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Sixty Years of Modern Human Origins in the American Anthropological Association

ABSTRACT We present a review of the history of scientific inquiry into modern human origins, focusing on the role of the *American Anthropologist*. We begin during the mid-20th century, at the time when the problem of modern human origins was first presented in the *American Anthropologist* and could first be distinguished from more general questions about human and hominid origins. Next, we discuss the effects of the modern evolutionary synthesis on biological anthropology and paleoanthropology in particular, and its role in the origin of anthropological genetics. The rise of human genetics is discussed along two tracks, which have taken starkly different approaches to the historical interpretation of recent human diversity. We cover varying paleoanthropological interpretations, including paleoanthropologists' reactions to genetic interpretations. We hope to identify some of the crucial inflection points in which the debate went astray, to rectify some of the points of misunderstanding among current scientists, and to clarify the likely path ahead. [Keywords: multiregional evolution, recent African origin, bottleneck, polygenism, race]

THE MODERN HUMAN ORIGINS PROBLEM has been with us in its current form for 60 years, through four generations of scientists. As we will describe, the fundamental issues were identified from the beginning, in the *American Anthropologist* (AA), and have changed very little since then. Some conceptual problems have been persistent: Because of its timescale and scope, modern human origins research requires us to understand details about the nature of speciation, the behavior of incipient species, and the relationships between material culture change and biological change that other problems may not require. These conceptual difficulties have often been clouded by epistemological problems, as scientists sometimes fail to make clear some of their important assumptions about the nature of species (can they interbreed with each other or not?) or the nature of genetic variation (is it closely tied to population size, and, if so, how and why?). Other times, scientists employ different epistemological approaches: Some “test” hypotheses by highlighting contrary data, while others pursue “consistency” approaches that highlight affirming data. These differences can lead different researchers to derive different results even if their data are the same.

Some of the most resonant ideas in the modern human origins debate are ideas that are wrong. By far the most pernicious is polygenism, the theory that human races have long, separate, and isolated histories. At the be-

ginning of the modern human origins debate, polygenism was accepted by many of anthropology's central figures (Bowler 1986; Brace 1981). Polygenist interpretations of human geographic diversity continued long after the strongest form of the theory—unique racial origins from different primate lineages—was thoroughly falsified (Brace 1982; Wolpoff and Caspari 1997). Polygenism survives both because scientists confuse it with modern gene-flow models (Cavalli-Sforza 1993; Gould 2002; Lewin 1993; Stringer and Andrews 1988; Stringer and Bräuer 1994) and, as described below, because some scientists continue to accept polygenist ideas.

Another of the wrong ideas of the past that continues to survive is the pre-*sapiens* theory, which claimed the existence of a human form within Europe during the Middle Pleistocene that had modern characteristics, uniquely related to living people (Hammond 1988) and unrelated to contemporary archaic forms. This theory, built on fossils with incorrect dates like Galley Hill, fossils with partial and possibly incorrectly reconstructed anatomy like Fontéchevade II, and the important Piltdown fossil that was an outright fraud, explains none of the extant Middle Pleistocene evidence from Europe, and today's paleoanthropologists rightly reject it. But its core assumption that “modern” and archaic human species long coexisted is an essential element of some current theories of human origins.

Here, we present a brief history of the debate and describe how it developed into a multidisciplinary confrontation of two core hypotheses: multiregional evolution (the ancestry of living humans includes ancient humans that lived across a broad geographic space encompassing more than one continental region of the Old World) and recent African origin (living and recent humans arose uniquely from a relatively small source population within the late Middle Pleistocene of Africa). Although some of the basic issues are much older, with particularly important contributions from earlier scientists like Gustav Schwalbe, Aleš Hrdlička, and others, it was primarily the early writings of Franz Weidenreich and William W. Howells that began to separate the issues surrounding “modern” human origins from the more general issues of hominid origins. We illustrate the roots of one of the largest problems in the modern human origins debate: its exclusion from the normal science traditions of biological anthropology. We describe the beginnings of genetic research into human origins from both regional and global perspectives, and contemporary fossil analysis. Finally, we discuss some future directions of modern human origins research.

THE OPENING OF THE DEBATE

While he was still director of the Cenozoic Research Laboratory and a professor at the Peking Union Medical College, Franz Weidenreich presented a paper summarizing the progress in paleoanthropology over the past decade at the Symposium on Physical Anthropology at the 38th Annual Meeting of the AAA in Chicago, 1939. This was published in *AA* the next year. Weidenreich stated the problem emerging from this progress as follows:

All the new specimens, along with the older material, form a rather continuous line of evolution. . . . Thus the question arises whether this line means an actual pedigree, assuming that *Pithecanthropus* and *Sinanthropus* are direct ancestors of Neanderthal man, and furthermore, recent man a scion of the latter, or whether these various types have to be accounted as but specialized and discontinuous side branches leading away from the main line of human evolution. [1940:380]

In his opinion:

The old theory, claiming that man evolved exclusively from *one* center whence he spread over the old world each time afresh after having entered a new phase of evolution, no longer tallies with the paleontological facts. [1940:381–382]

Presenting his account of how humans could have evolved across the inhabited world, Weidenreich made a series of proposals based on his own substantial research:

- None of the new specimens reveals any particularity which could be interpreted as a plain indication of a separate development.
- Just as mankind today represents a morphologic and generic [*sic*] unity in spite of its being divided into

manifold races, so has it been during the entire time of evolution.

- While man was passing through different phases, each one of which was characterized by certain features common to all individuals of the same stage, there existed, nevertheless, within such community different types deviating from each other with regard to *secondary* features. These *secondary divergences* have to be rated as regional differentiations and, therefore, as correspondent to the racial dissimilarities of present man. [1940:380, emphasis added]¹

To make sure his observations of secondary regional divergences could not be confused with Ernst Haeckel’s polygenic model of human evolution, with its independently evolving human lines, Weidenreich made two points. Regional evolutionary lines were distinct but not unique: Ancestral populations had many descendents and descendent populations had many ancestors.

At least one line leads from *Pithecanthropus* and *Homo soloensis* to the Australian aborigines of today. This does not mean, of course, that I believe all the Australians of today can be traced back to *Pithecanthropus* or that they are the sole descendants of the *Pithecanthropus-Homo soloensis* line. [Weidenreich 1943a:249–250]

Second, racial differentiation, past and present, was based on secondary features and did not require isolation.

The development and stability of . . . constitutional types and their occurrence in all racial groups of mankind today . . . give evidence that geographical isolation is not and cannot have been a prerequisite for the establishment of [differentiations] in man. [1946:86]

He called his theory “polycentrism.”

Two years later William W. Howells (1942) reviewed these problems, again in *AA*. Howells titled his section about Weidenreich’s explanation for the origin of races as “races derived from parallel phyla” (1942:182) and incorrectly described Weidenreich’s ideas as independent evolution:

- The present races have arisen from different strains of sub-sapiens species of the genus *Homo* by a process of convergence. [1942:183]
- Weidenreich would have convergence of several species all to produce, at least in implication, the same result: the modern races of *Homo sapiens*. [1942:186]

Although the description was false, it was a successful rhetorical strategy: After reading a polygenist rendition of polycentrism, it is easy to miss the strong polygenist assumptions behind many of Howells’s own ideas. Howells’s view was that *Homo sapiens* was very ancient and lived contemporaneously with archaic human species, because he assumed that the present human races already existed in ancient times:

The racial nature of the first chronologically established modern types, in the Upper Paleolithic of Europe . . . represent a fully developed white stock, with the Negroids of

Grimaldi corroborating the differentiation. No fundamental evolution since then can be demonstrated, and it is likely that by this time all the races had appeared . . . this calls for a long previous history for the species. [1942:191]

The differences between these races were not the products of natural selection but, instead, of divergence through isolation, caused by random genetic drift:

The great majority of racial features are obviously not adaptational, and consequently bespeak a more or less random fixation of random variations of color and details of shape, in different groups of *Homo sapiens* which attained a *relative isolation*. [1942:191, emphasis added]

In this view, human diversity—living or fossil—was evolutionary divergence caused by isolation.

Paleontology and zoology give a clear picture of the main evolutionary activity among the component populations of a single taxonomic group, and this activity is divergence. . . . [T]his principle might be supposed to have been the ruling one in human development, rather than to have been contravened by man as an exceptional case. [1942:190]

Both scientists refined their arguments in a lengthy exchange in *AA* and elsewhere (Howells 1944; Weidenreich 1943b, 1947). Every element, argument, and many of the nuances of the modern human origins debate can be found in this exchange, although paleoanthropologists would only rediscover many of the essential points much later.

Antiracism and the Modern Synthesis

After 1945, the accepted discourse within U.S. anthropology was increasingly antiracist. Simultaneously, the modern evolutionary synthesis diffused into biological anthropology. Sherwood Washburn's "new physical anthropology" (Washburn 1951) explicitly attempted to reorganize bio-anthropological research along modern evolutionary lines. This populational and antitypological mode of explanation fit an antiracist discourse, because it did not assume a deep historical basis for racial differences. In this and other ways, the evolutionary synthesis encouraged a new climate of normal science in the field.

Among the architects of the synthesis, the two to most extensively address human evolution were Ernst Mayr and Theodosius Dobzhansky. Both believed there was no strong evidence for any branching within the hominid lineage since its origin from some ancient anthropoid lineage. Mayr's work (1950), which attempted to simplify hominid taxonomies into three successive species, has been more remembered. But Dobzhansky's work was in many ways more explicit:

Our species, *Homo sapiens*, evolved from its ancestors . . . in an extensive territory, comprising perhaps most of the Old World. Evolutionary improvements, that is, new and adaptively superior genotypes, arose from time to time in various parts of this territory. The populations in which these improvements arose expanded and transmitted their advantages to more widespread populations. Where

two genetic improvements met, new populations of still superior adaptedness were formed, and expanded in turn. . . . To ask where *Homo sapiens* first appeared is therefore meaningless. Races and local populations are trial parties which explore the various possibilities of adaptation. The gene pool of the now living mankind contains genetic elements which were present in many and perhaps in all major populations of the past. [1955:3–4]

Dobzhansky's thoughts on human evolution, which were strongly influenced by Weidenreich's view of the fossil record (Dobzhansky 1944), did more than any other to construct a population genetics framework for both human evolution and diversification.

Paleoanthropologists viewed modern human origins in terms of European Neandertals and their peculiarities. Key European paleoanthropologists, notably Arthur Keith (1925, 1931) and Henri Vallois (1954), proposed that the ancestries of modern humans and Neandertals within Europe had been separate since at least the Middle Pleistocene, and that some Middle Pleistocene fossils represented a pre-*sapiens* form. This pre-*sapiens* theory precluded the Neandertals from human ancestry and focused on European evidence, though in abstract the theory did not require that the pre-*sapiens* ancestor be European. A few scientists either proposed or claimed evidence for a pre-*sapiens* lineage outside of Europe, including Hermann Klaatsch (1923) and Louis Leakey (1953), and even Howells's conceptions were similar to the pre-*sapiens* model, without any specific mention of Europe as a pre-*sapiens* homeland. The greatest interpretive crisis of the theory's typological perspective would come from the first notably variable fossil human sample to be recovered, the Mount Carmel sample from Skhul and Tabun caves. As analyzed by Keith himself with Theodore McCown (McCown and Keith 1939), the sample looked both Neandertal and modern. The variation was shared among specimens to such an extent that McCown and Keith could not sensibly divide them into discrete groups. Instead, they proposed that the sample represented a single population "in the throes of evolutionary change" from an ancient pre-*sapiens* form to the later Neandertals of Europe. For Dobzhansky and Mayr, the sample's mixture of features was proof not of one species evolving into another but, instead, of the persistent mixture of genes throughout the human species.

F. Clark Howell (1951, 1957) offered a third alternative, applying the concepts of the synthesis to the Neandertal problem in a very different way from that proposed by Dobzhansky. In his view, the Neandertal lineage in Europe had evolved over time in a direction away from modern humans, becoming progressively more specialized in their glacial adaptations. He asserted that this evolutionary specialization evidenced a lack of gene flow between evolving Neandertals and modern humans, and this isolation precluded any role for the later, or "classic," Neandertals in the ancestry of modern Europeans. Earlier Neandertals, such as those from Ehringsdorf and Krapina, might represent the common ancestors of both later Neandertals and modern people, who evolved in the interim

outside of Europe. Thus, the Mount Carmel population plausibly represented the human ancestors intermediate between recent Europeans and the early pre-Neandertals, and Howell called the sample "proto-Cro-Magnon." This pre-Neandertal hypothesis offered adaptive explanations for the proposed specializations of Neandertals, while emphasizing the populational aspects of evolutionary change from earlier Neandertals through the variable Mount Carmel sample up to recent Europeans.

However, there was growing opposition to the view that "classic" Neandertals or other ancient fossil hominids were too specialized to serve as human ancestors. The evolutionary synthesis provided the insight that evolutionary change could and often did occur very quickly, and this insight was included in the pre-Neandertal model. However, in what Dobzhansky called "an exaggerated reverence for the principle of irreversibility of evolution" (1962:181), the pre-Neandertal model assumed that the direction of evolution was somehow constrained so that Neandertal "specializations" could not reverse in evolutionary direction. C. Loring Brace (1962, 1964) offered an effective adaptive explanation for the evolutionary change from Neandertals to recent Europeans that incorporated many of the features then known to differ between the two groups.

As a near opposite of Brace, Carleton Coon emphasized what Brace ignored, the regional component of variation to the exclusion of global evolutionary changes. Coon's polygenic interpretation was that human races were so isolated that they could evolve independently at different rates and, thereby, crossed a "sapiens" boundary at different times (Coon 1962). The polygenic aspects of Coon's theory were racist and widely recognized to be wrong (Dobzhansky 1963, 1968; Hulse 1963; Montagu 1963; Oschinsky 1963; Washburn 1963 [based on the presidential address at the AAA]).

For most biological anthropologists, these difficult issues made little difference. By ignoring modern human origins, the field could consider both recent and ancient human populations in an adaptive context. Successful adaptive accounts of australopithecine differences and Neandertal characteristics both illustrate the kind of progress that might continue even without considering hominid relationships. Thus, much of the field avoided grappling with the multilineal and reticulate problems that modern human origins researchers could not escape.

GENETICS AND MODERN HUMAN ORIGINS

Genetic studies within anthropology grew with the influence of the modern synthesis and the "new physical anthropology" and came to play a key role in the modern human origins debate. Genetic evidence from blood types and other sources provided strong evidence that human races are biologically insignificant (Goodman and Armelagos 1996), undermining the argument that the human species must be ancient because its races are old (cf.

Howells 1942). Many anthropological geneticists came to deny the concept of race (Barkan 1992; Cartmill 1998), asserting that the pattern of human genetic variation cannot be apportioned or categorized into evolutionary lineages (Livingstone 1962), even those acknowledged to exist within a single species.

The emerging perspective of anthropological genetics renounced these simplistic formulations because genetic variation may have multiple explanations (Garn 1957). Under this evolutionary perspective developing in anthropology, human populations were ephemera, with extensive differentiation prevented by gene flow (Hulse 1962). Even language barriers were not barriers to reproduction, as evidenced by the manifest interbreeding among linguistically differentiated groups (Moore 1994), the ready adoption of new languages by entire peoples, the dissimilar patterns of linguistic and demographic changes, and the powerful lack of any genetic differentiation along present linguistic boundaries. Biology and culture shared no common pathways on an evolutionary timescale.

The simplest forms of genetic analysis continued to make many of the same assumptions of preevolutionary race histories—explaining human variation as the result of ancient hybridization of once-pure stocks. Many geneticists, especially those employing multivariate methods, neglected these insights and accommodated their evolutionary models to the assumptions of their statistical analyses. By far the simplest multivariate technique applied to genetic data is the construction of trees. These branching diagrams summarize the genetic distances among populations by assuming a history of progressive divergences from a single common ancestor. The compilation of genetic differences and their construction into a tree is a simple algorithmic matter, but all such algorithms assume that evolution has only one mechanism: divergence through isolation.

The findings from the analysis of genetic trees have always been very similar. Under the assumption that humans have only evolved by isolation and divergence, the earliest divergence was between African and non-African populations, with later divergences splitting Europeans from Asians, Asians from Americans, and so on. This result has held true for many different kinds of genetic data (e.g., Mountain and Cavalli-Sforza 1993; Nei and Roychoudhury 1974, 1982; Nei and Takezaki 1996). By themselves, genetic trees give no idea of the time period over which human genetic variation arose, but the issue could be addressed if geneticists were willing to make certain assumptions about the rate of differentiation. With constant evolutionary change and complete isolation after population divergences, African and non-African populations diverged 100,000 years ago.

Many have pointed out that these assumptions are invalid. For instance, Frank Livingstone wrote, "it would be highly unlikely that the genetic differences at any locus are solely due to, and therefore reflect accurately, the population history of the groups, or that the gene frequency

differences would reflect the history" (1973:48). Because the construction of trees must assume divergences followed by isolation, trees can only validly describe the evolution of populations that diverged in this manner. Depending as they do on a long history of isolation and divergence of human populations, these models actually require the revival of polygenist assumptions that have long been known to be wrong. As Alan Templeton (1998) noted in *AA*, a tree showing genetic relationships of extant human groups is actually a candelabra model, asserting independent histories for the human races and, thus, differing from the earlier polygenist models only by its recent placement of the common origin before racial divergence. Human populations do not fit these assumptions, and human genetic variation actually refutes such an evolutionary model.

Thus it may seem surprising that modern molecular geneticists would adopt the assumptions of 19th-century polygenists without alteration, but some researchers have given these assumptions unwavering support. For example, Cavalli-Sforza recently wrote:

The Ethiopians genotype is more than 50% African. It is difficult to say if they originated in Arabia and are therefore Caucasoids who, like Lapps, had substantial gene flow after they migrated to East Africa, or if they originated in Africa and had substantial gene flow from Arabia, but not enough to pass the 50% mark. We are not helped by knowledge of the origin of Afro-Asiatic languages, which are by far the most common ones spoken in Ethiopia but are also spoken in North Africa, Arabia, and the Middle East. [1997:7719]

Whatever else this kind of convoluted racial logic attests, it certainly shows the impotence of 60 years of biological anthropology to affect geneticists' assumptions about human evolution.

The Genetics of Bottlenecks

In 1972, John Haigh and John Maynard Smith made a surprising discovery about the β -globin gene (Haigh and Maynard Smith 1972). If humans had been numerous in the past, then genetic drift should have been weak, and β -globin should exhibit great diversity, especially considering its well-studied selective balance. The gene actually had surprisingly little variation, and Maynard Smith and Haigh suggested that the human population had once been very small, elevating genetic drift. The time of ancient small population size was assumed to be a "bottleneck," preceded by a population crash and followed by an expansion to the present population size.

Examination of other nuclear genes confirmed that human variation was lower than human population size would predict, but not until 1987 did these studies finally begin to influence paleoanthropology. In that year, Rebecca Cann et al. (1987) reported a low level of variation for human mitochondrial DNA (mtDNA) from humans of different geographic origins and asserted that an ancient bottleneck in population size was the cause. The research-

ers estimated that a common ancestor for all living human mtDNA existed between 140,000–280,000 years ago and surmised that a population bottleneck had occurred at this time. As it turned out, the central inference of the study, that a common mtDNA ancestor meant that all humans at that time belonged to a single population, was incorrect (Templeton 1993). Although the study did indeed demonstrate that our ancestors could not have lived in mutually isolated populations at that time, this finding was not news: Polygenism had been wholly discredited by anthropologists for 40 years. Although the researchers found greater variation in people of African origin than in non-Africans, the relevance of this finding was not clear: Either a more ancient African population or a larger African population could explain this observation.

The only salient finding was the low level of mtDNA variation and a possible bottleneck, because a very small ancient population size would imply that our ancestors had a limited geographical extent. Further studies of mtDNA and of the Y-chromosome also appeared to be consistent with a recent genetic bottleneck, because the variation in both genetic systems among living humans is very low (Dorit et al. 1994; Hammer 1995; Vigilant et al. 1991; Whitfield et al. 1995). It was this hypothesis of a recent bottleneck that, if true, could prove decisive in support of a recent single origin for living humans.

The inference of a bottleneck was several steps removed from the data. The real information coming from these genes, clarified by Henry Harpending, Alan Rogers, and colleagues during the mid-1990s (Harpending et al. 1993; Rogers and Jorde 1995; Sherry et al. 1994), was that the global gene pool represented by these genes expanded in the past. With a sufficient knowledge of the rate of mutational change in these genes, genetic researchers might discover both the timing and the magnitude of the change in size of these effective gene pools. Neither the history before this apparent expansion nor the underlying causes of it could be determined from mtDNA or Y-chromosomal data alone.

Impressive nuclear genetic data were available from the early 1970s, with more detailed global samples accumulating during the 1990s. By the late 1990s, most paleoanthropologists became aware of what had been empirically known for 15 years or more: Nuclear genes show that the effective gene pool of our lineage was small—equivalent to between 10,000–20,000 breeding individuals—during at least the entire Pleistocene. For each gene, a common ancestor of all the alleles extant in living humans once existed, and for all but a few genes these ancestors were dispersed across the past two million years.² It became clear that no gene preserved evidence of an ancient large gene pool. Without a gene pool crash from a large size to a much smaller size, there was no bottleneck, only a long history of a very small, effective gene pool, ever since humans existed.

So why did so many researchers after Cann et al. (1987) assume that a recent bottleneck was the prime explanation

of low human genetic diversity? It seems likely that the assumption was so widespread because the alternative seemed unthinkable. But the alternative to a single recent bottleneck turned out to be true: Humans never underwent a recent bottleneck because the effective human gene pool had never been large.

It's Not Easy to Be Small

There have been conflicting interpretations of low genetic diversity and its relation to the past size of the effective human gene pool. The first takes the evidence for a small ancient effective human gene pool at apparent face value and assumes it reflects a small ancient human population size. Promoted by Harpending and colleagues (Harpending et al. 1993; Harpending et al. 1998), the "weak Garden of Eden" model asserts that human populations once coexisted within a small geographic area at a limited population size, and that the geographic differences among living humans began to arise long before the dispersal of this small population around the world. As in Howells's (1942) model, human races have an ancient origin within a single pre-*sapiens* homeland:

We are descended from a population that was effectively a separate species for at least the last 1 or 2 million years. Although the size of this population must have fluctuated over time, it was often reduced to the level of several thousands of adults. Such a population would have occupied an area the size of Swaziland or Rhode Island rather than a whole continent, though episodic expansions would have covered a much larger area. [Harpending et al. 1998:1967]

Such an area would be much smaller than the pan-African distribution of Late Pleistocene human fossils, and it is very unlikely that any fossil evidence of this "separate" population could ever be identified.³

But does low genetic diversity necessarily reflect small population size? Genetic variation in *most* natural species is much lower than population size alone would predict under neutrality, often by several orders of magnitude (Nei and Graur 1984). It is unlikely that the broad range of animal species that show disparity of population size and genetic variation, from *Drosophila* to *Homo*, have all been greatly restricted in numbers until recently (Hawks et al. 2000). But if not, then other evolutionary mechanisms must have reduced genetic variation in most animal species. Such mechanisms have been the subject of inquiry in both evolutionary biology and anthropology (Gillespie 1991, 2001; Hawks 1999; Pannell and Charlesworth 1999, 2000; Takahata 1994; Whitlock and Barton 1997) and include different kinds of natural selection, population structure, or mating structure. Deciding which factors may have been important in human evolution and finding evidence for their action is a significant research problem that is currently underway.

Another approach to the question of small ancient human population size, promoted by Alan Templeton (1993, 1994, 1998), tests whether population movements

occurred at particular times in the past by finding disequilibria in the geographic distribution of genes. Using this method, human genes show that no single migration of all humans from a source occurred during the Middle or Late Pleistocene (Templeton 1998, 2002). Thus, models that require all human ancestors recently passed through a small population size bottleneck or occupied a very restricted geographic area during the Pleistocene, including the "weak Garden of Eden" proposal, must be wrong. Plainly, if Templeton is correct, then the modern human origins debate has come to an end, as no replacement model could possibly be true.

However, the debate continues, and one possible test of these interpretations is in evidence for population expansions. If the genetic variation of most human genes reflects a purely neutral evolutionary history, then these genes must be consistent with a massive expansion in population size, as the originally small gene pool of the Late Pleistocene ultimately grew to billions of people. Some genes, including mtDNA and the Y-chromosome, as well as a few nuclear genes, are consistent with substantial expansions during the Late Pleistocene. Many of these genes are from regions on the chromosomes with low or no recombination. In these regions it is easier to reconstruct the genealogical history, but they are more likely to have significant distortions from the effects of selection on linked sites (Gillespie 2001). Conversely, many other nuclear genes, including large-scale surveys of single nucleotide polymorphisms across the genome, significantly reject any population expansions during the Late Pleistocene (Hawks 1999; Przeworski et al. 2000; Wall and Przeworski 2000). Because some population expansions have occurred during human prehistory, genes that reject any such expansions must be explained. The question is whether such an explanation can refute the use of these genes to infer ancient demography and simultaneously support the use of other genes (Harpending and Rogers 2000) or whether, instead, the process of evolution makes all human genes useless for demographic inference (Hawks et al. 2000). Research along these lines continues, but like many other questions we have raised, the outcome clearly depends on the importance that selection is ultimately found to have in human evolution.

MULTIREGIONAL EVOLUTION

The current form of the modern human origins debate in paleoanthropology originated with Reiner Protsch's (1975) contention that modern humans could be identified as a distinct entity and were of African origin. He took a pre-Neandertal position but identified the earliest modern human contemporaries of Neandertals in Africa instead of in Europe. The next year, Howells (1976) put the question in the context of diffusion versus independent evolution. Other approaches to modern human origins were developing within paleoanthropology at this time, and the first fully developed statement of multiregional evolution was

published by Milford Wolpoff, with Wu Xinxhi and Alan Thorne, in 1984.⁴ The hypothesis was a direct outgrowth of Weidenreich's polycentric theory but relied on population genetics models and recognized that there were different mechanisms responsible for establishing the initial pattern of worldwide variation, when the world outside of Africa was first colonized, and for maintaining this pattern for much of subsequent human evolution, until it was increasingly obscured by the population size explosions that began at the end of the Pleistocene and continue unabated today. The multiregional hypothesis had to reconcile two apparently contradictory aspects of human evolution. There clearly were important, highly significant evolutionary trends reflected in the evolution of all human populations through the Pleistocene. These trends argued for a history of sharing genetic and cultural information. At the same time, there appeared to be evidence of continuity for different anatomical features in different regions of the world, spanning various durations of the Pleistocene. This observation argued for separation of populations within a species with population structure. Multiregional evolution relied on gene flow to explain both problems.

Because the authors argued that traits but not populations could show continuity, they focused on the evolution and dissemination of individual traits under selection to explain how changes occurred and why they persisted. They outlined the role of gene flow as part of an answer to the question of why the widespread human species with small populations (the Sewall Wright [1931, 1986] model of small, semi-isolated Paleolithic populations) did not speciate.⁵ The discussion of gene flow was organized by this issue and, following Mayr (1963), focused on its role in a species with population structure. Yet the emphasis on gene flow as the agent of species cohesion detracted from an accurate understanding of its role in linking populations across an adaptive landscape and disseminating important traits, despite the clear importance of clines balancing gene flow and selection in the model (Caspari 1997).

This discussion may have prompted other researchers to misconstrue some aspects of multiregional evolution (as discussed in Wolpoff et al. 2000). Some scientists assumed that an emphasis on the causes of long-term regional variation meant that multiregional evolution portrayed regional differences as the most important aspects of human evolution. Perhaps for this reason, or because of the continued confusion of Weidenreich's polycentrism with polygenism, many descriptions of multiregional evolution depicted it either as a candelabra without gene flow, or as a candelabra with weak lines of connection between thick vertical stems. This confusion is well illustrated by Stephen Jay Gould:

Multiregional evolution should be labeled iconoclastic, if not a bit bizarre. How could a new species evolve in lockstep parallelism from three ancestral populations spread over more than half the globe? Three groups, each mov-

ing in the same direction, and all still able to interbreed and constitute a single species after more than a million years of change? (I know that multiregionalists posit limited gene flow to circumvent this problem, but can such a claim represent more than necessary special pleading in the face of a disabling theoretical difficulty?) [2002: 911-912]

In actuality, "lockstep parallelism" is Coon's model (Caspari and Wolpoff 1996), not a multiregional one, as are assertions that multiregional evolution requires the "simultaneous" or "convergent" evolution of modern humans in different isolated populations.

Following the model's first publication, the fossil record provided significant additional support through new discoveries and more detailed and much more numerous observations of continuity in different regions (Duarte et al. 1999; Etlar 1996; Frayer 1993, 1997; Kramer 1991; Li and Etlar 1992; Pope 1992; Wolpoff et al. 2001; Wu 1997). However, these regional features are only a secondary pattern in human evolution as described by Weidenreich (1946, 1949), since major evolutionary changes occurred across the human range. Many new insights emerged to account for the worldwide pattern of evolutionary change; mechanisms compete to explain how evolutionary novelties spread through a species (e.g., Aiello 1993; Eswaran 2002; Smith et al. 1989), and although none are mutually exclusive, the pattern of global changes associated with modern human evolution has remained an unresolved issue (Relethford 2001). In particular, it is not clear whether the features distinguishing recent people from their ancestors arose independently or as a complex. The difficulties in defining either anatomical or behavioral "modernity" as a singular entity absent in archaic humans (Clark 2002; Sarich 1997; Tobias 1995; Wolpoff 1986; Wolpoff and Caspari 1997) may imply that these features did not disperse from a single place; however, this will not be easily resolved because different mechanisms may account for the dispersion of different features. The whole issue of modern human origins may be a perspective created only by the fact that we are moderns in the present looking into the past (Wobst 1990).

BUSHEL OF SPECIES

A few working paleoanthropologists accept the assertion that evolutionary change happens only at the time of speciation, and that species-level selection has been the principal mode of change among Pleistocene hominids (most notably Tattersall 2000; Tattersall and Schwartz 2000). For them there are six or more Pleistocene species of the genus *Homo* and there are even multiple species at single sites such as Dmanisi (Schwartz 2000) and Skhul (Schwartz and Tattersall 2000).

The punctuational mode of evolution represented by many hominid species of small geographical range, evolving by adaptive radiation and successive episodes of species selection, could be the basis of a plausible scenario to explain both the geographic differences in the hominid

fossil record and the genetic interpretation that the ancestral human population actually numbered less than 20,000 breeding individuals during the entire course of the Pleistocene. In this scheme, most—possibly all—known Pleistocene hominid fossils represent the multitude of species with no living descendants. The lineage leading to us was not a single species during the past two million years but was segmented into several successive species separated by punctuated speciation events, repeated genetic bottlenecks that further reduced the genetic variation of the eventual *Homo sapiens* population. This position has not been articulated either by population geneticists or by morphologists, and although it faces the substantial problems noted above, it constitutes a logical union of the two datasets.

The punctuational views that have been articulated reflect the most significant support for a total replacement theory, yet they have not greatly influenced the views of many paleoanthropologists. In part this may stem from an incomplete theoretical perspective that disputes the validity of the modern evolutionary synthesis. Punctuationalists equate synthetic theory with gradualism:

Thanks to the overwhelming triumph of the Evolutionary Synthesis . . . human evolution, like that of other organisms, came to be seen as a gradual, linear process that, come hell or high water, continued doggedly along a path of inexorable betterment. [Tattersall 2002:81]

Perhaps as a consequence, the punctuationalist perspective in anthropology has incorporated interpretations of the evolutionary process that are significantly at odds with the normal science tradition of biological anthropology. Again citing Tattersall's most recent discussion:

- Evolution is best described as opportunistic, simply exploiting or rejecting possibilities as they arise . . . there is nothing inherently directional . . . about this process. [2002:139]
- For true innovations to arise and become permanently incorporated into some component of the human population, it will be necessary for that population to become fragmented. [2002:189]
- There is no mechanism by which particular characteristics—still less, genes—can be singled out for favored or disfavored treatment. [2002:187]
- Either the whole creature (or species) succeeds reproductively, warts and all, or it fails. [2002:179]

Another problem is that it has been empirically difficult to identify and define fossil species by unique features. Even a single feature may be enough for species diagnosis in this framework, but examination of modern human skeletal collections almost invariably shows that the key characteristics of fossil human species are not absent from recent humans. If many closely related Pleistocene hominid species really did exist, an appropriate analogy would be the earlier Pliocene record of hominid evolution, but in this sample several species differing in adaptation overlapped extensively in almost every feature,

even features functionally related to their adaptive differences.

The punctuationalists agree with Howells (1942) that human races have been diverging from each other, or at least were until the technological shifts of the Holocene. An African replacement is one way to limit racial divergence under this model, by asserting that today's races share a very recent common origin in a single source population. In his support of a bushy fossil record, Gould's view is explicitly punctuationalist and his assessment of similarities, even *within* the human species, is based on phylogeny and not adaptation or a history of reticulation:

All modern humans form an entity united by physical bonds of descent from a recent African root; we are not merely the current state of a tendency as the multiregional model suggests. Our unities are genealogical; we are an object of history. [Gould 1988:21]

By rendering multiregional evolution as a polygenic theory, Gould promotes a recent African origin model as an antiracist alternative *despite its implicit reliance on a history of racial isolation*. This rhetorical strategy is the same as that used by Howells over forty years earlier.

EX AFRICA SEMPER ALIQUID NOVI?

Some paleoanthropologists do not embrace genetic or punctuationalist interpretations that suppose a complete replacement of archaic humans but emphasize that modern anatomy and behavior spread in a worldwide migration of ancient African peoples. A debate in *AA* in the middle of the 1990s (Frayser et al. 1993; Frayer et al. 1994a, 1994b; Stringer and Bräuer 1994) covers most of the outstanding issues. In their article, Christopher Stringer and Gunter Bräuer articulate a revised "Eve" theory, supplanting complete replacement with a theory in which modern humans appeared in Africa and then spread around the world where they interbred with the archaic humans they encountered, to a greater or lesser degree to account for instances when regional continuity between archaic and modern peoples may be established. This model is implicitly a multiregional view, albeit with an assumption that gene flow has been relatively insignificant among populations in the past. Other scientists with an explicitly multiregional perspective have focused on how a complex of features may have arisen and spread from an African source (e.g., Relethford 2001; Smith et al. 1989). For them, gene flow in the form of population movement and mixture is a primary cause of evolutionary change, while, in contrast, for the revised Eve theorists it is an ad hoc explanation of how there could be evidence of continuity when the evolutionary mechanism is population or species replacement.

Although there is a great diversity of opinion among paleoanthropologists on modern human origins, few substantial differences divide many of these views. Scientists such as Stringer and Bräuer (1994) have emphasized the

importance of population movements in spreading anatomical features, the presence of a complex of morphological differences separating “modern” and archaic peoples (Stringer and Andrews 1988), and the importance of genetic drift and small population dynamics in establishing complexes of new features. In contrast, multiregionalists including the present authors have questioned whether any complex of features defines modern people (Wolpoff and Caspari 1996, 1997), have emphasized the importance of natural selection in spreading advantageous features, and have focused strongly on the importance of similar changes in a global context throughout the Pleistocene. These conceptual issues, as well as terminological ones such as definitions of species, continue to divide the field. But there is increasingly little disagreement on many central issues. Most paleoanthropologists agree that ancient African populations had the greatest influence on global evolution, because of either their size or antiquity. Additionally, most agree that no anatomical changes provide clear marks of behavioral modernity as it arose, and that many humans with archaic anatomies were capable of modern behaviors. Finally, most agree that human evolution during the Late Pleistocene reflects significant population expansions and did not involve complete isolation among groups, and most are willing to accept that even the European Neandertals may have interbred with later humans. Thus, the majority of paleoanthropologists are today divided by the degree of importance they give to different evolutionary mechanisms, and the amounts of contributions from different ancient populations to the modern gene pool, but not by whether any contribution existed.

THE FUTURE

From a scientific perspective, modern human origins research is proceeding at an admirable pace, with new important discoveries nearly every month. These discoveries have constrained the range of possibilities within both paleontology and genetics. The observation of low variation among recent humans has been drawn into sharp relief both by the accumulation of genetic evidence during the past four decades and by the even longer-term statistical work on various anthroposcopic traits. Certainly humans are variable, particularly in an anatomical context, and humans are polytypic in a geographic context. Yet as great as the entire global range of human anatomical variation may be, it is so small that it fails to encompass most known hominid fossils from only 50,000 years ago. The variation among human genes, both within and among populations, is equally slight, and exactly the same can be said of the small but growing sample of ancient mtDNA: It all lies outside the range of modern variation. If selection on human anatomy and behavior, abetted by social or cultural factors, were the cause of our similarity, then the evolution of recent people may have involved a large population spread across large regions of the world. But if

genetic drift was the cause, with only limited contributions of selection or other factors, then the evolution of recent people must have occurred within a very small population, one that must have been geographically restricted.

Within human paleontology, disagreements about the relative importance of evolutionary mechanisms and the actual patterns of morphological change persist, although most agree that some gene flow occurred between archaic human populations. The broad agreements that do exist have been obscured by terminological confusion, especially involving the definition of ancient species, since scientists who use taxonomic names to denote morphological differences but not true reproductive boundaries mask the importance of gene flow. Also, many paleoanthropologists continue to use models that require isolation between human races, even though we know that such isolation has never existed. We believe that such conceptual problems persist because modern human origins research has never been integrated into the scientific context of modern biological anthropology, and long-discredited theories continue to have significant impact.

Even greater polarization exists among geneticists. Some equate genetic variation with population size, leading to the interpretation that our ancestors lived only in a small area prior to a Late Pleistocene expansion in population size. This interpretation has become increasingly inconsistent with paleontological models, even those involving a recent African replacement, because of its implication that no gene flow occurred in the past. When combined with models that view human geographic differences as a tree of population divergences, such interpretations become increasingly divorced from reality. Other genetic models that include ancient gene flow exist, but these do not themselves provide mechanisms to explain the level of human genetic variation. Thus, making a decision regarding these genetic issues will require the elaboration of evolutionary mechanisms of change, similar to paleontological perspectives.

In our view, much future progress on these issues will be analytical. Paleontological data accumulate relatively slowly, and while our empirical knowledge of human genetic variation accumulates ever more rapidly, we lack satisfactory ways to explain the genetic patterns that we have already observed. To proceed, we must recognize the past, by acknowledging both that some theories were proven wrong long ago and that others are not so different as rhetorical formulations may make them seem. Put most simply, we must resolve the role of selection in human evolution.

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NOTES

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1. In this article, *generic* is used several times when *genetic* is clearly meant. This is most likely an error in typesetting, as the English words are quite similar to their German counterparts.
2. Such as the major histocompatibility complex genes, whose variation has been maintained by selection for millions of years (Ayala 1995).
3. If such a small isolated population ever existed for very long; a better hypothesis to account for these data might be frequent and recurrent branching speciations along the human lineage during the Pleistocene, each involving a small initial population size with many simultaneous evolutionary changes because of drift and selection.
4. This history is described in Stringer 1994 and Wolpoff and Caspari 1997.
5. This was in response to an article by Ehrlich and Raven (1969) reporting low levels of gene flow between natural populations and questioning the validity of the biological species concept.

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