



The four faces of Eve: hypothesis compatibility and human origins

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Abstract

Several different sources of evidence have been used to support a recent African origin for our species. It is commonly assumed that these sources of evidence support the *same* recent African origin. However, a close examination of the evidence available from four sources, including paleontology, archaeology, the level of human genetic variation, and the geographic structure of human genetic variation, shows that this is not the case. Each of these in effect supports a different recent African origin, and no hypothesis of a recent origin is compatible with more than two of them at a time. In contrast, all of these sources of evidence may be consistent with a multiregional model for our recent evolution. © 2001 Published by Elsevier Science Ltd. All rights reserved.

1. Introduction

The recent African origin theory, or Eve theory as it is sometimes called, predicts that all humans living today trace their ancestry to a single population living in Africa sometime during the Late Pleistocene. In its simplest form, this explanation for human origins entails two things. First, the human population ancestral to living humans was small at its origin and later expanded both in number and in geographic range. Second, the human contemporaries of this expanding population were completely replaced by them and went extinct without issue. The simplicity of this theory has resulted in active inquiry as to whether it in fact validly describes human origins.

The theory has been supported by a number of researchers using, at turns, morphological, archaeological, and genetic evidence. Some of the reasons that this theory has gained support are historical, rather than scientific (Wolpoff and Caspari, 1997). However, one scientific rationale drives much of the research into recent human origins: namely, the perceived morphological, genetic, and behavioral similarities of living and recent humans. It has been widely assumed that these similarities are consistent with each other in supporting a single

scenario of human origins (e.g., Stoneking, 1994; Stringer and Bräuer, 1994; Klein, 1995).

In fact, because two distinct categories of genetic evidence have been analyzed — the geographic pattern of genetic variation and the overall level of genetic variation — there are four distinct sources of evidence that have been used to evaluate hypotheses of human population history. Although it is widely assumed that these four sources of evidence each support the same recent origin hypothesis, there have been troubling indications that these sources of evidence are in fact inconsistent with each other. Incompatibilities have arisen because while several specific historical trajectories may include a recent African origin, only a subset of these histories may be consistent with any particular set of data. In such a situation, the subset of population histories allowed by one set of data may fail to include those allowed by other sets of data. In terms of the recent African origin model, the important constraints on population histories include the timing of population expansions, the pattern of Late Pleistocene geographic dispersals, and the subsequent pattern of gene flow among recent human populations.

We discuss each type of evidence below. For each category, we list the range of population histories consistent with the available data under the assumption of a recent African origin, as well as notable inconsistencies with other data sources. Finally, we suggest alternative interpretations of the available data that are compatible with all sources of information. We examine whether the range of population histories compatible with all of them precludes a recent African origin interpretation.

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2. Behavioral evidence

The major source of behavioral evidence pertaining to recent human evolution is the archaeological record of the Late Pleistocene. This record is very detailed in Europe and Western Asia, and relatively less detailed in East Asia and Africa. Therefore, discussions of recent origins have largely focused on the role of technological change in Europe and Western Asia, where a transition between Middle Paleolithic Mousterian assemblages and various Upper Paleolithic assemblages occurred between 47,000 and approximately 30,000 yr ago (Bar-Yosef, 1994; Klein, 1995).

Interpretations of a recent African origin on the basis of this evidence have focused on the nature of this transition and the hominids associated with these assemblages. It has long been posited that the transition between European and West Asian Middle and Upper Paleolithic assemblages was rapid and involved different hominid groups.

The largest problem with behavioral evidence for a recent African origin is the lack of apparent biological causation for new behaviors. One area where this problem surfaces is in the Mousterian of Western Asia, where between 100,000 and 45,000 yr ago near-identical assemblages are produced by a range of hominids, some of which have been described as “anatomically modern” and others described as Neandertals. This is recognized by Klein (1999, p. 590), who posits that the behavioral changes associated with recent humans did not arise along with their observable anatomical features, but instead appeared as a result of a fortuitous mutation in the brain. This saltationist explanation can probably be discarded, since the favorable mutation required is far too complex to be likely (contra Bickerton, 1990) and would have to spread rapidly through the African population and into other populations, including the so-called archaic ones such as the Châtelperronian Neandertals of France, who used bone tools, body ornamentation, and other innovations. Uncoupling culture and biology, as this explanation for the Eve theory requires, is expected within a single human species, but would be unexpected if the populations were of different competing human species.

The archaeological evidence of “modern” behavioral innovations among archaic peoples, and the evidence of “archaic” behavioral patterns in the earliest “modern” peoples, remains a significant stumbling block for the recent origin interpretation. The explanation that behavior and anatomy only first became congruent more recently than 50,000 yr ago is an important constraint in the timing of modern human origins imposed by archaeological data.

We believe that the best explanation for this situation lies in the assumptions made about the archaeological markers of “modern” behavior, the main marker being

the appearance of blade-making techniques (cf. Howell (1959), and authors following him to at least as recently as 1997: Relethford, 1995; Boyd and Silk, 1997; Foley and Lahr, 1997; Sherratt, 1997). In fact, laminar technology appeared hundreds of thousands of years before the Upper Paleolithic, both in Africa and in other parts of the world. No case of early blade production can be linked to the much later Upper Paleolithic proliferation of blades, though, or to any major change in hominid behavioral capacity, according to Bar-Yosef and Kuhn (1999). Nor can blades be linked to “anatomical modernity”. As we noted, some early “moderns” did not use blades, just as even recently blades were very widespread in only some parts of the world. Alternatively, not only did late Neandertals in France manufacture blades, but so did very early ones at sites such as Biache. Bar-Yosef and Kuhn (1999, p. 333) summarize the situation as follows: “there is no clear association between the production of elongated blades — prismatic or Levallois — and any single feature of hominid anatomy or behavior”. The Upper Paleolithic did not originate in Africa and spread from it across the world (Marks, 1992), and, if valid, these considerations imply that there is no archaeological evidence for *any* migration of modern humans out of Africa at all. It also follows that authors who use the appearance of MSA blades in Howieson’s Poort assemblages from South Africa as evidence that modern humans first evolved there are incorrect (Stringer, 1989; Deacon, 1992).

3. Anatomical evidence

Anatomical evidence for the recent evolution of modern humans comes from the fossil record between about 150,000 and 50,000 yr ago. A recent African origin has been interpreted either because of the presence of traits in late Middle and early Late Pleistocene Africans that are common in recent humans, or because of the patterns of similarities among recent and Late Pleistocene groups.

The first of these two approaches is primarily definitional. Researchers have defined recent humans as a monophyletic group — “anatomically modern” humans — and have applied this definition to more ancient specimens in order to identify the first members of this group. A number of such definitions have been proposed (Day and Stringer, 1982, 1991; Stringer and Andrews, 1988). Using these definitions, researchers have identified early Late Pleistocene humans living in either Africa or Western Asia as the apparent precursors of living humans. Other groups, which lack the entire pattern of traits found in recent humans, are found by this procedure to be either too primitive or too specialized to be human ancestors.

The second approach encompasses a variety of statistical approaches to examine the relationships of various Middle and Late Pleistocene hominids to recent human

groups. These have taken the form of principal components analyses (Stringer, 1996), comparisons of trait frequencies (Lahr, 1994, 1996), and matrix tests (Waddle, 1994; Sokal et al., 1997). The findings of such comparisons have been that recent humans, as a group, are more closely related to either African or Near Eastern hominids of the early Late Pleistocene than to any other early Late Pleistocene groups.

Under the assumption that recent humans have a single common origin, both the approximate population size of this early “anatomically modern” population and the pattern of subsequent geographic dispersals required by this hypothesis are fairly clear. Dates for specimens from Africa classified variously as “anatomically modern” (Stringer, 1994), or “near modern” (Klein, 1999) occur between 150,000 and 80,000 yr ago in both East and South Africa, though the associations of all these dates with specimens have been questioned (Frayser et al., 1993). The addition of “anatomically modern” humans from Mt. Carmel in Western Asia implies a geographic distribution for this group of, at minimum, 10 million square kilometers, roughly equal to one-third the land area of Africa. At a minimal population density of 0.03 breeding adults per square kilometer, this implies a population size of 300,000 breeding adults during this time period. Further, the presence of these humans in Western Asia by 90,000 yr ago implies at least one early dispersal, corroborated by the possibility of a “modern” presence in Australia (Roberts et al., 1990, 1994) and in China (Wolpoff, 1999) by 60,000 yr ago.

It has long been recognized that the appearance of “modern” humans in the late Middle Pleistocene of Africa is not coincident with the transition to Upper Paleolithic, or Late Stone Age technological assemblages, which for the moment we are willing to accept as indicators — although not *unique* indicators — of “modern” behaviors. Further, even the apparent dispersal of these humans into Western Asia predates the Upper Paleolithic in the area by as much as 50,000 yr. These inconsistencies have been explained in two ways. First, it has been posited that the early dispersal of humans into Western Asia did not lead to colonization of other areas of the Old World (Klein, 1999). If this were true, then a later dispersal of LSA-bearing humans may have comprised the true replacement wave, though the first appearance of “moderns” in East Asia is not coincident with African or West Asian technocomplexes (Lin, 1996; Wu, 1998). Second, as discussed in the previous section, it has been posited that the development of Upper Paleolithic technologies was not linked to the appearance of “modern” hard tissue anatomy, but instead to fortuitous (and invisible) changes in brain structure that only occurred later (Klein, 1999).

Aside from the apparent contradictions created by anatomical studies of human fossils, there are a number of methodological problems that make it difficult to

support a recent African origin on the basis of anatomical evidence. For example, the use of certain traits or groups of traits in definitions of “anatomically modern” humans ignores the possibility that traits common in recent humans have their origins at different places and times. The ubiquitous distribution of such traits is taken to indicate the group’s monophyly, although it may reflect no more than widespread, persistent genetic exchanges in the later Pleistocene and Holocene. Further, though many of the traits common in recent humans are present in early Late Pleistocene Africans and West Asians, their distribution is far from universal within this sample (Smith, 1994). If we continue to assume a recent origin, then either the true source population for recent humans is substantially later in time (and thus far cryptic to paleontology), or humans evolved multiregionally, at least within Africa, until a near-universal distribution of “modern” traits was attained.

Neither of these possibilities alleviates the most serious problem with a recent origin, which is that none of the techniques used to support such a model can differentiate this model from a less restrictive, isolation-by-distance model for recent human evolution. Under such a model, human populations are connected by gene flow in a way that depends on their size and distance from each other. If isolation-by-distance were the correct description of our evolution, then living humans would be more similar to a single population in the past than to others, and this population would either be the largest or the most central. Among continental areas, the largest human population in the early Late Pleistocene likely was the African population (contra Klein, 1999), by virtue of both habitable geographic area and favorable climate. Further, the geographic center of the human population was Western Asia. These facts would seem to make it inevitable that techniques based on similarity, including those using cladistics, will appear to support a Western Asian or African origin for recent humans, regardless of whether such an origin in fact occurred.

The simplest way to distinguish a recent single origin from an isolation-by-distance model is to test for gene flow between ancient human groups, either by comparing these groups directly or by looking for evidence of regional continuity between Late Pleistocene groups and more recent humans. When such tests have been carried out, they have invariably demonstrated some level of gene flow between ancient groups and more recent peoples in the same areas (Smith et al., 1989; Frayer, 1992, 1993; Frayer et al., 1993, 1994; Etlar, 1996; Duarte et al., 1999; Kennedy, 1999), even when the studies’ conclusions have disagreed with this assertion (Lahr (1994, 1996), as discussed in Relethford (1998)). The implication of these studies is that more than one Late Pleistocene population contributed to the ancestry of living humans. Surprisingly, even strong advocates of a single origin do not disagree that some small contribution of archaic

peoples may have occurred (Cann, 1992; Stringer, 1994; Stringer and Bräuer, 1994), though this would seem to invalidate the recent African origin model from a genetic perspective, as discussed below. If such contributions were regular enough to leave their mark on the sparse fossil record, they were regular enough to have the genetic consequences we describe.

4. Geographic variation of human genes

The variation in human genes associated with geography is similar in concept to the study of human anatomical variation. However, there is no fossil record of past human genetic variation, so that all comparisons must rely only on the observed variation of living humans. In many ways, this makes the analysis of geographic variation in genes more model-bound than is the case for anatomy. This problem is partly alleviated by the availability of more analytical techniques for genetic data, but it remains an area of disagreement.

Examinations of the geographic structure of human genetic variation have involved classical markers, protein polymorphisms, restriction fragment length polymorphisms (RFLPs) and single nucleotide polymorphisms (SNPs) (Nei and Roychoudhury, 1974, 1982; Cann et al., 1987; Mountain and Cavalli-Sforza, 1994, 1997; Goldstein et al., 1995; Nei, 1995), as well as sequence variation in human mitochondrial (Vigilant et al., 1991) and nuclear DNA (Harding et al., 1997). These observations may be divided into two categories, including comparisons of the level of variation among regions, and the timing of splits between regions.

It has been recognized for over a decade, that African populations have a higher level of genetic variation than non-Africans, first from the analysis of the DNA of the mitochondria (Cann et al., 1987), and later from other genetic systems (Mountain, 1998). This observation is consistent with an earlier origin of African populations than in other regions of the world, and is the primary reason why genetic studies have favored a recent origin in Africa as opposed to some other region.

The second kind of analysis of geographic variation has attempted to trace the dispersals of recent humans as they left Africa (Cavalli-Sforza et al., 1993). These analyses examine either the gene frequencies or other genetic characteristics of living human populations and attempt to fit these to a tree of descent. In such analyses, the deepest split in the obtained tree of populations is assumed to represent the original divergence of a single ancestral human population. A number of studies have found that the two branches stemming from this original bifurcating divergence represent living Africans on one side and living non-Africans on the other side (Nei and Roychoudhury, 1974, 1982; Goldstein et al., 1995; Nei, 1995). The date associated with this original split varies

little even among studies using different evidence, and the means of these studies fall within a relatively narrow range, between 115,000 and 156,000 yr ago. The actual dates of population divergence are probably earlier, for two reasons. First, these dates assume no gene flow among populations after they diverge from each other, but if we were to assume past levels of genetic distance similar to those observed among human populations today ($0.1 < F_{ST} < 0.15$), the true divergence time would approach infinity as the number of migrants among regions approaches one to two individuals per generation. Second, these studies assume a constant inbreeding effective size for humans of 10,000 individuals; however, any expansions in this number during the last 100,000 yr will cause estimates of divergence time to be underestimated.

Populational analyses have been supported by global studies of single genetic loci. For example, Relethford and Harpending (1994) found evidence for ancient population structure in the geographic variation of mitochondrial DNA, implying a history of population divisions at a time before population growth is evidenced at this locus. Likewise, other nuclear loci including beta-globin (Harding et al., 1997) and PDHA-1 (Harris and Hey, 1999) argue for ancient population divergences, though these may differ from the population studies in that at least some divergences are significantly more ancient than 200,000 yr (Harding et al., 1997). Such ancient intercontinental divergences do not contradict more recent estimates of population divergences *within* continents between 50,000 and 100,000 yr ago (Su et al., 1999), both because the spread of humans after their initial dispersal was not instantaneous, and because greater gene flow within as opposed to between regions will result in greater underestimates of within-continent divergences.

The contradictions between this source of evidence and those listed previously primarily relate to the timing of events and the levels of intergroup gene flow. Paleontological data do not require a recent African origin to be accompanied by complete isolation of populations, and indeed such isolation would be surprising given the historical levels of interchange among human populations. However, in order for the dates of genetic divergences to be consistent with the dispersal dates derived from paleontology, it is *necessary to assume* the complete isolation of populations after they diverge from each other. For this reason, Templeton (1998) calls the recent African origin model a “candelabra theory”, because any level of gene flow among groups will elevate the divergence dates above the range allowed by paleontology. However, if no gene flow occurred among human groups later than 100,000 yr ago, the spread of “modern” features within at least the African population during this time period cannot be explained. The conflict with archaeology is even worse than with paleontology if we assume the Upper Paleolithic is the earliest evidence of modernity, since

there is no magic date that allows the population divergences estimated from genetics to be consistent with the spread of Upper Paleolithic technologies after 50,000 yr ago. We must conclude that there is no recent African origin hypothesis that can have support from both archaeology and the geographic distribution of our genes. Each of these interpretations refutes the other.

The problems with observations of geographic variation in human genes are largely the same as those facing studies of anatomical variation. Just as in the case of anatomical variation, the observation of a greater level of variation within Africa is also consistent with a larger population size in Africa than in other regions (Relethford and Harpending, 1994; Relethford, 1995, 1998), and there is as yet no way to distinguish between these hypotheses. For this reason, greater African than non-African variation is consistent with a recent African origin, but cannot demonstrate it.

More seriously, all of the genetic analyses listed above assume that a bifurcating tree is a sufficient description of population relationships, and therefore must *assume* complete isolation of human populations (i.e. Templeton's depiction of a "Candelabra model"). Rather than testing a tree model against other possible descriptions of the data, such as isolation-by-distance, these analyses effectively *assume* that gene flow among populations cannot have existed in the past. However, studies have consistently shown that a tree is a poor fit to human genetic data (Templeton, 1998). Testing procedures that allow gene flow to be an option have repeatedly shown that human genes are consistent with a long history of isolation-by-distance among continental regions (Templeton, 1993, 1998). Such a history would unambiguously falsify a recent African origin.

5. Level of human genetic variation

A second avenue of genetic research addresses the overall level of genetic variation in humans. This subject has become important because the level of genetic variation present in humans today may be related to the size of the human population in the past. If it could be demonstrated that this population size was very small, then it is unlikely that such a small population could inhabit a large area of the world (Harpending et al., 1998). In this case, only inhabitants of a very small area could be ancestral to living humans, while inhabitants of other areas apparently went extinct.

The level of genetic variation is now known for a moderately large number of genetic systems. Under an assumption that evolution has proceeded by genetic drift in a random-mating population, the level of variation in a genetic system is a function of the number of individuals in the population. Therefore, genetic variation is often expressed in terms of the inbreeding effective size of the population, or the size we would expect the population to have if it had obeyed a neutral Wright–Fisher model. Estimates of effective population size for many human genetic systems are presented in Table 1; these appear to imply a human inbreeding effective size of around 10,000 during the Pleistocene.

The ratio of census (i.e. true) population size to inbreeding effective size in humans is often assumed to be about three to one (reviewed in Hawks et al., 2000), which would imply that the inbreeding effective population size roughly approximates the number of breeding adults (Harpending et al., 1998). This assumption would imply that the human population ancestral to us was limited to a size of around 30,000 individuals, or 10,000 breeding

Table 1

Inbreeding effective size estimated for human genetic systems. The methods used to estimate inbreeding effective size vary among publications. Most assume a constant population size, which may inflate the effective size estimate if populations have recently expanded. HLA interallelic data may be affected by balancing selection (Ayala, 1995); the relevance of the estimate given here has been questioned (Erlich et al., 1996)

Genetic system	Published N_e estimate	Sources
Human-specific <i>Alu</i> polymorphisms	17,500	Sherry et al. (1997)
48 nuclear genes	10,000	Li and Sadler (1991)
β -globin	10,000	Harding et al. (1997)
HLA intrallelic data	10,000	Takahata and Satta (1998)
HLA interallelic data	100,000	Ayala (1995)
Single nucleotide polymorphisms	10,000–100,000	Wang et al. (1998)
ZFY	3000–28,000	Dorit et al. (1995)
YAP	2000–26,000	Hammer (1995)
ZFX	3000–15,000	Huang et al. (1998)
Microsatellites	10,000	Jorde et al. (1997)
Mitochondrial DNA	8700	Cann et al. (1987)
PDHA1	18,000	Harris and Hey (1999)
LPL	10,000	Clark et al. (1998)
Dystrophin	10,000	Zietkiewicz et al. (1998)

adults, during most of the Pleistocene (Takahata, 1993; Harpending et al., 1998). Since this number is so much smaller than that estimated for a transcontinental population size for Pleistocene humans, some researchers have concluded that the ancestors of living humans occupied only a limited range (Harpending et al., 1993, 1998), and that the fate of most Pleistocene humans was extinction. This scenario would be consistent with a recent African origin model for our evolution.

To tell whether this explanation for the level of human genetic variation is consistent with other lines of evidence, it is necessary to determine when, if ever, the small population of ancestral humans this explanation entails may have expanded in number. A number of researchers have studied the DNA of human mitochondria, in which the distribution of variation indicates a possible worldwide population expansion between 40,000 and 70,000 yr ago (Harpending et al., 1993; Rogers and Jorde, 1995). Additionally, mtDNA appears to support the interpretation of later expansions in some geographic areas, such as Europe, which may be consistent with the archaeological record for the spread of Upper Paleolithic assemblages (Sherry et al., 1994). This recent population expansion is also consistent with some analyses of human microsatellite variation (Kimmel et al., 1997) and Y-chromosome variation (Seielstad et al., 1999).

However, such a recent expansion contradicts evidence from paleontology for a wide distribution of “anatomically modern” humans by 90,000 yr ago, minimally across all of Asia and into Australia. Even strong arguments for a speciation in the African Late Pleistocene imply a population size of approximately 300,000 breeding adults. Weaker arguments, which allow some level of interbreeding among “modern” and other contemporary populations, imply a population size two to three times as large. Neither would seem to be consistent with the evidence from mitochondrial DNA or other genetic systems.

Furthermore, a small ancestral population size is inconsistent with the genetic evidence for geographic expansion. As discussed above, nuclear genes imply an ancient population structure among continental regions, with a split between Africans and non-Africans before 100,000 yr ago. Surprisingly, mitochondrial DNA also shows evidence of ancient population structure, predating evidence for population expansion (Harpending, 1996). As discussed in the previous section, the pattern of geographic variation in human mitochondrial DNA most closely fits an isolation-by-distance model, so that we may account for this by positing that human populations remained small for a time after geographic expansion, while continuing to exchange migrants with each other. The problem with this scenario is that continuing gene flow among regions would increase the time needed for human populations to differentiate, forcing the split between African and non-African populations evident in

nuclear genes to be as ancient as 200,000 yr or earlier. Such an ancient date would not only be inconsistent with a recent population expansion, but also with the intermediate date for African origins invoked to explain paleontological data, and the recent date invoked to explain archaeological data.

6. How can we resolve these contradictions?

From the discussion above, it should be apparent that the various data used to support a recent African origin for our species are in fact inconsistent with each other. The patterns of inconsistencies are listed in Table 2.

The geographic distribution of human genetic variation clearly favors an early dispersal from Africa. This is not inconsistent with the paleontological evidence for the spread of “modern” features, but implies a larger population size over this time period than seems to be allowed by the level of genetic variation. It also requires that the spread of Upper Paleolithic technologies and other behaviors was accomplished by diffusion into populations that were established much earlier than 40,000 yr ago.

In contrast, a late dispersal would appear to coincide with technological changes in at least Western Asia and Europe, and would appear to be consistent with genetic evidence for a recent population expansion. However, the geographic range occupied by ancestral “modern” humans is too great to be consistent with a population size of 10,000 breeding adults. Yet if these ancestral humans occupied a smaller region, thus far hidden to paleontologists (Harpending et al., 1998), it remains unexplained how the genetic differentiation of human groups arose over 100,000 yr ago. Since this estimate requires the unrealistic assumptions of no gene flow among groups and no population size increases within the past 100,000 yr, it would seem that an even more ancient differentiation occurred, which would be consistent with fine-scale studies of geographic variation (Templeton, 1998). How ancient? Because the level of gene flow cannot be less than zero, the timings of population divergences derived from genetic data have a solid lower bound. A smaller African population of 10,000 breeding adults may have existed among other morphologically similar populations and given rise to later humans, but the observed geographic differentiation of living humans refutes this claim, and paleontology is unlikely ever to have the resolution necessary to support it.

Many have tried to resolve these problems by positing that most of the ancestry of recent humans came from a single area, but some small level of interbreeding or hybridization with hominids from other areas occurred, which may have been more or less extensive (Smith et al., 1989; Stringer, 1994; Stringer and Bräuer, 1994; Hammer et al., 1998). Such models fall along a continuum of models that incorporate gene flow among ancient

Table 2
Patterns of consistency among data sources addressing a recent African origin. Other population histories besides those listed here are possible, but these are the best-supported hypotheses given the existing data. Intermediate hypotheses are discussed in the text

Population history	Appears consistent with ...	But inconsistent with ...
Initial population size of 300,000, dispersal by 90,000 yr, no intergroup gene flow	Paleontology, geographic variation of human genes	Spread of Upper Paleolithic, level of human genetic variation
Initial population size of 10,000, dispersal by 90,000 yr, no intergroup gene flow	Geographic variation of human genes	Paleontology, spread of Upper Paleolithic, level of human genetic variation
Initial population size of 300,000, dispersal at 50,000 yr	Spread of Upper Paleolithic, Paleontology (assuming a late dispersal)	Geographic variation of human genes, level of human genetic variation
Initial population size of 10,000, dispersal at 50,000 yr	Level of human genetic variation, spread of Upper Paleolithic	Paleontology, geographic variation of human genes

groups. Though the importance weighed to single populations may differ among these models, they are all essentially multiregional (Relethford, 1998). Rather than formulating the model with the most minimal level of gene flow, as some authors have attempted (Stringer, 1989, 1994; Bräuer, 1992; Stringer and Bräuer, 1994), it is more useful to examine a null multiregional model of isolation-by-distance over the Late Pleistocene, and ask whether any of the available data contradict it.

As noted above, neither paleontological nor genetic data are inconsistent with an isolation-by-distance model for human diversification. In fact neither of these data sources can be consistent with complete isolation among human populations, because genetic data do not fit a bifurcating model (Templeton, 1998), and because traits common in recent humans attained a high frequency only gradually within Late Pleistocene Africans and other populations. This would imply an early and gradual emergence of modern human form on a background of genetic exchanges among populations. The level of gene flow required for this model is small: at equilibrium among human populations with F_{ST} equal to 0.1, only about two migrants need to move between populations per generation (Relethford, 1999).

The spread of Upper Paleolithic technologies may be explained under this model in part by diffusion. This is not a severe requirement, since either diffusion or multiple independent inventions are required to explain technological changes in Europe even if complete replacement is assumed to have occurred (Otte and Keeley, 1990; Marks, 1992; Olszewski and Dibble, 1994; Klein, 1995; Straus, 1997). Further, the evidence for a different pattern of behavioral changes in East Asia (Lin, 1996; Wu, 1998) and the evidence for Middle Pleistocene emergence of “modern” behaviors such as art (Bednarik, 1995) and water transit (Sondaar et al., 1994) suggest that recent human behaviors did not evolve as a single package, universally co-associated, but instead had a more gradual origin. This does not deny the importance of migrational events, as evidenced by the spread of agricultural peoples into Europe (Chikhi et al., 1998), which may provide a model for earlier European events (Bar-

Yosef, 1994). It merely suggests that mass migration was not the only mechanism for behavioral change through time.

The major obstacle to the broad acceptance of this synthetic model is the level of human genetic variation, which has provided a stumbling block for every human evolutionary hypothesis. This is because a population size of 10,000 breeding adults is inconsistent with the habitation of large areas of one or several continents. A recent African origin might be consistent with such a small population size over a very limited amount of time either in the late Middle or early Late Pleistocene, but stunningly, genetic data imply that this condition lasted for most of the past two million years (Harpending et al., 1998; Takahata and Satta, 1998; Hawks et al., 2000), up until less than 70,000 yr ago (Harpending et al., 1993), or even more recently (Hawks et al., 2000). Such a long period of small population size conflicts with every hypothesis for human origins based on paleontology, leading to arguments that the true source population for our species must be cryptic (Harpending et al., 1998).

However, this conflict is largely based on a misconception about what genetic estimates of inbreeding effective population size actually mean. Comparisons with other species indicate that inbreeding effective population sizes estimated from the level of genetic variation are typically several orders of magnitude lower than the true population size (Nei and Graur, 1984; Gillespie, 1991; Templeton and Read, 1994; Whitehead, 1998). Further, many factors are known to reduce genetic variation relative to population size (Nei and Graur, 1984; Frankham, 1995) and several are likely to have characterized humans during the Pleistocene (Takahata, 1994; Hawks et al., 2000). Fossil and archaeological evidence for human prehistory cannot be consistent with a census population size on the order of 10,000 throughout the Pleistocene (Hawks et al., 2000). Because there is no reason from the comparative genetics of other species to favor such an interpretation of the inbreeding effective population size calculation, it should be clear that the assumption that genetic variation may accurately estimate ancient population sizes should be set aside. Then, no known genetic evidence

would contradict an isolation-by-distance model for Pleistocene human evolution (Templeton, 1997, 1998).

It would therefore appear that an isolation-by-distance model is one possible resolution of the different sources of data addressing human origins. It should be noted that such a model is not merely consistent with multiregional evolution, *it is multiregional evolution* (Wolpoff et al., 1984; Relethford, 1998; Templeton, 1998). It is possible that additional data will show that some other explanation for the data, possibly involving large migrations, is better supported than strict isolation-by-distance. However, as we have seen, no explanation involving a unique descent of recent humans from only a single geographic subset of earlier humans can explain the data presented here. Because no single recent origin theory can be consistent with the pattern of observed morphological, genetic, and archaeological data, the true explanation for recent human evolution must be a multiregional one.

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