 60,000–70,000 years merely to cross the distance to East Asia.

This also explains the differing cultural associations of modernity in Europe and Asia. In contrast to the situation in Europe, there was no obvious cultural change in Asia associated with anatomical modernity. While the Aurignacian Upper Paleolithic culture, developed in West Asia around 50,000 years ago, was carried into Europe, the earlier Middle Paleolithic cultures that spread as far as Siberia in the north and India in the south (Clark 1992) may have been carried along by the earlier Asian waves. The reason that these cultures were not carried all the way to the Far East is possibly that they were "lost" from the wave front (for example, when the latter passed over a region with inadequate-quality lithic material). As with neutral genes, once lost from the wave

19. That the wave paths in figure 1 correspond to the present-day or historical ranges of large language families seems to hint that the protolanguages of these families were spread by the diffusion wave of modernity. This, of course, would ascribe to language families much earlier origins than is now commonly accepted.
20. The diffusion wave, which requires a considerable influx of moderns to propagate, could have been stopped even if some population and genetic exchange did occur across the Turkish straits.

front an inherited culture would not have propagated further with the wave.

THE GENETIC AND FOSSIL EVIDENCE FROM AUSTRALASIA

The island populations of Australo-Melanesia show genetic depth and diversity second only to those of sub-Saharan Africans (Nei and Roychoudhury 1982, Cavalli-Sforza, Menozzi, and Piazza 1994). The Australian fossil record has also shown the clearest evidence of continuity linking present-day Australian Aborigines through 10,000–15,000-year-old Australian fossils to archaic Indonesian and Chinese fossils (Wolpoff, Wu, and Thorne 1984, Hawks et al. 2000). This is quite at variance with, say, the situation in Europe, where much of the genetic and fossil evidence arguably supports an abrupt transition with seemingly little continuity. The explanation may be that the diffusion wave was disrupted when the wave reached Indonesia because demic diffusion was prevented from carrying the modern genotype into Australo-Melanesia by the intervening seas.

Thus one scenario explaining the Australian evidence could be that the earliest settlement of Australo-Melanesia, some 60,000 years ago, was by anatomically archaic people, possibly a gracile Asian "premodern" type (Thorne 1977). The "African modern" diffusion may have occurred by intermittent migrations beginning as late as 15,000–20,000 years ago, after the diffusion wave reached Indonesia, leading to hybridization with the earlier population. This would explain the evidence of recent (terminal Pleistocene/Holocene) evolution in Australian populations (Brown 1992), the greater Australo-Melanesian genetic depths, and the evidence of morphological continuity. This scenario is supported by the fact that the oldest known Australian fossil has neither close morphological affinities to early modern Africans nor "African" mtDNA (Adcock et al. 2001).

EARLIER REVOLUTIONS

The modern human revolution may not have been unique in human evolution. There seems to have been a previous diffusion wave from East Asia—anthropologists have noted the similarity of some of the premodern Chinese fossils (e.g., Dali) to late Middle Pleistocene Africans (e.g., Jebel Irhoud) that were transitional to modernity (Stringer 1992, Pope 1992). Corroborative genetic evidence of a "back-to-Africa migration" has been detected from Y-chromosome and β-globin studies (Hammer et al. 1998, Templeton 1998).

This fossil and genetic evidence may thus be explained by postulating a premodern wave out of East Asia. This wave may even have been the first phase of the modern human revolution, the wave out of Africa being the second, for some "modern" features such as thin cranial walls combined with large cranial capacity seem to have evolved earliest in East Asia (Pope 1992).

Apart from this, there may have been other human "revolutions." That other transitions, from *Homo*

erectus to "late" *H. erectus* and to archaic *H. sapiens*, occurred is evident from the fossil record. Thus, human evolution in the Pleistocene may have been driven by a shifting-balance process that created regional phenotypes by genetic drift and local selection, propagating by diffusion waves those that were globally advantageous. The latter process—rather than speciation—possibly caused the revolutions apparent in the human fossil record. Thus, intraspecies revolutions may even have led humanity through the various transitions in human evolution—supporting the possibility of there having been no cladogenetic speciation (as opposed to anagenesis) within the genus since the advent of *Homo* (Wolpoff, Wu, and Thorne 1984).

THE GENESIS OF *HOMO*

If the shifting-balance process was a primary mechanism in human evolution, the pattern of human evolution would have been uncommon, probably unique among the primates. The great apes do not show the low genetic diversity that is characteristic of humans and has been explained here as the signature of the final phase of the shifting-balance process. The operation of Wright's process, which would throw up advantageous gene *combinations*, could perhaps explain the profound adaptive advances of humans over their genetically closest relatives.

If the shifting-balance process operated in human evolution, it would seem to follow that hominid populations had been largely segregated in the small-deme and low-interbreeding social structure that would have allowed advantageous gene combinations to develop locally and then propagate globally. None of the great apes have this social structure, and if hominids had it this could explain the uniqueness of human evolution.

Perhaps such a social structure developed from one similar to the multimale communities of chimpanzees when collective hunting engendered a group cohesiveness that would have been impossible in the largely foraging apes. If so, the recent evidence (Heinzelin et al. 1999) that hunting and/or scavenging (probably collective) were prevalent among the later australopithecines is suggestive. It is possible that the posited social structure developed among these hominids, led rapidly to the genesis of *Homo*, and crucially influenced human evolution for another 2.5 million years. The great social and demographic changes since the Neolithic age may finally have stopped human evolution by Wright's process.

Conclusion

This paper is an exposition of a theory proposing that the last major episode in human evolution was caused by the diffusive spread of an advantageous modern human genotype. The theory is predicated upon a quantitative model that is an extension of the single-gene Fisher-Kolmogorov equation generalized to consider the diffusive movement of an advantageous genotype consisting of many genes controlling multiple coadapted traits.

Many of the direct implications and predictions of the model are testable against the known empirical facts. I argue that the empirical evidence points to the conclusion that assimilation, not replacement, best explains the genetic data. The theory offers an explanation for the disappearance of archaic humans that reconciles—within the framework of Sewall Wright's shifting-balance theory—the fossil, genetic, and archaeological data that have generated an extended debate among anthropologists, geneticists, and prehistorians. In short, this paper suggests a comprehensive solution to the problem of modern human origins.

The course of human evolution was possibly characterized by several episodes, or "revolutions," in which advantageous genotypes created regionally by a shifting-balance process spread as diffusion waves across global populations. At the root of the uniqueness of human evolution possibly lay a social structure—of small demes with low interbreeding rates—that allowed a development by Wright's shifting-balance process. This social structure, which would also have influenced the development of human intelligence and behavior, was, I suggest, the unique determinant factor in human evolution.

Comments

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As an archaeologist interested in our origins who tries —with limited success—to keep up with the burgeoning genetics literature, I was fascinated to read Eswaran's beautifully constructed, elegantly written, and methodologically sophisticated essay. Using Sewall Wright's shifting-balance theory (1932), he makes a strong case that most of the features associated with anatomical modernity originated in Northeast Africa as a coadapted gene complex that spread relatively rapidly (2,000–4,000 generations) throughout the Old World because it offered a strong selective advantage over the genotypes of the archaic hominids descended from the early Pleistocene radiations usually associated with *Homo erectus*. Using Monte Carlo simulations, Eswaran models that spread not by some variant of the migration scenarios commonly invoked by recent-African-origin advocates to account for replacement but by a "diffusion wave" of modernity consisting of small modern populations expanding continuously along a narrow (200–800 km wide) but rapidly moving wave front by means of small random movements, hybridization, and natural selection favoring propagation of the modern genotype. In doing this, he gets around what I take to be the major obstacle to most of the recent-African-origin scenarios—the fact

that the alleged peregrinations of moderns left no traces in the archaeological records of Europe and western Asia (Clark 1992, 1999, 2002; Clark and Lindly 1989; Clark and Willermet 1997). Whether the replacements implied by these scenarios are evident in the fossils is also hotly contested (cf., e.g., Stringer 1992, Stringer and Gamble 1993, Stringer and McKie 1996 with Wolpoff et al. 1984, 1994, 2001). What is so compelling about Eswaran's account is that it explains *how* and *why* modern form might have arisen and spread and thus lends greater support to the multiregional-continuity model, which has a fully developed conceptual framework (see, e.g., Wolpoff et al. 1984; Wolpoff 1989, 1992), than to that of recent African origin, which does not. Most of the genetics studies with which I am familiar (especially those based on nonrecombinant DNA) are essentially atheoretical pattern searches that assume that mutations are adaptively neutral, leaving me to wonder what adaptive advantage—however defined—might have been conferred on anatomical moderns that supposedly allowed them to replace archaics throughout their ranges. Certainly no such adaptive advantages are evident in the archaeology.

Extreme replacement scenarios like those promoted by Stringer and McKie (1996), Mellars (1996), Klein (1999), and others are only part of a bewildering array of recent research that is "selectively consilient" with particular scenarios developed in genetics and molecular biology. Generally speaking, paleoanthropologists are ill-equipped by inclination and training to digest and assimilate this mountain of information, couched in a lexicon with which we have only a passing familiarity. However, the sheer volume of post-1990 publication should remind us that the genetic evidence is not as cut-and-dried as it is commonly presented as being. Many workers in both camps appear to assign an unwarranted priority to the evidence for pattern in the genes, as if the meaning of pattern were uncontroversial within genetics and did not need to be reconciled with pattern in the fossils and the archaeology. Originally, much of this research focused on the mtDNA scenario proposed by Cann, Stoneking, and Wilson, (1987), with its implication that no admixture between Neandertals and moderns could be accommodated. If true, it implied that differences between moderns and earlier hominids had to be at the species level. There was little appreciation by paleoanthropologists that, within the corpus of mtDNA research available through the late 1980s, other base-pair substitution rates were published and defended which implied a hominid radiation out of Africa after ca. 2 million years ago, corresponding either to the appearance of *H. erectus* (usually considered a grade) or the appearance of *H. sapiens* (Wolpoff 1989, Wolpoff et al. 1993); that the Cann rate implied an absurdly late ape/human split, at ca. 3.5 million years ago, for which there is no fossil evidence whatsoever; and that, through the late 1990s, other large, complex, stable, and ancient genetic systems (nDNA single nucleotide, RFLP, and short tandem repeat [microsatellite, minisatellite, *Alu*-insertion] polymorphisms; β-globin; the Y-chromosome HLA complex) had been investigated, along with continued research on mtDNA

and on classic nDNA genetic markers (summarized in Howell 1999:191–244).

This research produces estimates of the age of the most recent human mtDNA ancestor that range from 0 to 806,000 years (95% confidence interval, data from 12 studies postdating 1991). Coalescence estimates of modern human ancestry based on Y-chromosome and nDNA polymorphism data (11 studies postdating 1995) range from 62,000 to 1,300,000 years. While the weight of mtDNA and Y-chromosome research published so far is consistent with *some* kind of recent-African-origin model, it is important to remember that the histories of particular genetic systems are not the same as population histories (if they were, each genetic system would have the same history) and that the genetic evidence as a whole does not uniquely support a recent (< 100,000 years B.P.) divergence date for *H. sapiens* or imply a speciation event, a radiation or range extension out of Africa, or a physical replacement (by whatever mechanism) of one form of hominid by another. There continues to be little appreciation by archaeologists and human paleontologists that molecular biology has an internal dynamic characterized by the same kinds of controversy and debate found in other disciplines (Lewin 1988*a*, *b*, *c*, Pennisi 1999, Strauss 1999).

As a convinced multiregionalist, I like Eswaran's paper because it proposes a plausible scenario to explain the appearance of modern form without the necessity for invoking migration (Clark 1994). Be that as it may, it is still difficult to escape the impression that debate about the meaning of pattern in the genetic data is as subject to the particular scenarios set up for it as the controversies raging around the archaeological and paleontological evidence.

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This paper will quickly become a central part of the canon of biological anthropology. Eswaran starts with a very simple model of the appearance of a new advantageous trait complex in a subdivided population—selective advantage along with demic diffusion—and derives a rich variety of consequences of the process. The simple model explains the available genetic and morphological data better than anything we have had until now and gives us many testable predictions.

Two major traditions of evolutionary theory emerged during the first half of the past century, one due to R. A. Fisher and one to Sewall Wright. Fisher emphasized the spread of advantageous mutations and their accumulation in large populations. Wright emphasized the importance of combinations of traits, coadapted gene complexes, and believed that subdivided populations undergoing drift would function like semiautonomous experiments generating combinations of traits. When an advantageous complex occurred it would then spread

throughout the whole population. Since the 1970s the Fisher point of view has dominated evolutionary biology: Hamilton, Williams, Dawkins, Maynard-Smith, and Grafen are all firmly in the Fisher tradition. Wright's ideas have received less visible attention.

Eswaran brings Wright's ideas to the puzzle of modern human origins in this paper, and I predict that his approach will quickly be applied to similar problems elsewhere in evolutionary biology such as the spread of Africanized bees in the New World. The core of his achievement is the brilliantly simple implementation of the idea of a gene complex: an individual enjoys the selective advantage of modernity if he is a homozygote at all of N genetic loci. With this simple parameter we can model the spread of a single gene ($N = 1$) all the way to a new species (N large). Thus the multiregional and Garden of Eden hypotheses are extreme cases of the general model.

With only the evidence of mitochondrial DNA, we were almost satisfied a decade ago with the idea that the origin of modern humans was a speciation event, but subsequent genetic evidence (e.g., Harpending and Rogers 2000) and issues involving the apparent discordance between anatomical and technological modernity have essentially falsified the speciation model. At the same time, the overwhelming evidence of greater Sub-Saharan African genetic diversity along with diversity clines away from Africa deny the simple Fisherian picture of ongoing accumulation of advantageous mutations from throughout the species of archaics. Eswaran shows how a new gene complex could have spread, transforming the species while allowing the incorporation of genetic material from archaic populations that were "replaced." The process demands a relatively high level of breeding isolation between moderns and archaics, since the genes of any hybrids are, with high probability, lost. As an approximation the admixture rate must be less than the selective advantage of the new morph for the process to proceed.

The wave of advance of the new morph is essentially a rolling bottleneck. As the wave front progresses from place A to B to C and so on, the colonizers of B are a sample of the population of A, the colonizers of C a sample of B, etc. This is like a continuous founder effect that destroys much genetic diversity as it passes, while behind the wave front population size rebounds rapidly. The populations behind the wave front are nearly completely isolated from the front. The result is that DNA should show the signature of population expansion from a small number of founders and that the time of expansion should vary continuously with time since the wave passed. This pattern of strong signatures of expansion but with widely different inferred times of expansion is exactly what is seen in the mitochondrial DNA mismatch distributions (Harpending et al. 1993).

The paper is full of unexpected insights, one of which deserves more elaboration than it receives in the paper. Many gene trees show that the root is in sub-Saharan Africa, meaning that on one side of the root there are Africans and on the other side both Africans and non-Africans. This is routinely taken to indicate an African origin of human genetic diversity, but it indicates something much more interesting. In a random mating population the probability that a sample of n genes includes the root is $(n-1)/(n+1)$ (Nordborg 2001). This means, for example, that if 100 people (200 genes) left a single population of ancestral Africans the probability is nearly unity (199/201) that they would take the root with them so that world gene trees would show Africans and non-Africans on both sides of the root. The widespread pattern of Africans only on one side of the root must mean that the ancestral population of Africans was highly subdivided and that the origin of moderns was from the edge of Africa, as Eswaran states.

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Eswaran offers an intriguing and sophisticated model for the causes of morphological change in Upper Pleistocene human evolution and subsequent modern genetic diversity. His model of modern human origins requires that "modernity" (i.e., modern morphology) have some selective advantage over archaic morphology in order to account for the propagation of his "diffusion wave." He tentatively proposes that reduced childbirth mortality might represent that advantage. My comments are restricted to that aspect of his paper.

Reduced childbirth mortality is an appealing and plausible but (as Eswaran would acknowledge) undemonstrated proposition. Childbirth represents a time in the human life cycle when we can see dramatically and graphically the impact of natural selection. The relationship between the size of the infant's head and shoulders and the size and shape of the mother's birth canal (Rosenberg and Trevathan 2001, Trevathan and Rosenberg 2000) is critical to successful passage of the infant from the mother's body. When disproportion or dystocia occurs in humans, the results include injury to or death of the mother and/or infant, any of which would impact the overall reproductive success of the mother. All other things being equal, slight changes in the size or shape of the infant's head or trunk or the mother's pelvis would certainly affect the birth process. Eswaran argues that many of the distinctive features of modern *adult* cranial morphology are associated with a decrease in the anterior-posterior diameter of the modern cranium and that a reduction in that dimension *in infants* would lead to easier and less risky birth and hence would constitute a selective advantage for modern humans.

However, there is currently no evidence that such a reduction in birth difficulty actually took place with the origin of modern humans. The pelvis has represented a compromise to the conflicting selective forces created by its simultaneous functions in locomotion and obstetrics since the origin of bipedalism. Rosenberg and Trevathan (2002) have argued that childbirth in humans has been difficult enough to benefit from the interven-

tion of a birth attendant for over a million years. Evidence from archaic humans in Europe and Asia demonstrates that the relationship between maternal pelvic size and infant size (inferred from maternal body size) is indistinguishable from that seen in modern humans. If, as hypothesized by Eswaran, there were a reduction in childbirth mortality related to decreasing anterior-posterior diameter of the infant head in early modern humans, we would expect to find *relatively larger* birth canals in modern humans than in Neandertals or their penecontemporaries, and we do not (Rosenberg 1988, 1998). Thus there does not seem to be any evidence for a *reduction* in the risks of childbirth associated with the transition to modern humans.

This observation does not necessarily undermine Eswaran's overall model, since his argument does not depend on this particular selective advantage of modern human morphology. However, for the part of the model involving natural selection, some alternative to decreased cephalopelvic disproportion must be proposed as the advantage associated with modern human form.

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It is refreshing to see a serious attempt to use population-based genetic theory to model and provide some clarification to the complex process of human evolution that is generally referred to as "modern human origins." In this elegant demonstration, Eswaran has done what has been needed for some period of time; he has provided an explicit model with explicit assumptions to model the populational and genetic processes by which modern human biology may have spread and eventually become the dominant form across the Old World.

As much as I am pleased by his paper, and not solely because it matches to some degree my previous views that some form of the assimilation model of modern human emergence (Smith, Falsetti, and Donnelly 1989) best fits the available fossil, molecular, and anatomical data (Trinkaus and Zilhão 2002), I believe that it suffers from a problem shared with the majority of the current and past models of modern human emergence: namely, it tries to explain too much of a geographically and temporally complex process with a single mechanism or prime mover. I am convinced that the "diffusion-wave" model was a major player in a number of regions and time periods during the process of modern human emergence (which, after all, took more than 70,000 years to occur and involved all of the inhabited Old World), but I remain unconvinced that it can explain all of the factors to which Eswaran applies it without too heavy a dose of special pleading.

There are also aspects of the model that push the limits of our current paleontological knowledge. For example, one of the key elements of the model is a significant adaptive advantage for a set of coadapted genes, of which

Eswaran invokes anatomical ones to reduce parturitional and infantile mortality. However, despite differences in adult facial size, there is little difference in archaic-versus-modern early juvenile facial size (despite early developmental differences in morphology) (Ferembach et al. 1970, Madre-Dupouy 1992, Tillier 1999), and there would have been less in neonates. Adult brain size, and hence neonatal brain size, are essentially the same (Ruff, Trinkaus, and Holliday 1997), and female pelvic-aperture size either remained the same or decreased slightly (Rosenberg 1988, Rosenberg, Lu, and Ruff 1999). Cranial vault thickness did not change (Lieberman 1996), and significant decreases in robusticity are limited to the upper limb and clearly not systemic (Trinkaus 2000). There appears to have been a reduction in developmental stress (Brennan 1991), but this occurs principally with later juveniles (Ogilvie, Curran, and Trinkaus 1989). If there is any indication of possibly increased fertility among early modern humans, it would be related to the apparently greater adult longevity of early modern humans (Trinkaus 1995), a reflection of decreases in behaviorally based stress levels and not something that would be directly controlled by subtle anatomical differences. There are cases of significant survival of congenitally impaired early modern humans (Tillier et al. 2001, Trinkaus et al. 2001), but there is also evidence of late archaic humans' surviving for extended periods with serious traumatic and/or degenerative disabilities (Trinkaus 1983, Lebel et al. 2001).

It also needs to be emphasized that the biological similarities and differences commonly noted across the late-archaic-to-early-modern transition occurred in two very different technocultural contexts. At least in the western Old World, the initial establishment of early modern humans (including their temporary spread into the southwestern Near East) was entirely Middle Paleolithic, whereas the major spread of modern humans (to which the diffusion-wave model would apply) was entirely Upper Paleolithic. Moreover, during the time period for which there was some degree of overlap of late archaic and early modern humans within regions (basically between 35,000 and 29,000 B.P. in Europe), there are insufficient fossil remains to assess what the differential adaptive and demographic patterns might have been, and the few available specimens indicate a mosaic pattern of functional anatomical features (Trinkaus et al. 1999, Churchill and Smith 2000).

Therefore, although I applaud Eswaran for his elegant and explicit attempt to provide a model for the population dynamics of modern human emergence, I think that it provides a useful model for our ongoing investigation of regional population dynamics rather than a universal explanation for the emergence of modern humans. It also helps to emphasize that the two phylogenetic models of modern human emergence which dominated human paleontology for the last decade of the 20th century, the strict Out-of-Africa with replacement and the original multiregional model (the "standard" version as quoted by Eswaran), have one thing in common: they are both

wrong. It is time to move on to more dynamic models that incorporate regional and temporal diversity.

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Eswaran models a mechanism for correlating adaptive change across the entire species range. His model explains one possible mode of multiregional evolution for Pleistocene humans, but it is important not to overstate its importance either by presenting it as a *unique* mode of change or by implying that the observed course of events in the Late Pleistocene necessarily requires a *unique* explanation.

Multiregional evolution (as described by Relethford 2001; Templeton 1997, 2002; Wolpoff 1989; Wolpoff, Hawks, and Caspari 2000) is a theory relying on well-understood forces of evolution to explain the pattern of variation and change for Pleistocene human evolution by resolving the apparent contradiction between specieswide changes and regional continuities of local features. Local variation is promoted by differences in selection as well as isolation by distance and unequal reciprocal gene flow[1] in the absence of selection. Clinal distributions are created by balances of gene flow (mostly from the center to the edges of the human range) and selection or drift. Features defining common evolutionary trends can disperse throughout the species when reciprocal gene flow is predominantly directional, for instance, the largely center-to-edge pattern originally identified as a key element of multiregional evolution. Dispersal is more rapid when the characteristics are promoted by selection or when they respond to cultural changes that spread. In either case some unique local variations persist for shorter or longer periods because there are no instances of complete population replacement everywhere (Wolpoff et al. 2001).

A significant issue in multiregional evolution is how new features, in particular, features that come to characterize the whole species, disperse together. One would expect that a dispersing population mixing with other populations would break apart and attenuate the package. This is one reason that many multiregionalists argue that new features had independent origins and appeared together only after they had dispersed individually and that other researchers, convinced that complexes of features have dispersed together, turn to a population *replacement* explanation for it such as the Eve theory.

Eswaran uses Wright's adaptive-landscape model for a new insight, to explain how a complex of features might disperse together as a diffusion wave through popula-

tions without any population movement. His explanation focuses on the spread of "modernity."

The model predicts a successful diffusion wave within a limited range of parameters: strong selection promoting the dispersing gene complex and limited intermixture. Eswaran suggests that the source of this strong selection is a reduction of birth mortality. He cites Rosenberg's (1992) discussion of the evolution of human birthing difficulties in support of his argument, but Rosenberg notes that birthing difficulties can be inferred more than a million years before the modern humans whose new morphology presumably "solves" them. Further, the enlarged pelvic inlets and outlets characteristic of "modernity" that make births easier are found in female Neandertal (Rosenberg 1998) and earlier pelves (Arsuaga et al. 1999). Two Neandertal populations (Krapina [Wolpoff 1979] and Sima de los Huesos [Bermúdez de Castro and Nicolás 1997]) have high childhood mortality and low adult survivorship, which means that they could not also have had high birthing mortality because they would not have had enough surviving children to persist. As it is, Wolpoff (1979) calculated that the live births at Krapina must have been spaced very close together for the Krapina "population" size to have been stable.

A more significant question is whether "modernity" is actually a unique complex of features and even whether it can be validly defined apart from the description that modernity depicts people as they are today and in the recent past. If modern humans were a new species or an overwhelmingly superior anatomical and/or behavioral variant they should have a package of unique, distinct features, but repeated attempts to identify such a package (Day and Stringer 1982, 1991) fail to include all recent (Wolpoff 1986) or living (Brown 1990) people. This suggests that modernity is not a morphological complex but a perspective created by the fact that we view the past from the present.

Questioning whether this particular explanation of a diffusion wave is valid does not affect the issue of whether multiregional evolution works. It does address how it *might* work, but there is nothing in the multiregional hypothesis implying that only one mechanism has been operative in dispersing features. With pleiotropy and hitchhiking when there is selection, a number of models could explain the simultaneous adaptive spread of more than one trait. How many traits must disperse together before simpler selective models are no longer adequate?

I am not opposed in principle to the idea that a package of related features could have spread around the world, presumably from a single source—this is the assumption of the (poorly named) "assimilation"[2] explanation of multiregional evolution proposed by Smith, Falsetti, and Donnelly (1989), and a single-source explanation is favored by Relethford (2001). But the fossil evidence has never provided much support for the idea as an expla-

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1. Gene flow refers to the movements of genes, which may or may not involve the movements of peoples but in either case is reciprocal and requires interbreeding between people from different groups—varyingly called mixture, admixture, assimilation, or hybridization.

2. All explanations of how multiregional evolution works necessarily involve gene flow, which implies interbreeding, and therefore all are "assimilation" models.

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nation of modern human origins. Still, there is no question that in some form or other Eswaran's diffusion-wave model is quite likely a valid explanation for the multiregional pattern of any one of a number of specieswide events in human evolutionary history. It is a significant and particularly insightful description of how multiregional evolution might be expected to work when a specieswide change involves a package of characteristics that have a single origin but are related only by the common adaptation they promote.

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A popular interpretation of the results of genetic studies of the origins of modern humans is that no Neandertal genes survive among today's Europeans. This interpretation is in turn used to argue for the total replacement of anatomically archaic Eurasian populations by anatomically modern groups migrating out of Africa. Eswaran's "diffusion-wave" model shows that those present-day genetic patterns can be more parsimoniously explained through the operation of such ordinary population biology mechanisms as demic diffusion and admixture. In fact, the model suggests that such patterns are better explained by hybridization than by total replacement and that hybridization "could have been the principal reason for the disappearance of the archaic morphology."

I cannot but agree with these conclusions, since I have been arguing along similar lines (Zilhâo 2001a:72):

> It is quite likely that between 100,000 and 40,000 years ago a large majority of all the planet's human beings lived in Africa, where the modern morphological form evolved. If these African groups also had a higher fertility, as is commonly the case with warm climate populations of the same species when compared with those from colder climates, we can plausibly explain what happened [the "extinction" of Neandertals through assimilation by moderns]. When Africa became "full" of Africans, Africans started to disperse into the neighboring regions. . . . Given enough time, even a very small difference in fertility would put the much smaller and more scattered populations of Neandertals at a demographic disadvantage, especially if interbreeding was common.

This quotation highlights where it is that I disagree with Eswaran. His model requires two assumptions: that a strong adaptive advantage for the "modern" genotype exists and that the rate of interbreeding between demes is low. He also suggests that the advantage may have lain in the particular features of anatomical modernity, for instance, in bringing about reduced childbirth mortality: "an increase in fertility due to this advantage is sufficient to explain the modern transition." He also assumes that population density is constant across time and space,

which entails making all group-demes of the same size and each made up of a single genome.

There are a few problems with these assumptions. First, as is pointed out by Eswaran himself, in order for the model to work, the magnitude of the difference need be no greater than archaic populations' having 7 children per mother versus modern ones' having 7.5. Such differences in fertility, however, are of the same order of magnitude as those between warm-temperate and arctic populations of contemporary hunter-gatherers (Binford 1983), all of which are anatomically modern. Consequently, the selective advantage assumed by Eswaran is not necessarily related to body morphology, and the model cannot be used to support the notion that moderns had reduced childbirth mortality because of "a decrease of the anterior-posterior diameter of the modern cranium" and "concomitant modifications of the pelvis."

Second, one of the simulation's basic mechanisms, the mating procedure, is probably realistic. Under Eswaran's rules, for the model to work mating inside the deme (which, if I understand him correctly, is a hunter-gatherer band of normal size, i.e., ca. 25 people) must be much more common than mating outside it; as he points out, "the interbreeding rate between human groups would need to have been very constrained to allow the spread of complex advantageous genotypes." However, this condition contradicts the rules of exogamy, which, as Wobst (1974, 1976; see also Smith 1992) has shown, are demographically obligatory to secure a group's reproduction in the long run. Important aspects of lithic technology are widespread in the late Lower and the early Middle Paleolithic, implying information exchange networks encompassing vast areas. Such networks must have functioned as overlays on the exchange of individuals between demes in the framework of exogamic mating, whose rules, therefore, must have been in place well before the worldwide spread of anatomical modernity.

However, if differential fertility is related not to an advantageous genotype but to cultural-environmental constraints, as suggested by the ethnographic data, the need to constrain the interbreeding rate disappears. Moreover, this rate is also likely to have been extremely variable, for example, low in situations in which mutual avoidance was possible, high in geographical culs-de-sac (Zilhão 2001b). My question, therefore, is whether the same outcome (i.e., the disappearance of archaics through their assimilation into moderns dispersing out of Africa) might not be obtained assuming an imbalance in population density and population size between the core area of the world's population of humans, occupied by moderns, and the peripheral areas, occupied by archaics. Although this biogeographical scenario remains to be modeled, it seems empirically more realistic than Eswaran's. I compliment him on an elegant demonstration but would welcome similar quantitative testing of alternative mechanisms.

Reply

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I was gratified to read the commentators' remarks on my paper. Clark and Harpending, evaluating the diffusion-wave theory on the basis of the archaeological and the genetic evidence respectively, give it very favorable reviews. The other commentators, while not unqualified in their approval, are also positive and constructive. I offer the following response in the same spirit.

While Trinkaus could be right in this opinion that the problem of modern human origins may not be solved by any single overarching theory, I believe that the search for such a comprehensive solution is at least an antidote to the tendency to offer explanations for particular parts of the empirical data that may be incompatible with the whole—what Clark has referred to as "selective consilience." This is not to say that all aspects of the modern-human transition need be explained by diffusion waves. It is clear that geographical obstacles would break the wave, as I suggest happened in Australo-Melanesia. Similar disruptions but of lesser degree may have occurred where mountain ranges or dense forests created obstacles to demic diffusion. Similarly, even if the theory is largely correct, regional refinements may be needed to accommodate local empirical data. However, given the heat of the debate and the variety of data involved, it is unlikely that the problem of modern human origins will be collectively considered solved by physical anthropologists, geneticists, and archaeologists unless all the data held dearest by each discipline can be explained by a theory largely invoking a single mechanism. Only a theory fostering a genuine consilience among the different disciplines is likely to be accepted.

Zilhão has questioned some of the assumptions of my model. A few of these (e.g., constant population density, a single genome per deme) were made only to simplify the modeling. The suggestion of a 7.5/7.0 modern/archaic live-birth-rate ratio serves only to illustrate the selective advantage ($\alpha = 0.07$) assumed. (My belief that this advantage was primarily morphological will be discussed below.) I am aware that the low-interbreeding assumption violates the accepted view of Paleolithic societies as exogamous (e.g., Wobst 1976), but, as I point out, a fundamentally exogamous population structure will not allow the propagation of advantageous gene combinations.[1] I thus propose that a low-interbreeding population structure was common to human societies throughout the Pleistocene—which could have had pro-

found implications for human evolution (see below). Finally, while alternative scenarios for an African expansion by migration and hybridization could be explored, they would need to explain—along with the peculiarities of the empirical genetic and archaeological evidence—why, despite hybridization, the archaic morphology disappeared so completely.

I appreciate Wolpoff's point that definitions of modernity based on a given set of features have failed to include some living or recent people. However, these exceptions have been from Australia, where, as I have noted, the diffusion-wave mechanism would not spread the advantageous modern genotype. For Australia I have proposed a migration-and-hybridization (gene-flow) scenario that could "explain the evidence of recent (terminal Pleistocene/Holocene) evolution in Australian populations (Brown 1992), the greater Australo-Melanesian genetic depths, and the evidence of morphological continuity." That gene flow would not propagate sets of co-adapted traits or erase ancient genetic diversity as does the diffusion wave may explain the distinctiveness of the Australian evidence.

While it is not central to my theory, my hypothesis regarding the key advantage of anatomical modernity has received much attention. This hypothesis is conceived at two levels:

1. The same characteristic morphological features herald anatomical modernity across the Old World. For example, early modern Chinese were morphologically much closer to early modern Africans than they were to archaic Chinese (Stringer 1992). This seems to indicate replacement. Yet the genetic data suggest significant assimilation of archaic human genes. A resolution of this paradox is that the morphological changes were themselves shaped by selection, which then fixed them across the world. A cultural, linguistic, or mental advantage is unlikely to be accompanied by distinct morphological changes (at least not in the pelvis!) except in the case of population replacement, which is why I suggest that a purely morphological advantage must be involved.

2. As for the basis of this advantage, it seems to me that the congruence of the specific changes in robusticity, facial projection,[2] skull shape, thickness, and density,[3] and pelvis structure powerfully suggest adaptive modifications shaped by childbirth.

While I agree with the commentators that this hypothesis remains to be tested, I do not believe that, given the paucity of current evidence, we can rule it out altogether as they seem to have done. To do so would mean asserting the counter-hypothesis that even given the known sensitivity of human childbirth difficulty to *small* changes in the shape and dimensions of the maternal pelvis and the neonate cranium (see Rosenberg's

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1. Note, however, that the diffusion wave of modernity, say, could well have propagated even if there had been partial breeding isolation only between modern and non-modern "types" and not within subpopulations of the same type. The assumption of the partial isolation of all demes is a stricter one that makes the theory compatible with Wright's and allows a more general view of human evolution to be proposed.

2. A unique modern feature, the chin, may be seen to be the natural by-product of a reduced mid-face when the jaw is prevented from becoming too small to fulfill its masticatory purpose.

3. Greater cranial thickness and density were evident in Neandertal neonates (see, e.g., Golovanova et al. 1999:81–2), which would surely influence childbirth mortality even if the relative maternal-pelvis/infant-cranium ratio were held constant.

comment) we are sure that the *marked* changes[4] in these features that accompanied the archaic/modern transition really did not impact childbirth mortality. A single parameter such as the pelvis/cranium ratio can be only a rough indicator of birth difficulty, especially if this ratio remained constant across the archaic-modern transition as Rosenberg suggests it did.[5] It is likely that, when more complete information on archaic female pelves[6] and infant crania is obtained, the passage of the latter through the former will need to be modeled before definite conclusions can be drawn.

There has presumably been a continuous pelvic adaptation to human childbirth for the past 2 million years because of the selection pressure of increasing neonate cranium size. Thus enlarged pelves in Neandertals and other late archaic humans are only to be expected. I have merely suggested that some co-adapted changes in the pelvis and the cranium further eased the birth process for modern humans and significantly decreased childbirth mortality in yet another step in a continuously evolving "solution" to the childbirth problem.[7] Finally, I have no doubt that the Neandertal live birth rate was adequate to sustain their population, for otherwise they would not have lasted 200,000 years. But natural selection chooses among competing phenotypes, and the anatomically modern one may have been better—in terms of offering greater childbirth survivability—than the Neandertal one.

I hope that more data and further study will resolve this issue. At the very least this hypothesis, by suggesting that modern anatomical features were adaptive, cautions against jumping to conclusions regarding the conspecificity of archaic and modern humans from the morphological differences between them.

Finally, I emphasize that the diffusion-wave theory is based on a modified version[8] of the three-phase shifting-balance theory of Wright (1932). This is significant because Wright's process, if it operates, could increase the pace and scope of the evolution of a species beyond what is attainable by Fisherian mass selection alone. This may help to explain the uniqueness of human adaptation and intelligence. We can speculate that the evolution of humans was largely determined by the small-deme, low-interbreeding social structure required for Wright's process. Thus the invocation of Wright's theory in human evolution has rich consequences in need of further in-

vestigation. It allows us to go beyond the problem of modern human origins to the whole of human evolution.

Indeed, I believe that two other disciplines—evolutionary psychology and historical linguistics—should perhaps spare a glance at this theory, for, apart from the increased scope of evolution offered by Wright's process, an evolutionary environment dictated principally by life in small competitive demes is likely to have had a profound effect on the evolution of the human mind and emotions, with implications that would bear investigation. As for historical linguistics, the correspondence of the pattern of diffusion waves (fig. 1) with the pattern of language families is striking and—apart from suggesting the need for a radical reassessment of the age of language families—may offer explanations for the existence of the linguistic superfamilies that have been proposed and have been the subject of much controversy for the past half-century.

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4. The differences between archaic and modern infant crania have been thought sufficient to be at the species level (Stringer and McKie 1996:88). There were also significant differences between Neandertal and modern pelves (Rak 1990)

5. But see Tague (1992:19), who suggests that Neandertals had a less favorable cephalo-/maternal-pelvic relationship and so would have had more difficult childbirth than modern humans.

6. The only known complete Neandertal pelvis (from Kebara) is presumed to be male.

7. Which is still not completely "solved," for natural childbirth in humans remains the most difficult among the primates. Even after the modern transition, the disappearance of browridges, etc., may have been driven by selection pressure to decrease childbirth mortality still further.

8. For it insists on mobile demes.

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