

Towards a Theory of Modern Human Origins: Geography, Demography, and Diversity in Recent Human Evolution

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ABSTRACT The origins of modern humans have been the central debate in palaeoanthropology during the last decade. We examine the problem in the context of the history of anthropology, the accumulating evidence for a recent African origin, and evolutionary mechanisms. Using a historical perspective, we show that the current controversy is a continuation of older conflicts and as such relates to questions of both origins and diversity. However, a better fossil sample, improved dates, and genetic data have introduced new perspectives, and we argue that evolutionary geography, which uses spatial distributions of populations as the basis for integrating contingent, adaptive, and demographic aspects of microevolutionary change, provides an appropriate theoretical framework.

Evolutionary geography is used to explore two events: the evolution of the Neanderthal lineage and the relationship between an ancestral bottleneck with the evolution of anatomically modern humans and their diversity. We argue that the Neanderthal and modern lineages share a common ancestor in an African population between 350,000 and 250,000 years ago rather than in the earlier Middle Pleistocene; this ancestral population, which developed mode 3 technology (Levallois/Middle Stone Age), dispersed across Africa and western Eurasia in a warmer period prior to independent evolution towards Neanderthals and modern humans in stage 6. Both lineages would thus share a common large-brained ancestry, a technology, and a history of dispersal. They differ in the conditions under which they subsequently evolved and their ultimate evolutionary fate. Both lineages illustrate the repeated interactions of the glacial cycles, the role of cold-arid periods in producing fragmentation of populations, bottlenecks, and isolation, and the role of warmer periods in producing trans-African dispersals. *Yrbk Phys Anthropol* 41:137-176, 1998. © 1998 Wiley-Liss, Inc.

TABLE OF CONTENTS

Origins and Diversity: Historical Perspectives on Recent Human Evolution	139
Evolutionary Geography	145
Population survival, range, and demography	146
Modern Human Diversification	148
Neanderthals and modern humans	148
Ancestral bottlenecks and the establishment of modern humans outside sub-Saharan Africa	160

Spatial structure of the ancestral population	160
Population structure prior to Upper Pleistocene expansions	163
Secondary bottlenecks and the differentiation of human populations	165
Human diversity within and out of Africa	167
Discussion and Conclusions	168
Dispersals of modern humans	168
Diversity through time	168
Extinction	169
Microevolutionary events	170
Role of geography in recent human evolutionary history	170
Acknowledgments	171
Literature Cited	171

The evolution of modern human origins has dominated the last decade of research and controversy in palaeoanthropology. The character of this debate contrasts with those in the early part of this century, when there was insufficient data or chronological resolution to separate out confidently distinct evolutionary events in hominid evolution, and with those in the middle part of the century, when early hominid research pushed modern human evolution into the background. The emergence of the "modern human problem" has posed a major challenge to palaeoanthropology, as is evidenced by the persistence of two competing theories. This apparent impasse between the so-called multiregional (MM) and single origin (SOM) models has been ascribed to either lack of data or a clash between molecular genetic and palaeontological evidence or to competing intellectual paradigms (Clark and Willermet, 1995). We would argue that the evidence now available allows the solution of the modern human problem at the level of these two models but that much remains to be done in terms of relating the evolution of modern humans to evolutionary theory and mechanism and in integrating models of origins with the evolution of human diversity.

The purpose of this paper is to explore the problem of modern human evolution in terms of a number of broader issues in evolutionary theory. The first of these is that problems of phylogenetic origins such as that of modern humans cannot be isolated from the more general issue of population diversity and variation; hence, any theory of modern

human origins must also account for changing patterns of diversity across some origin threshold. The problem of modern human origins could thus be approached as that of human diversity through time. Second, it must be recognized that the issue of the origins of modern humans is essentially a microevolutionary one. Multiregional models have stressed the lack of speciation in later hominid evolution (Wolpoff et al., 1994), and single origin models have often demanded reproductive isolation between hominid populations and speciation events (Stringer and Andrews, 1988). In practice, the scale, both in terms of chronology and biology, is clearly on the edge of where species boundaries may lie. Given the need to explore detailed geographical and temporal patterns within a larger framework, demographic rather than species-based aspects of evolutionary theory should be considered. Finally, similarly to many interesting problems in evolution, modern human origins rest as much on geographical patterns as on chronological ones, and the archaeological and fossil records provide access to these. However, the consideration of spatial patterns requires an understanding of the theory underlying the possible roles played by geography on the evolution of populations within a lineage.

This paper is divided into three parts. First, we outline how issues of origins have historically been intimately related to both scientific and more general notions of human diversity and how the current debate fits within this history; second, we outline some of the principles of evolutionary geogra-

phy that provide a framework for considering recent human evolution and discuss how these can be used to explore the complex pattern of modern human diversification; finally, we use these principles to explore the actual patterns and mechanisms involved in the separation and subsequent diversification of the populations ancestral to living humans today.

ORIGINS AND DIVERSITY: HISTORICAL PERSPECTIVES ON RECENT HUMAN EVOLUTION

Although the current debate on modern human evolution is phrased in terms of origins, the question of human diversity has always been an integral part of it. This is clear in the development of the current debate, which, although it emerged as an issue in prehistory (Bowler, 1986; Smith and Spencer, 1984, and papers therein), rapidly became a forum for discussions of the genetic variation found in the human population today. This interest is not new. The diversity of humans around the world has long been a source of both scientific and religious discussions, and theories explaining how it has arisen are numerous. The rise of evolutionary theory in the last 150 years did little to change the actual perception of human differences. It mainly placed these within a new context, that of proximity or distance from hominid fossil forms and non-human primates. Interpretations at the turn of the century focused on two alternative and often extreme models of modern human origins. Attempts at asserting the application of a Darwinian perspective to the origin of people saw the rise of the first unilineal models—from *Pithecanthropus* to Neanderthals to humans—such as those of Manouvrier, Haeckel, Cunningham, and Schwalbe. These were first contested not on the basis of the nature of the phylogenetic relationships but on the placing of these fossils in the human family by contemporaries like Virchow and Turner. However, once the hominid character of Neanderthals was accepted, the actual descent of humans from them, particularly Europeans, was questioned. It was thus that researchers like Boule, Keith, Breuil, and Elliot Smith argued that Neanderthals represented an extinct branch of

humanity, a view defended by some, like Vallois, until the middle part of the century. Hrdlička and Weidenreich, former students of the early unilinealists Manouvrier and Schwalbe, were the main dissenting voices. Hrdlička studied not only the European Neanderthal remains but traveled to Rhodessa to examine the newly found fossil of Kabwe. He proposed a new unilineal model in which there was a Neanderthal phase in the evolution of humans. Weidenreich, following his study of the *Sinanthropus* fossils and their comparison to *Pithecanthropus* remains, proposed a model similar to Hrdlička's but which stressed the descent of living Asians from *Sinanthropus* and living Australians from *Pithecanthropus* (Weidenreich, 1943) (in his model, Neanderthals actually represent a side branch, and modern Europeans are descendants of the Levantine fossils). Although drastically different regarding the role of archaic hominids in modern human evolution, all these early and mid-twentieth-century views highlighted regional differences among present human populations and did not emphasize the evolutionary mechanisms that were being discussed and explored at the time by founders of the modern synthesis such as J. Huxley or Simpson.¹ These two approaches, one emphasizing direct ancestry, continuity, and regional stability, the other temporal and spatial discontinuities, essentially set the framework for the subsequent decades of research on the evolution of human diversity.

Each of these models also has implications for broader interpretations of human diversity, especially whether all humans are very similar and have virtually identical evolutionary heritages or not and why differences between populations have evolved. It is here that ideas on human diversity have perhaps been most changeable, and it is clear that anthropological studies and the perception of population differences have also had sociopolitical dimensions. During the early part of this century, the emphasis

¹Carleton Coon represents an interesting figure in this watershed between pre- and post-neo-Darwinism in that, although his major works were published in the 1950s and 1960s (Coon, 1962), his framework for considering evolutionary diversity in humans was essentially that of the prewar anthropologists.

was on the differences between human populations and the expectation that pure regional types or races had once existed. This view fueled eugenic and racist movements in the US and Europe. The fact that anthropological research had provided a scientific flag for these movements had a profound effect on the future development of the discipline. Partly to compensate for earlier excesses, postwar anthropological research had to prove to the academic world that it had no eugenic and racist tendencies. For the three subsequent decades, anthropologists focused on research that stressed the genetic similarities between human groups, the plasticity of the human phenotype and its relation to environmental factors, local adaptation rather than migration as the source of variation, and the functionally unique aspects of human societies. Studies on the evolution of human diversity or the role and direction of migrations in the development of diversity became rare or absent. A corollary of these developments was the general abandonment of human morphology as a source of information for phylogenetic studies at the level of human populations. It is interesting that while the study of fossil hominid skeletal remains received a major boost from the 1950s to the 1980s, particularly all the then newly found australopithecines, the study of the evolution of modern humans and their differences through skeletal remains was left aside. This is not to say that no research on modern human skeletal samples was carried out throughout this time period. Two areas had a significant development. On the one hand, the principles of palaeopathological diagnosis and bioarchaeology were developed, and this field became and still is a very active one within anthropology (Larsen, 1997). On the other, the use of multivariate statistics for the analysis of cranial measurements became established, and a number of studies investigated the relationships among present human populations using these methods. However, with the exception of works like those of W.W. Howells (1973, 1976, 1989), these studies were carried out at the level of present regional populations and did not dwell on the issues of the origin of modern humans and global human diversity.

Therefore, when palaeoanthropology regained a deeper interest in the origin of modern humans in the early 1980s, the status quo was a theory that stressed the local evolutionary character of human populations and variation as a product of immediate environmental adaptation rather than population history. This view saw human plasticity in the face of environmental needs as the key mechanism and strongly rejected hypotheses of wide-ranging migrations and dispersals as a source of diversity. Weidenreich's multiregional theory, which lacked a theoretical mechanism for the maintenance of worldwide parallelisms for the regional evolution of humans from archaic ancestors, was reworked into a coherent model of clinal evolution in which gene flow homogenized differences and prevented speciation (Wolpoff, 1989; Wolpoff et al., 1984).

Nevertheless, there was a contrast between the widely held belief that in East Asia and Australia there had been continuity of occupation and descent from *Homo erectus* onwards, as proposed by Weidenreich in the 1930s–1940s on one hand and on the other the persistent controversy over the contribution of Neanderthals to the modern human gene pool and the relative age of modern humans in Africa and the Middle East. Neanderthals are the best-represented fossil hominid in terms of number of fossils, anatomical completeness, and age-sex distribution. Various recently dated sites suggest that there may have been over 100,000 years between the first appearance of modern humans in Africa and the last appearance of Neanderthals, making these two hominid groups contemporaneous for the greater part of their history. If the dating of sites like Saint Césaire and Zafarraya is correct (Lévêque and Vandermeersch, 1981; Lévêque et al., 1993; Hublin, 1996), it is also the case that these two populations may have overlapped by some 10,000 years in Europe (Strauss, 1993–1994; Hublin et al., 1995; Grün and Stringer, 1991). Therefore, Neanderthals are also very recent, and the consensus that grew during the 1980s about their limited geographical distribution and the apomorphic character of their anatomy became very difficult to integrate with long-term claims (Brace, 1964) that late Neander-

thals show morphological changes that could be interpreted as signs of admixture (Mellars, 1996; Stringer and Gamble, 1993). The re-dating of the fossil sample from Krapina to 130,000 years ago (Ka) (Rink et al., 1995), long argued as progressive between Neanderthals and Upper Palaeolithic Europeans, and the character of recent fossils like Zafaraya and St. Cesaire have confirmed that Neanderthals show no trends towards increasing modernity. Thus, the absence of truly transitional fossils in this area raised again the question of extinction and replacement vs. admixture. Although the fossils are unlikely ever to rule out any admixture, the contribution of Neanderthals to European morphology appears to have been minimal or completely lacking (Bräuer, 1992; Holliday, 1997; Stringer, 1992, 1993; Stringer et al., 1984).

New studies have also brought the notion of regional continuity outside Europe under closer scrutiny. There is indeed regionality to be found today in some of the so-called continuity traits (the characters proposed as evidence for Asian and Australasian morphological continuity from Asian *Homo erectus* to modern populations) as well as in other traits not included in the multiregional model. However, the original descriptions of the traits and their linkage to a model by Weidenreich were either largely qualitative or based on relatively small samples. Statistical approaches and larger samples have generally failed to corroborate the earlier observations, and greater consideration of the polarity of these traits as well as functional patterns of human cranial morphology has greatly limited the evolutionary significance of many of them (Groves, 1989; Groves and Lahr, 1994; Lahr, 1994, 1996; Lahr and Wright, 1996; Lieberman, 1996). Indeed, from a historical point of view, more in-depth studies led even some of those who originally defended the view of long-term morphological continuity in Southeast Asia to reject much of the basis for multiregionality, as indicated in this passage from Macintosh and Larnach (1976):

Macintosh (1963)...supported Weidenreich's opinion that special features of the *Pithecanthropus-Soloensis* forehead have undergone very little change in the Australian. We no longer hold any such view....A compari-

son of Australian skulls with those of *Homo erectus* shows the complete absence of the *Homo erectus* cranial pattern in the former....[I]t [is] extremely unlikely that they [Ngandong] can be ancestral to Australians.

The problem of both Far Eastern and European links of archaic hominids with recent human populations hinged on two issues: the relative age of morphologically different populations and the relative proximity of living human populations to their supposed regional archaic ancestors. While new dates have tended to show the contrast between Africa and elsewhere with regard to the age of the modern population, a number of studies have also established the morphological unity of all modern humans. Metric analyses have overwhelmingly shown that living human populations share far more with each other than with their local antecedent populations (Howells, 1973, 1989; Stringer, 1996a,b; Stringer et al., 1997; van Vark and Bilsborough, 1991; van Vark et al., 1992). The modern human morphological homogeneity, the discontinuities in the fossil record outside Africa, the chronological contrast between the first appearance of modern humans in Africa and in the rest of the world, and the tropical body proportions of the earliest modern Europeans in contrast to those of Neanderthals led to a wide acceptance of a view developed gradually and independently since the late 1970s of a single origin, a recent origin, and an African origin (Bräuer, 1989; Holliday, 1997; Howells, 1976, 1989; Lahr, 1996; Lieberman, 1996; Stringer et al., 1984; Turbón et al., 1997; Waddle, 1994). In addition, from the mid-1980s the uniformity of the modern human morphology has found a reflection in the overall genetic homogeneity of modern humans.

In 1987, the publication of a phylogenetic analysis of human mitochondrial DNA (mtDNA) sequences was among the first attempts to use molecular genetics to explore human (as opposed to hominid) origins (Cann et al., 1987). The surprising claim at the time was that human populations today are descended from a small ancestral population living in Africa within the last quarter-of-a-million years. In effect, the growing field of molecular anthropology has confirmed and elaborated on this claim. The

initial proposition was twofold: that in terms of mtDNA lineages African populations were significantly more diverse than others and that all human mtDNA lineages coalesced between 200 and 150 Ka. High levels of African diversity have now been confirmed for mtDNA, a number of microsatellites, and for a number of loci on the Y chromosome (Armour et al., 1996; Bowcock et al., 1991, 1994; Hammer, 1995; Hammer et al., 1997; Hasegawa and Horai, 1991; Hasegawa et al., 1993; Horai et al., 1993, 1995; Nei and Graur, 1984; Pääbo, 1995; Rogers and Jorde, 1995; Stoneking, 1993; Stoneking et al., 1997; Takahata, 1993; Tamura and Nei, 1993; Tishkoff et al., 1996; Vigilant et al., 1991; Whitfield et al., 1995). This diversity can be measured at a number of regional scales; for example, the Turkana are more diverse than all Europeans, and East Africa is the most diverse region (Watson et al., 1997). Diversity is high, whether measured in terms of the number of lineages present or in terms of the evolutionary distance between haplotypes. Early attempts to represent this diversity in terms of tree structures rooted in Africa were subject to methodological and sampling criticisms (Maddison et al., 1992; Templeton, 1993, 1997), but more sophisticated analyses have confirmed the initial results (Nei and Takezaki, 1996; Penny et al., 1995). Recent work on the beta globins has also shown higher African diversity, but it has also indicated patterns of intercontinental diversity that, it has been claimed, do not support a restricted geographical distribution of human ancestral populations (Harding et al., 1997). However, the ancient population structure reflected in this slow mutating system cannot be interpreted spatially from the present distribution of β -globin lineages. In this sense, they neither support nor refute the out-of-Africa model but can be incorporated within it.

The second proposition—that the last common mtDNA ancestor of all humans (“Eve,” or the point of coalescence of lineages) lived in the recent past—has also been supported by studies of other, independent, fast mutation loci. Many analyses, using mtDNA, Y markers, and microsatellites, have yielded estimates between 180,000 and 125,000

years (Hammer et al., 1997; Pandya et al., 1997; Stoneking, 1997; Tishkoff et al., 1997; Wallace et al., 1997). These recent dates of coalescence of modern human lineages are in contrast to the single result obtained from a fossil hominid, a Neanderthal, whose sampled part of the mtDNA is calculated to coalesce with that of living humans between 600 and 500 Ka (Krings et al., 1997). The amplification of 378 bp of the mtDNA control region of the Neanderthal type specimen resulted in a lineage that differs from the standard living human (“Anderson”) reference sequence by 27 substitutions. Living humans differ from each other on average by 8–12 substitutions, showing that the Neanderthal mtDNA obtained is three times more different than the difference between any two average modern lineages.

The context in which to interpret the significance of these findings is demography. Genetic diversity is a function of ancestral population size and the mutation rate of the system under study. Modern humans lack genetic diversity in relation to other species (Ferris et al., 1981; Horai and Hayasaka, 1990; Kocher and Wilson, 1991; Li and Sadler, 1991; Morin et al., 1993; Rogers and Jorde, 1995; Ruvolo et al., 1993; Wilson et al., 1985), interpreted as the outcome of a bottleneck in our relatively recent evolutionary past, when a significant portion of ancestral mtDNA diversity was lost (Bowcock et al., 1991; Brown, 1980; Haigh and Maynard Smith, 1972; Harpending et al., 1993; Jones and Rouhani, 1986; Nei and Graur, 1984; Maynard Smith, 1990; Rogers and Jorde, 1995; Takahata et al., 1995; Wills, 1990). Estimates of the size of the effective ancestral population to all humans suggest that during the bottleneck it was composed of >10,000 individuals. Furthermore, it has been estimated using Alu insertion polymorphism data that the population before the bottleneck took place was not very large either, numbering approximately 40,000 individuals (Sherry et al., 1997). Only if ancestral populations had been very large could we accommodate both the Neanderthal and modern mtDNA diversity within a single breeding group, and that was not the case. Therefore, the differences found between modern humans and the Neanderthal

mtDNA sample, together with the estimates of small ancestral population sizes, provide strong support for the view that humans and Neanderthals represent separate hominid lineages. Furthermore, palaeodemographic models have also shown that the hominid population was never large enough to sustain the gene flow necessary to maintain the long-term global homogeneity required by the multiregional model (Mandercheid and Rogers, 1996).

In summary, therefore, empirical evidence has been accumulating relatively rapidly, in both palaeontology and genetics, in favor of a recent, localized, and African origin for the ancestors of modern humans. We are thus approaching a moment of tangible empirical consensus over the broad pattern of the evolution of modern humans. This has led to a number of recognizable positions. One is a firm commitment to the maintenance of orthodox views represented by the multiregional model. This takes the form of both critical skepticism and a reevaluation of the meaning of multiregionality (Templeton, 1997; Wolpoff and Caspari, 1997). A second is what may be described as the "out of Africa as normal science" position. This is the view held by some geneticists, who have attempted to pinpoint the time and geography of various gene histories as represented by coalescent points and genetic distances. A third position would be that a single origin in Africa in the relatively recent past provides merely the framework for considering broader evolutionary issues relating to human diversity and evolutionary mechanisms. It is this third position that we believe requires further elaboration. Among the important questions that remain are those related to the processes involved in the evolution of human diversity from an ancestral source, the pattern of population differentiation, the time span involved, and the localized or global character of the mechanisms acting upon it. The link between this third position and the historical shifts during this century are perhaps worth mentioning briefly (Table 1). The trend towards continuity gene flow models has been the dominant one and is consistent with both sociopolitical views emphasizing continuity and overlap between populations and with

some of the neo-Darwinian ideas of population variability and local adaptive patterns. In contrast, the single origin model has often appeared to be a throwback to an earlier and premodern synthesis view of evolution. It demarcates populations geographically and sharply, it depends upon major migratory events, and it pays little or no attention to either mechanisms of gene flow or natural selection. The early modern populations migrating out of Africa may have more in common with Elliott Smith's hyper-diffusionism than with modern evolutionary biology.

It is these contrasts that lie at the heart of the modern human origins problem. Empirically, the SOM is the better model, but it is consistent with outmoded evolutionary ideas, whereas the multiregional model has little empirical support but is very much in line with conventional population genetics and adaptive processes. Resolving these paradoxes requires either a major reworking of the empirical evidence or an examination of how a broad model of a single origin of modern humans in Africa can be brought in line with current and developing views of microevolutionary processes.

There are two reasons why the latter is the way forward and why we are in a better position now than half a century ago to deal with the evolution of human diversity. The first is empirical and methodological advances. The palaeoanthropological database now available, compared to that before the war when diffusionist models predominated, is greatly improved. The models of Weidenreich and Elliott Smith were based on a handful of fossils—the *erectus* specimens from Zhoukoudien, *Pithecanthropus*, some Neanderthals, and isolated African finds like Kabwe (in addition to the confusion caused by Piltown). Today there is a large number of fossils from the Middle and Upper Pleistocene, and these are geographically widespread. However, new methods are providing new evidence. In the last 15 years, major developments have occurred within two areas of research with direct implications for the question of modern human origins—palaeochronology and molecular anthropology. Major advances in palaeochronology are related to the development

TABLE 1. History of studies of human origins¹

Date	Consensus model for human origins	Key anthropologists
1860–1920	Unilineal progressive evolution: all evolution seen as a progressive trend, driven by orthogenetic processes, leading to modern humans; no geography and no point of origin; key issues related to whether there were any intermediate steps (Neanderthals, etc.) and how they should be ordered; living human diversity seen as ladders along a progressive continuum	Manrouvier Cunningham Schwalbe Haeckel
1900–1950	Typological trees: most fossils seen as side branches away from the main line, generally becoming extinct; lack of continuity and an emphasis on parallel evolution; key controversies related to which if any fossils (e.g., Piltdown) did lie on the true line of descent; living human diversity seen as part of the tree of hominid variation; the origin of modern humans located with particular fossils	Keith Boule Breuil
1940–1990	Anagenetic polytypic evolution: development of the modern synthesis led to a recognition that variation within populations and species could occur and that populations would be transformed gradually by selection; emphasis placed on continuous variation, gene flow, and progressive adaptive change; living human diversity part of a spectrum of variation; model was transformed into the multiregional model in the 1980s as a means of accounting for spatiotemporal patterns within a population genetics framework; no point of origins; gene flow the principal mechanism of evolutionary change against local adaptive pressures	Coon Weidenreich Mayr Brace Wolpoff/Thorne
1980–	Divergence and replacement: emphasis on geographical variation, mechanisms of speciation, and the role of isolation in evolution led to renewed interest in more taxonomically diverse models of human evolution; emphasis increasingly placed on localized events such as range fragmentation and genetic bottlenecks underlying evolutionary processes, with correlated interest in dispersals, replacements, and extinctions; model was very much driven by a greater use of genetics and a more precise chronology; living human diversity as a marker of recent historical patterns; human origins located at a particular point in time and space (Africa, late Pleistocene)	Howells Stringer Wilson, etc. Bräuer/Smith (intermediate hypotheses of an African origin with admixture between modern and archaic hominids)

¹ Four phases in the history of studies of human origins can be recognized. These overlap considerably in time, and to some extent represent an ongoing conflict between unilinear/progressive/polytypic models stressing gradual transformation and adaptive radiation models emphasizing the divergence, isolation, and extinction of populations and species. The current conflict between multiregional and single origin models represents the latest manifestation of the debate, which primarily reflects interpretations and applications of the contemporary interpretation of evolutionary processes in general.

of new dating techniques, like thermoluminescence (TL) and electron spin resonance (ESR), which have been essential for the reshaping of the chronology of the period 200 to 50 Ka. The wide application of molecular genetics to anthropology can be associated with the development of PCR technology allowing the fast processing of molecular data, in this case molecular data regarding human population characteristics, while in analytical terms it is clear that computability is what gives modern science its edge. However, it is also the case that present studies of modern human diversity build upon the knowledge gathered by both pre- and postwar physical anthropologists, so that phylogenetic studies of the phenotypical differences among living and fossil modern populations use complex statistical methods in order to include concepts of trait polarity, identify allometric components of

variation, and investigate how and to what extent environmental factors contribute to the observed variance. Although it is not yet widely recognized, the inclusion of these caveats into the phylogenetic analyses of modern human skeletal information has resulted in the successful applicability of such data to the question of modern human origins, as shown by the consistency between patterns of relationships among populations derived from genetic and cranial data (Lahr, 1996) and the similar levels of interpopulation variance explained by either source (Relethford and Harpending, 1994).

The second reason is that the gene flow model is itself no longer central to the current understanding of evolutionary patterns among other animals. Partly this is the recognition that models such as the shifting balance model that have been used to underpin the MM were in fact developed by Wright

(1931) to deal with small-scale local population differences, not intercontinental demes over millions of years (Maynard Smith 1989). As such, the MM is in fact not as consistent with neo-Darwinian mechanisms as has been claimed. In contrast, detailed studies of the morphology and genetics of a wide range of species have shown that dispersals, geographical variation, and local events are the means by which diversity is generated rather than uniform and constant gene flow (Avice, 1994). In other words, local geographical and often discrete events structure evolutionary patterns. Evolutionary mechanisms underlying events such as the origins of modern humans are therefore likely to be very much linked to detailed geographical patterns.

The discussion above suggests that there is now a consistent chronological and spatial framework for studying modern human origins but that more detailed hypotheses are required to explain the relationships between a single localized event and subsequent population differentiation and dispersals. The increase in the fossil sample, the greater temporal and geographical resolution, and the shift in focus in evolutionary theory towards discrete events show that it is both possible and necessary to look at the single origin model of modern humans in the context of evolutionary mechanisms. These are developed here in terms of evolutionary geography, which is discussed in the next section.

EVOLUTIONARY GEOGRAPHY

Evolutionary geography may be described as the branch of biology that investigates the role of spatial factors in the evolutionary process. It differs from phylogenetic biogeography in that it operates at a variety of scales and in that its main aim is not the biogeographical reconstruction of phylogenetic patterns but the investigation of the environmental (biotic and abiotic) and demographic conditions for both vicariance (abiotic range disruption) and dispersal events in the history of a lineage as well as the evolutionary causes and consequences of such events.

Geography has been conventionally identified as playing three major roles in the

evolutionary process. First, it acts by creating the contingent factors that affect macroevolutionary processes in terms of large-scale climatic and tectonic events. However, the hidden variance in macroevolutionary events strongly suggests that contingent mechanisms do not provide an adequate explanation for the evolution of individual species and populations within them (Foley, 1994, in press). The second aspect is its role in promoting allopatry and consequently speciation or differentiation. The allopatric effect of geography on evolution is not restricted to a taxonomic level, for spatial relationships at the subspecific, specific, and higher levels may and have been found. However, a strong case may be made for the role of geography in shaping selective factors that govern microevolutionary processes in terms of localized pressures on survival, range, and demography and therefore on the evolution of populations or subspecies. Third, environmental variation is strongly spatial in character and thus provides the actual adaptive framework for the changes that occur in populations (Foley, in press). Evolutionary geography, in other words, uses spatial patterns to bring together contingent, adaptive, and demographic aspects of evolutionary change.

Three different dimensions—temporal, spatial and demographic—may be attributed to any given population. The first of these relates to the duration of a population as a distinct entity, from the moment of its founding or separation from the ancestral source to its disappearance either by extinction or by reintegration into the ancestral or another population. Rates of divergence could also be considered part of the temporal dimension of a population. The spatial dimension relates to the geographic range of a population and its interaction with the environment, while population size and structure make up the demographic parameters. Geography will affect and in many cases account for an important part of the variation in all these. It thus becomes necessary to understand the relationships between geography and the temporal and demographic dimensions of a population in order to identify certain principles that may help clarify the evolution of diversity within a

species. The general principles of evolutionary geography underlying the ways in which new populations become established, survive, and/or disappear are considered below.

Population survival, range, and demography

A population of a species becomes an evolutionary entity upon the occurrence of some level of genetic separation from an ancestral source; in most cases, this involves a degree of allopatry. Such allopatric populations may be formed without any dispersals on the part of individuals, such as when barriers are formed within a species range. The evolutionary outcome in such cases of vicariance will depend on whether populations become separated permanently or temporarily, with large or small daughter populations, and with or without novel selective pressures. On the other hand, the formation of allopatric populations following range expansions (dispersals) results from population contraction due to an incapacity to sustain continuously the expanded range. Depending on factors like the duration of the fullest range expansion and the population density supported by the extreme environments occupied at that time, allopatric populations resulting from the breakup of this range will be under the influence of both new selective pressures and drift. Therefore, one of the first factors to be taken into account in considering the evolution of a population is its geographical relationship to its parental group—whether it lies within the overall range or not.

Once an allopatric population has become established, it may follow one of three courses: maintain population stability, contract, or expand. The first of these depends upon the original population size and its achievement of a mortality-survival equilibrium with the carrying capacity of the environment. In evolutionary terms, such a population represents a source of discrete diversity, for it maintains its own trajectory without impinging upon those of other populations of the species for as long as the allopatry is maintained (Fisher, 1930; Avise, 1994). This is important, because the issue here is not whether gene flow can occur but whether it actually does, and this can be

independent of formal issues having to do with the process of speciation. The second case, population contraction, is the obvious outcome when mortality exceeds survival, which may take a population towards a new platform of size in which equilibrium is maintained or extinction occurs. Extinction of populations that went through a period of strong genetic drift represents an important loss of interpopulation diversity at the level of the species. The last case, population expansion, may have two outcomes. On the one hand, if the population expands over its original range, it may again establish contact with the parental group and, depending on the time since separation and the amount of differentiation acquired, be reintegrated into a single form and thus disappear as an entity. This will result in an increase of overall intrapopulation variance. On the other hand, if the population expands into new territories it may, by subsequent contraction, give rise to the whole process of separation that originated it in the first place, originating allopatric populations now separated by two branching events from the parental source. An important aspect of this process is that in the sequence of population *a* expanding and through subsequent contraction forming two allopatric populations, *a* and *b*, and later population *b* expanding and through subsequent contraction forming allopatric populations *b* and *c*, depending on the amount of change (due to either selection or drift) that took place during the establishment of *b* as a distinct entity, the differences between *a* and *c* may be very significant. Particularly in the case of the subsequent extinction of *b*, the relationship of *c* and *a* may be unclear. Therefore, the second factor to be taken into account when considering the evolution of a population is the duration of that population as a localized unit and its role in subsequent substructuring of the species.

A population's response to selection will determine whether it will expand or contract and thus the conditions for isolation or contact. Both contractions and expansions (dispersals) can have major evolutionary consequences. Although the causes of contractions are likely to be ultimately ecological and can occur both as part of an expan-

sive process and independently, their primary consequences lie in the greater probability of genetic change occurring in smaller and more isolated populations. Populations that maintain a private trajectory within the species due to isolation represent a temporary stable situation, the outcome of a discrete branching event with the potential for allopatric speciation. Nonetheless, it is dispersals and expansions that bring populations into new territories and in contact with other populations of the species or closely related species, affecting existing patterns of diversity (Fig. 1).

Range expansions are likely to occur as a result of the interaction between the characteristics of the population and the nature of the environment. Either or both may change. Where just the environment changes, there may be increased population density without expansion (a new carrying capacity equilibrium) or range expansion as the result of shifting barriers as particular environments themselves expand. In either case, the result is demographic changes which maintain the relationship between resource exploitation and available resources. This kind of fluctuating demography must be the norm in evolutionary time. These outcomes, either increased density without range expansion or expansion into new habitats, may also result when some element in the behavior of the population changes as a result of some selective shift (e.g., a technological or adaptive development). However, these are qualitatively different. The establishment through a behavioral change of a new carrying capacity equilibrium within the occupied environment or the occupation of ecologically new environments implies a change in resource exploitation that removes existing barriers (either in terms of dietary composition or resource acquisition). These events are likely to be rare in comparison. Finally, it is also possible for changes in the environment and the behavior of the population to occur interactively.

The key point is the link between demography and spatial distribution and hence the geographical nature of evolutionary processes. Environmental and behavioral changes induce changes in both population density and carrying capacity, and, after a

new ecological equilibrium is restored, changes in the spatial relationships between individuals, groups, and populations will have occurred. Such changes affect the cost-benefit ratios of adaptive strategies. However, independent of the immediate effects of greater population density or of a greater exploited area, environmentally induced changes in population demography will be subject to the stability of the new environmental conditions. Typically, these greater demographies and/or areas would not be sustained under climatic deterioration, resulting in contraction and even population crashes. Depending on the magnitude and duration of the contracted phase or bottleneck, such successive demographic expansions and contractions within the history of a lineage may increase the rate of that lineage's divergence due to recurrent periods of drift. On the other hand, it is the appearance of new modes of exploitation that may transcend particular environments and thus allow significant range expansions or dispersals and occupation of a new environment with the potential for stability of occupation independent of environmental fluctuations. For example, Pliocene and Pleistocene hominid species differ in their relationship between species diversity and range size, paralleling primate and carnivore patterns, respectively (Foley, 1991). Thus, it may be inferred that the habitual exploitation of a more carnivorous diet early in the Pleistocene temporarily removed a level of environmental barriers that allowed the dispersal of hominids far beyond their sub-Saharan range and the establishment of hominid populations in tropical Asia (Gamble, 1993; Foley, 1991, in press), with major consequences for the subsequent evolution of the lineage's diversity. Therefore, the third factor to be taken into account when considering the evolution of a population is whether an observed population expansion is associated solely with environmental changes (either by changing the range of that particular environment or by increasing resource availability) or with significant changes in subsistence that led to the dispersal of the population into an altogether different environmental niche.

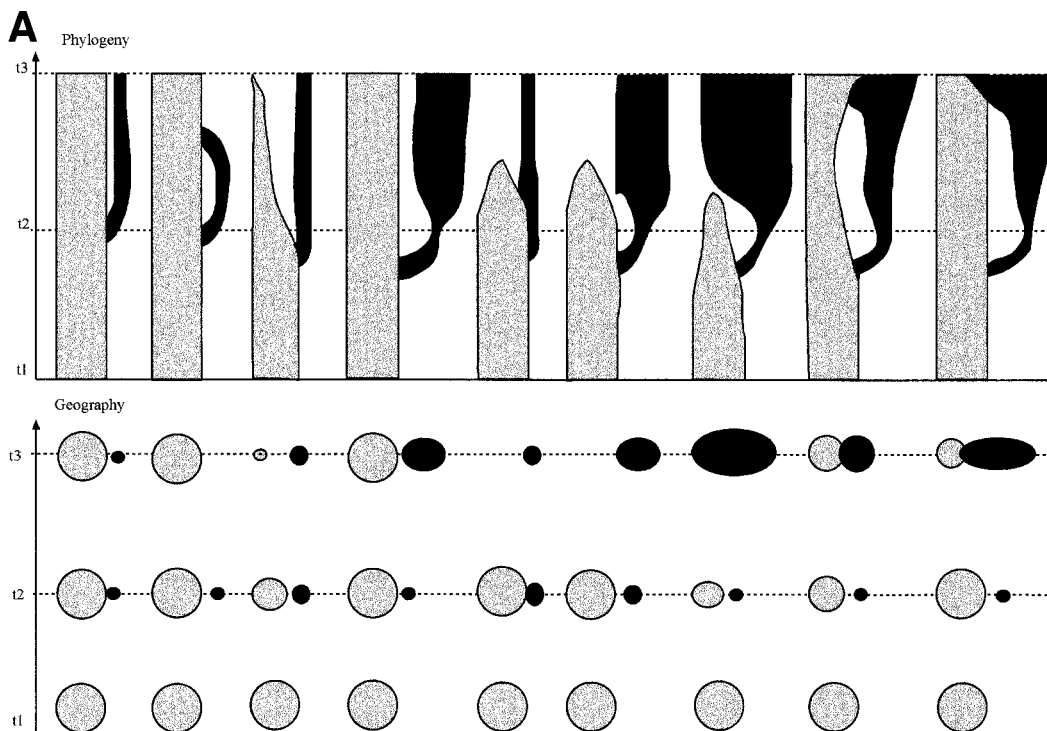


Fig. 1. **A:** Relationship between the phylogenetic history of populations and spatial distributions illustrated in terms of two populations within an evolving lineage. The top part of the diagram shows the phylogenetic relationships, the bottom half a schematic representation of population distribution and size. The parent population (lighter shading) gives rise to a daughter population in all examples. However, the outcome varies according to changes in spatial distribution of both parent and daughter populations. In some cases, both persist at varying scales, in others only one, either through extinction or replacement or else through resorp-

tion back into a single population. **B:** Relationship between phylogenetic history and evolutionary geography in a single complex example. Over time (t1-t3), the population expands and contracts and becomes fragmented or homogenized. This can happen repeatedly. Observations of diversity will vary according to the time slice, and at any one time the overall diversity will be a cumulative palimpsest of historical changes in distribution. This model does not take into account the possibility of small-scale background gene flow but emphasizes dispersal events and population contractions/extinctions.

Therefore, the three key considerations are 1) the geographical relationship between parent and daughter populations, 2) the longevity of the population and its subsequent role in further substructuring and diversification, and 3) the relationship between environmental change and behavioral innovations in relation to range expansion.

MODERN HUMAN DIVERSIFICATION

If geographical factors play a significant role in the evolution of populations in general, how have they affected the particular case of modern human evolution? This section attempts to integrate the principles of

evolutionary geography in the formulation of interpretative hypotheses for specific points in the evolutionary history of humans. Two of these points will be addressed: first, the phylogenetic relationship of Neanderthals and modern humans and, second, the ancestral bottleneck in modern human history and the establishment of modern populations beyond a sub-Saharan African range.

Neanderthals and modern humans

Neanderthals represent a group of hominids that may be identified morphologically by a number of apomorphic traits (Klein, 1998; Rak, 1986, 1993; Stringer and

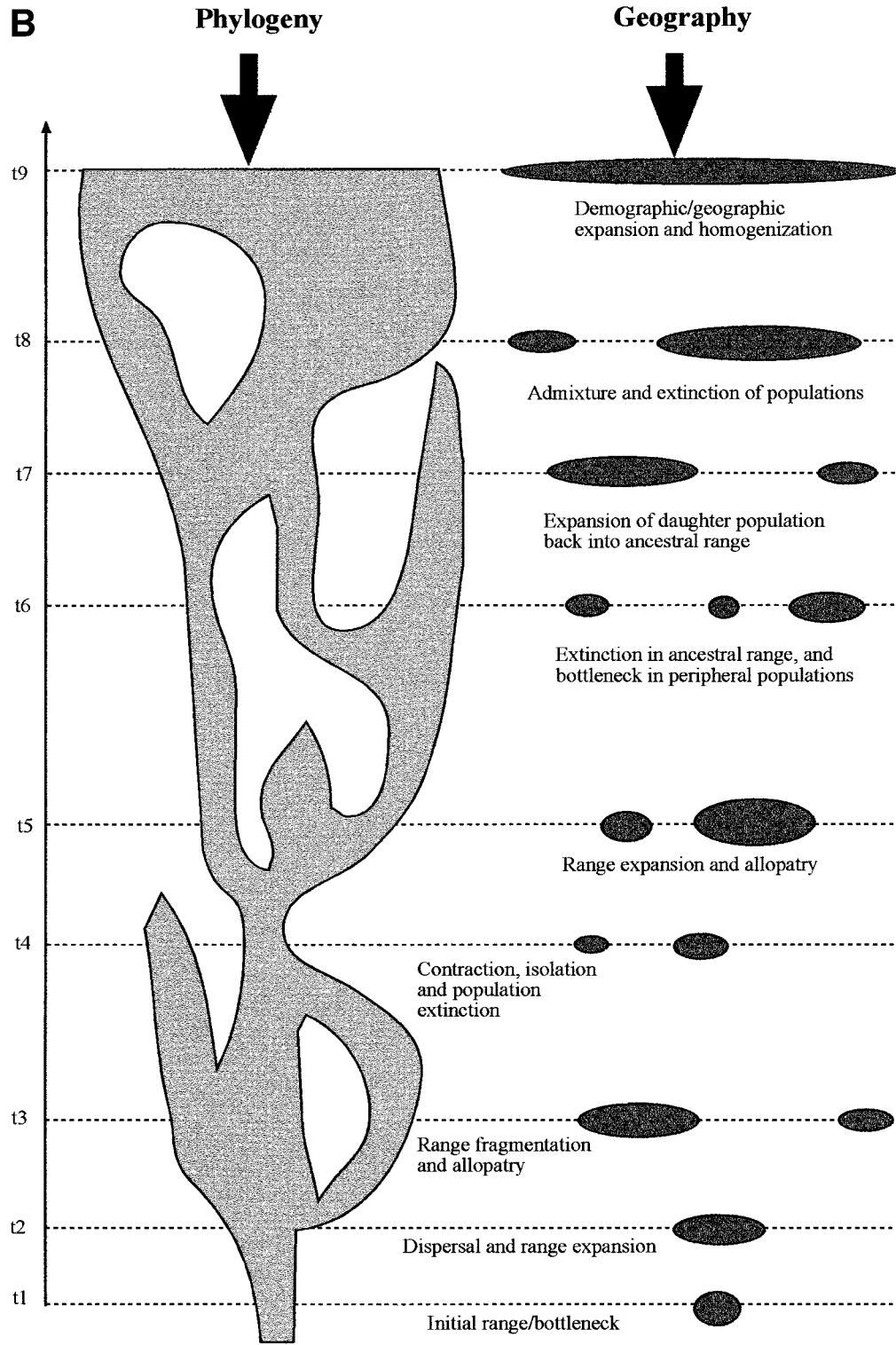


Fig. 1.

Gamble, 1993; Trinkaus, 1987; Trinkaus and Howells, 1979). Because of their comparatively rich record, temporal and spatial dimensions may also be attributed to them with some certainty. The first forms that possess the suite of features that came to characterize the group appear during the last interglacial (or stage 5 of the marine isotope climatic sequence) (Saccopastore, Krapina), but these features are found in mosaic form in fossils from 200 Ka onwards (Biache, La Chaise-Suard, La Chaise Bourgeois-Delauney) (Stringer, 1995). Neanderthal traits have also been identified in earlier remains—Swanscombe, Steinheim, Atapuerca Sima de los Huesos—but the precise dating of these remains is unconfirmed. Nevertheless, we may infer that the selective pressures acting upon these traits to create the combination of features that results in “a Neanderthal” were those imposed by the harsh environments of stage 6 (200 to 125 Ka). This is consistent with their body proportions, which show adaptations to very cold climates (Ruff, 1994). That Neanderthals and their specific traits evolved in Europe contemporaneously with the evolution of modern humans in Africa is therefore well supported by fossil evidence. The question arises about where the ancestors of the populations that evolved the distinctive Neanderthal traits were, and four possible answers exist (Fig. 2).

The first (Fig. 2A) is that European hominids had a long-term local evolutionary trajectory, with continuity from the first occupation of the continent—some 800,000 years. This model is based on the recent discovery of early Middle Pleistocene fossils in the site of Gran Dolina, Atapuerca, Spain, described as a distinct species (*H. antecessor*) and the interpretation of aspects of their morphology as evidence for long-standing continuity towards Neanderthals (Bermudez de Castro et al., 1997). Three criticisms can be made of this model, however. The first is that the present record of *antecessor* comprises juvenile remains, and therefore the morphology represents both ontogenetic and phylogenetic variation. Second, the other European hominid fossil from the period 800 to 500 Ka (Ceprano, Italy) has been described as *H. erectus* (Ascenzi et al., 1996),

without any particular affinities towards either Neanderthals or modern humans. And finally, palaeontological and archaeological data suggest periods of important subsequent exchange with African hominids, arguing for important discontinuities and external influences in the European Middle Pleistocene record.

The second possibility (Fig. 2B) is that the late Middle Pleistocene population of Europe ancestral to Neanderthals had a local origin in the earlier European Middle Pleistocene archaic population (composed of fossils like Arago, Bilzingsleben, Boxgrove, Mauer, Petralona, Steinheim, Swanscombe, Vertesszöllos). There are similarities between this group and the contemporary African archaic population (composed of fossils like Bodo, Kabwe, Elandsfontein, Ndutu), like reduced superstructural development, facial projection, and increased endocranial volume, although postcranially they retain plesiomorphic traits like an external iliac buttress, large cortical thicknesses, and femoral shaft width (Rightmire, 1996; Ruff et al., 1993; Stringer, 1995). The similarities between the European and African mid-Middle Pleistocene fossils have been taken to indicate common ancestry and led to the proposal that these fossils, previously called by the phylogenetically unhelpful name “archaic” *Homo sapiens*, represent a new species, *Homo heidelbergensis* (Groves, 1994; Rightmire, 1988, 1996; Stringer, 1993). This species would have had an African origin in the early Middle Pleistocene, with the fossil of Bodo representing the earliest known specimen (dating to ~600 Ka [Clark et al., 1994]). The appearance of African animal species in southwestern Asian biotas around 500 to 450 Ka (Tchernov, 1992a) and the first appearance in Europe of the Acheulean (mode 2)² archaeological tradition from Af-

²The archaeological terminology of Clark (1968) is used here. He suggested that stone tool assemblages, regardless of their typological details, could be grouped into a series of broader technological modes that can be defined as follows: mode 1, chopper tools and flakes; mode 2, bifacially flaked hand axes, usually struck off large flakes; mode 3, tools made from flakes that have been struck from prepared cores; mode 4, tools made from blades, often with reduced platforms; mode 5, microlithic flakes and tools. Mode 1 comprises the Oldowan and persistent

rica (Klein, 1995) are further evidence for the dispersal of faunas, containing hominids, from Africa into Eurasia at this time (Klein, 1995; Foley and Lahr, 1997). As African *H. heidelbergensis* gave rise to the late Middle Pleistocene African population ancestral to the first modern humans (Bräuer, 1989, 1992; Rightmire, 1989; Stringer, 1989), the Neanderthal and modern human lineages would be separated by at least half-a-million years. This hypothesis has two implications. First, periods of contact between Africa and Europe during the approximately 800 Ka of glacial cycles were rare and fortuitous. Second, there must have been large levels of parallelism, particularly in terms of brain size and behavior, in the evolution of the Neanderthal and modern lineages.

The third possibility (Fig. 2C) is that the late Middle Pleistocene population of Europe ancestral to Neanderthals and the late African Middle Pleistocene population ancestral to modern humans have a closer common origin. This model is based on the observation that Neanderthals, late African archaic, and early modern humans shared the same archaeological tradition (mode 3 industries). This tradition was not present in Africa over half-a-million years ago when the second hypothesis would posit a common ancestor. Mode 3 technologies would thus have had to evolve independently, once in Europe and once in Africa, or else there would have had to be cultural exchange with no genetic admixture over a long period of time. An alternative explanation is that there was a dispersal of populations with Levallois technology (mode 3 industries) from Africa to Europe around 250 Ka (the date of the fossil from Florisbad, found in association with Middle Stone Age/mode 3 artefacts [Grün et al., 1996]), when interglacial conditions would have again facilitated hominid and faunal dispersals out of Africa (Foley and Lahr, 1997). This hypothesis has three implications. First, dispersal events be-

tween Africa and Europe would have taken place several times as certain processes during glacial episodes temporarily removed geographical barriers and allowed population expansion. Second, the morphological similarities between European *H. heidelbergensis* and late archaic hominids directly ancestral to Neanderthals reflect a form of iterative evolutionary process by which shared traits represent homoplasies, especially facial features associated with cold adaptation. Third, the behavioral parallels between Neanderthals and modern humans as observed in the archaeological Middle Palaeolithic/Middle Stone Age record (mode 3) reflect synapomorphic cognitive change.³

Finally (Fig. 2D), it is possible that there was in fact continuous contact, gene flow, and exchange of populations between Africa and Europe throughout the middle Pleistocene and as such no relatively discrete events as implied by the previous models. However, such a model is largely inconsistent with both the palaeontological and archaeological divergences that can be seen, as well as with paleoclimatic and paleogeographical reconstructions which imply only intermittent contact.

Evolutionary geography provides a framework for assessing these competing hypotheses. The key element is the conditions promoted by glacial cycles. Although important cooling of the Earth's climate began at the end of the Pliocene (Denys, 1985; Loubere, 1988; Rea and Schrader, 1985), cyclical glacial fluctuations are believed to have started around 800 Ka (Roberts, 1984; Shackleton, 1987). The first full glacial stage is recognized in the marine sequences as stage 22, within the Matuyama subchrone and before the Jaramillo event, and there-

Asian pebble tool tradition; mode 2 refers primarily to the Acheulean of Europe, western Asia, and Africa; mode 3 is the Middle Stone Age in Africa and the Middle Palaeolithic (i.e., Mousterian and Levallois technology) of Europe; mode 4 is the Upper Palaeolithic of Eurasia and the Middle East, while mode 5 covers a global range of late and post-Pleistocene Later Stone Age and Mesolithic assemblages. See Foley and Lahr (1997) for a discussion of the mode system of archaeological classification.

³This model interprets the development of prepared core technologies as a significant phylogenetic and functional event and posits that the distribution of prepared core technologies as they develop and evolve during the later Pleistocene reflects both an apomorphy of a particular population and a unique evolutionary event. A less extreme interpretation would be that prepared core technologies developed relatively rarely, spread by a mixture of diffusion and population movement, and thus still provide a population marker, albeit one less tied into technology. An alternative view would be that prepared core technologies develop many times independently and therefore do not serve as a population or behavioral marker. The case for treating mode 3 technologies as phylogenetically significant is considered in full by Foley and Lahr (1997).

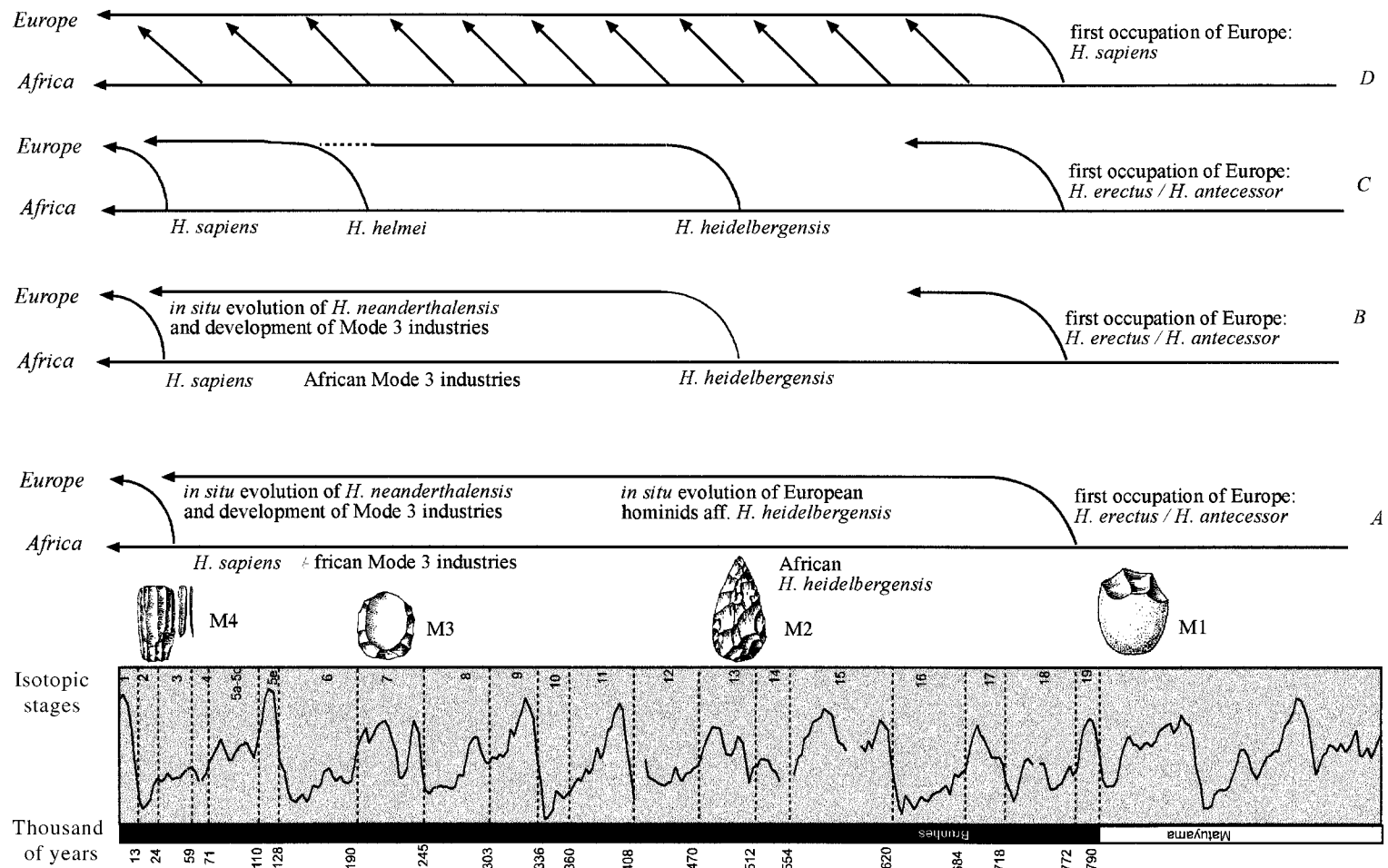


Fig. 2.

fore between 900 and 790 Ka. The succeeding glacial cycles are similar in character (i.e., show the slow buildup of continental ice sheets and a rapid period of deglaciation followed by a warm interglacial stage). However, they differ markedly in degree, extent, timing, and rate of glacial growth, as shown by the details provided by marine isotope curves (Malatesta and Zarlenga, 1988; Sachs, 1973; Sarntheim et al., 1986; Shackleton, 1987; Zimmerman et al., 1984) (see Fig. 2). In spite of these differences, they were cyclical events with recurrent outcomes which affected equatorial and northern latitudes in predictably different ways. Maximum cold in the north, with its resulting reduced areas and southward shift of climatic belts, translates globally into maximum coolness and low sea-level stands and especially aridity in many parts of the tropics. This process is followed by the release of water trapped in the northern hemisphere glaciers, which is responsible for the global rise in sea level and for pluvial and high lake

level short episodes in equatorial regions (Bradley, 1985; Hamilton, 1976; Hooghiemstra and Agwu, 1988; Ritchie and Haynes, 1987; Street and Grove, 1979). These fluctuations have specific consequences for African and European faunal geographical ranges (Fig. 3).

Large mammalian faunas in both continents undergo a period of range expansion during interglacials, while only Eurasian faunas seem to have shifted ranges during glacial buildup (in Africa, extensive aridity causes the contraction of available ranges and a level of isolation and endemism). In the case of Europe, interglacial faunal expansions associated with the retreat of ice and tundra occurred along the Eurasiatic plains to the northeast and occasionally towards the southeast, reaching the Middle East (although the Taurus-Zagros mountain range and the interglacial forests of the Greek and Turkish peninsulas acted as important barriers to movement in this direction [Heintz and Brunet, 1982]). During glacial periods, European animal ranges shifted southwards as continental areas became covered by ice sheets and permafrost terrain. At these times, the Middle East acted as a cul de sac, for these northern elements could not overcome the Saharan barrier at its maximum extent during glacial stages (Tchernov, 1992a,b,c, 1994). Therefore, the main direction of Palearctic expansions was east-west, as reflected by past and present animal distributions. In the case of Africa, population expansions were associated with increased moisture occurring particularly during the early phases of interglacials. These expansions were also directional, as forests expanded equatorially and savannas in a northerly direction across the Sahara. During these episodes, the Ethiopian faunal range also encompassed the Sahara, northern Africa, and the Levant, which shows indications of savanna conditions (*Struthio camelus* and *Camelus dromedarius* fossils [Payne and Garrard, 1983; Tchernov, 1992a]), while movement into Europe would reflect a subsequent dispersal if the Taurus-Zagros barrier were transcended. Therefore, the main direction of nonforest Ethiopian expansions was north-south, reaching into the Levant through the Sinai peninsula.

Fig. 2. Representation of four models for Neanderthal ancestry. The evolution of the Neanderthal populations is dependent upon a model for the colonization of Europe and the continuity of the European hominid population. Four models are set out below against the context of the marine oxygen isotope core (Shackleton, 1987) and Clark's technological modes (Clark, 1968). **A:** Dispersal of *H. erectus/H. antecessor* from Africa with mode 1 industries and long-term regional continuity within Europe, resulting in the evolution of European Middle Pleistocene populations. Affinities of these and African hominids, both in morphology and behavior, would represent parallelisms. **B:** Dispersal of *H. erectus/H. antecessor* which does not result in the permanent occupation of Europe. Subsequent dispersal in the mid-Middle Pleistocene by *H. heidelbergensis* with mode 2/Acheulian tradition from Africa, resulting in the establishment of African and European lineages ~500 Ka, which later differentiate in modern and Neanderthal populations. Behavioral and morphological (encephalization) similarities between modern humans and Neanderthals would represent parallelisms. **C:** Dispersal of *H. erectus/H. antecessor* which does not result in the permanent occupation of Europe. Subsequent dispersal in the mid-Middle Pleistocene by *H. heidelbergensis* with the Acheulian tradition from Africa, followed by another dispersal episode of late Middle Pleistocene African hominids (*H. helmei*) with mode 3/Middle Palaeolithic industries ~ 250 Ka, resulting in the establishment of the immediate ancestors of Neanderthals. Morphological similarities between mid- and late Middle Pleistocene fossils in Europe would represent parallelisms or admixture within Europe. **D:** Continuous dispersal of populations across the Mediterranean from *H. erectus/H. antecessor*, with no marked discontinuities in the Afro-European populations through the Middle Pleistocene.

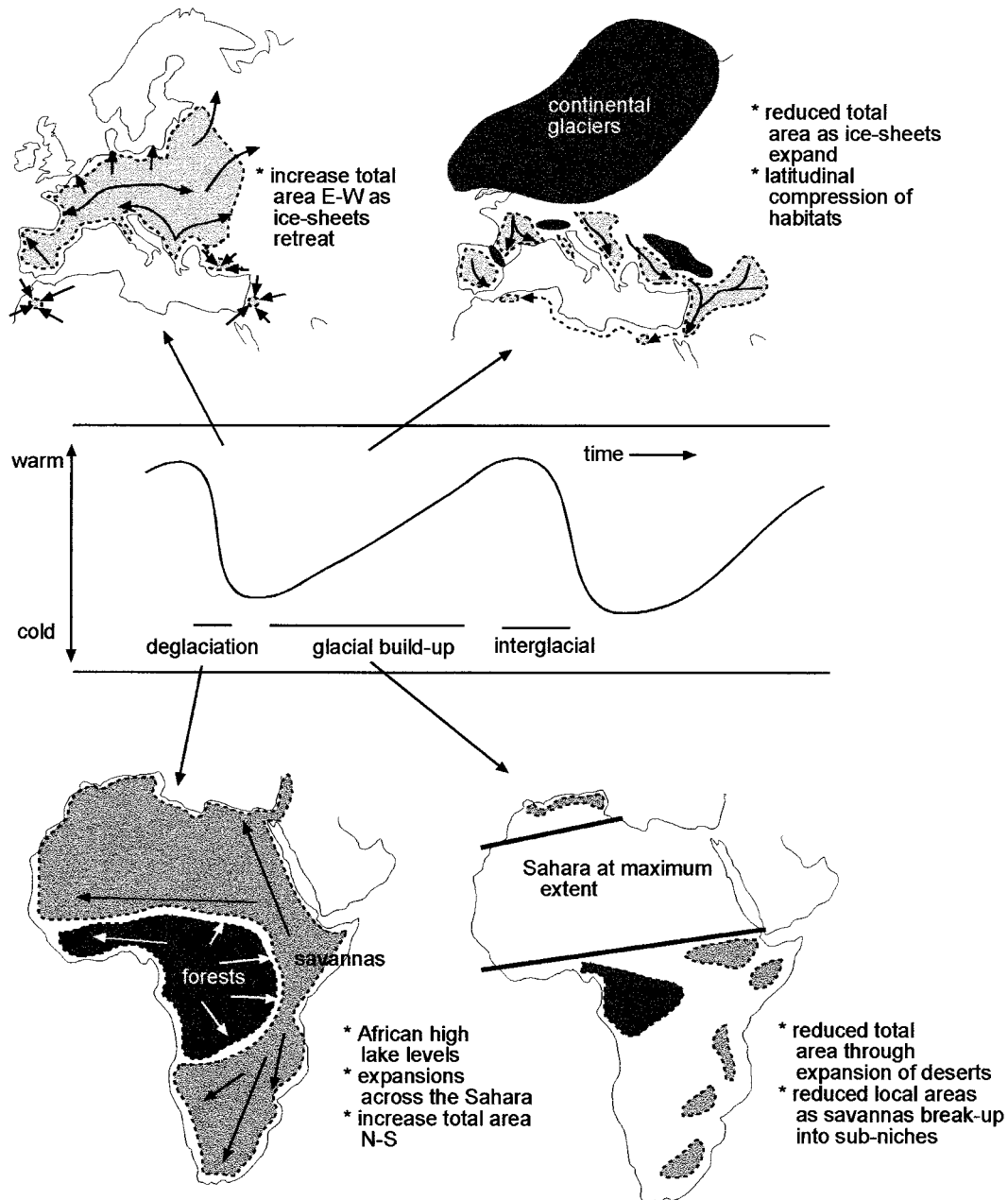


Fig. 3. Schematic representation of the effects of a glacial cycle (slow buildup of continental ice sheets in high latitudes followed by rapid deglaciation and a relatively short period of interglacial conditions) on African and European faunas.

These expansions are reflected in Middle Pleistocene fossil assemblages of Europe and especially the Middle East (Tchernov, 1992a,b,c; Turner, 1984), in which the appearance of African, Palearctic, and Oriental

elements reflects different phases within glacial cycles. Although there are very few mid-Middle Pleistocene palaeontological sites in the Levant (Gesher Benot Ya'acov, Giv'e at Shaul—dated to approximately 400

Ka or stage 11, the beginning of the long Interglacial phase known in terrestrial sequences as the Holstenian/Hoxnian), these clearly show evidence of Afro-Eurasian biotic exchange (Geraads and Tchernov, 1987; Hooijer, 1959, 1960; Tchernov, 1992a). Unfortunately, the number of later Middle Pleistocene sites is also small, and their precise dating less certain. The faunas they contain show an influx of Palearctic elements (like *Talpa*, *Sciurus*, *Capreolus*, *Lepus europaeus*, *Microtus guentheri*, *Ursus arctos*, *Mammuthus primigenius*, and *Felis sylvestris* [Tchernov, 1992a,b]). The sites, associated with the geographically restricted Acheulo-Yabrudian (Zuttiyeh, Tabun E) have been tentatively dated to the end of stage 7 and stage 6 (220/200 to 150/140 Ka) (Bar-Yosef, 1992a,b). The Tabun D levels of the Tabun cave have also been dated to the end of stage 6 (Bar-Yosef, 1992a,b, 1994), and it also has palearctic elements, including recent Euro-Siberian species (Tchernov, 1992a,b). The assemblage at Qafzeh both lacks these Palearctic elements present in Tabun E and D and has a large number of East African savanna and Arabian species (like *Arvicanthis ectos*, *Mastomys batei*, *Gerbillus dasyrus*, *Suncus murimus*, *Alcelaphus busephalus*, *Equus tabeti*, *E. africanus?*, *Struthio camelus*, and *Camelus dromedarius* as well as some Eurasian forms like *Dicerorhinus hemitoechus* and *Capra aegagrus* [Tchernov, 1992a,b]). It represents evidence of a short period during which the Middle East was again the northernmost limit of the African biome and is consistent with Qafzeh's dating to the last interglacial, or stage 5 (Bar-Yosef, 1992a,b; Valladas et al., 1988; Schwarcz et al., 1988). The faunas of Hayonim and Kebara show again the prevalence of Palearctic elements, consistent with their stratigraphic position within the last glacial cycle (Valladas et al., 1987).

Therefore, significant dispersals of African faunas into the Middle East occurred at least twice: first during the mid-Middle Pleistocene (Holstenian/Hoxnian interglacial, stage 11) and later during the early Upper Pleistocene (Eemian/Ipswichian interglacial, stage 5). However, three facts indicate that this reconstruction is incomplete. First, the richer European record shows the introduction of African elements in the early

Middle Pleistocene (Cromerian or stage 19), like *Panthera leo* and *Crocota crocuta* (Turner, 1984), an event that is not recorded in the Middle Eastern sequence. Second, the Middle East lacks palaeontological sites that may be attributed to stage 7 (~250 Ka),⁴ when mode 3 technology seems to appear in the European archaeological record. Third, the very ephemeral presence of African species in the Skhul deposits (Tchernov, 1992b) may indicate very short-term shifts of the faunal ranges that are nevertheless significant for the reconstruction of hominid dispersals.

Two conclusions relevant for the hypotheses of Neanderthal ancestry outlined above can be drawn from the palaeogeographical data. First, instead of rare and fortuitous events, periods of contact between African and Eurasian biomes are to be expected as part of glacial cycles, though with different extents depending on the specific character of each cycle. Second, the process is one-way; the direction of movement was always from Africa to Eurasia. Eurasian elements that expanded into the Levant at the onset of colder climates did not permeate into sub-Saharan faunas throughout the period concerned, reaching in a few occasions as far as eastern North Africa, or rarely the Maghreb (Jaeger, 1975; Tchernov, 1992a). In terms of Middle Pleistocene hominid movements, we may therefore expect African dispersals into the Jordan valley to have taken place several times in association with the early parts of interglacials (stages 19, ?15, 11, ?9, 7a + 7b, 5e) (Fig. 4).

The biogeographical evidence would thus suggest that hominids, adapted to more tropical environments, would have expanded northwards as far as the Middle East as these habitats themselves expanded during early phases of interglacial episodes. These expansions would have consisted of populations tracking the fluctuations of their na-

⁴Tchernov (1992b) attributes a stage 7 date to Oum Qatafa. The fauna of this site does not contain Palearctic elements (*Lepus*, *Talpa*, *Sciurus*), and the micromammals are most comparable with those of the Tabun G levels (Bate, 1943) but which, under the new chronology for the Tabun sequence, could be older (Bar-Yosef, 1992a,b). The first intentional use of Levallois technique (mode 3 technology) within what are called Upper Acheulean Levels in the Middle East has a stage 7 date—at the site of Berekhath Ram, underlying a layer of lava dated K/Ar to 233 Ka (Goren-Inbar, 1985).

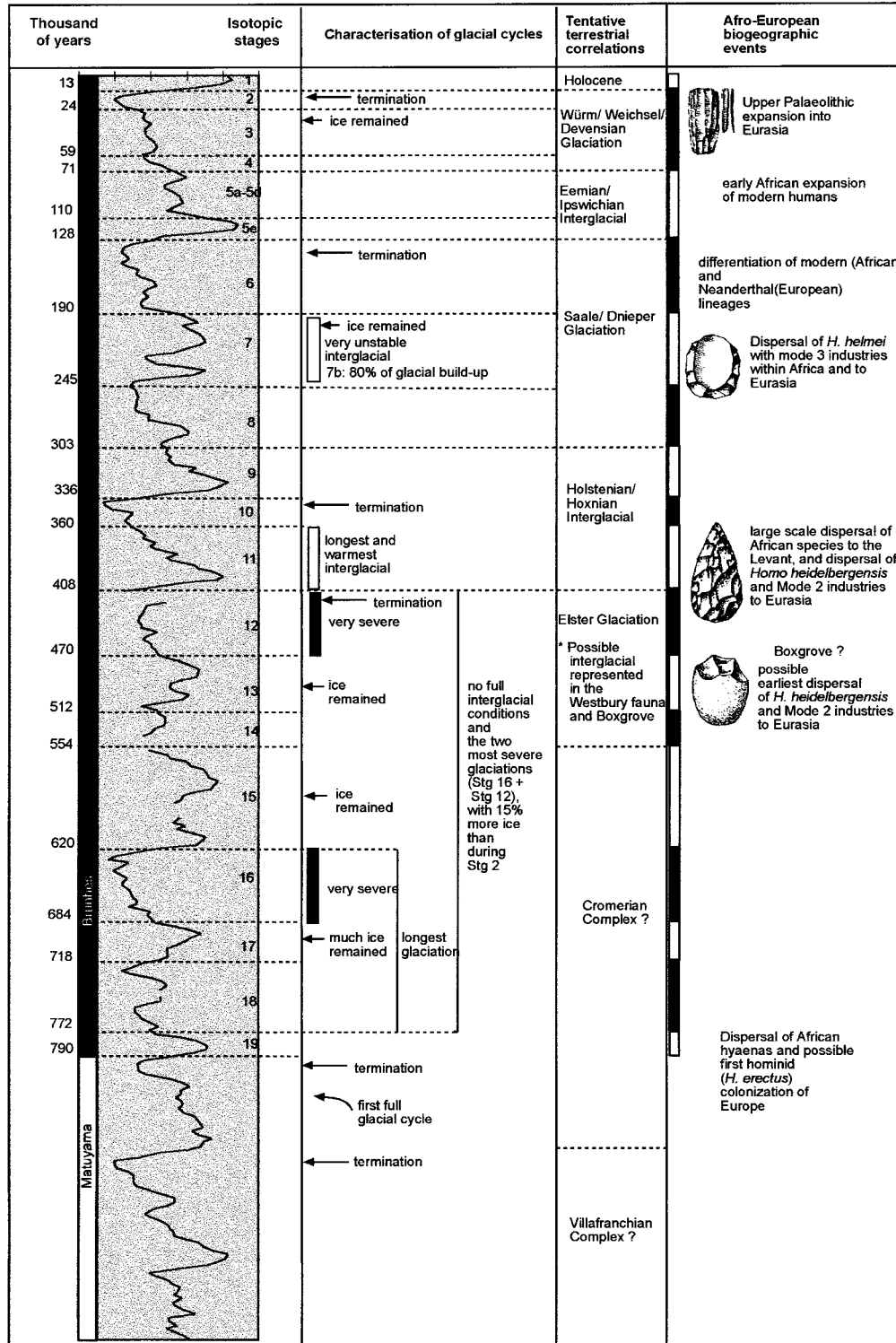


Fig.4.

tive habitats. However, it may be argued that a combination of biological and behavioral evolutionary novelties allowed, in at least four cases, the invasion of Europe, which would have involved breaking into new habitats. These four instances would be reflected in the first appearance of hominids in Europe ~800 Ka, that of *H. heidelbergensis* and the mode 2 Acheulean tradition ~500 Ka, that of late archaic hominids and mode 3 technology ~250 Ka, and that of modern humans with Upper Palaeolithic technology ~50 Ka. If primary dispersals consist of population expansions in response to an enlarged distribution of native habitat, then the colonization of Europe represented secondary dispersals across significant habitat boundaries. These secondary dispersals would have been by genetically distinct populations, as they would have occurred from populations in northeastern Africa and the Middle East that were already peripheral to and distanced from the original ancestral African source. Once in Europe, hominids would have become subsequently more specialized under allopatric conditions as they responded to the selective pressures posed by the onset of glacial climates.

If this reconstruction were correct, it would be most consistent with the third hypothesis regarding Neanderthal ancestry posed above: that Neanderthals and modern humans share a recent common ancestor within the last 250,000 years and the cognitive development represented by the implementation of Levallois core preparation (Foley and Lahr, 1997). This view is also consistent with the mtDNA data from the Neander specimen. The history of a population and that of a gene differ in their reflection of demographic parameters; the time of coales-

cence will precede by x generations the time of population vicariance (Fig. 5). The coalescence of human and Neanderthal mtDNA lineages ~500 Ka (approximately the time of separation of African and European *H. heidelbergensis*) would suggest that the separation of the population ancestral to both humans and Neanderthals occurred some time afterwards (Krings et al., 1997), consistent with a later dispersal, as reflected in the Middle Stone Age/Middle Palaeolithic archaeological records.

The model described above, derived from evolutionary geography, suggests that there is an additional layer of Afro-European dispersal in the evolutionary history of *Homo* than is usually recognized. Evidence for this layer is mainly archaeological and palaeontological, but it also finds support in the hominid fossil record. The immediate ancestors of the ancestors of European Neanderthals would have dispersed within and out of Africa during stage 7 or even possibly during the main interstadial of stage 8. Fossils like Florisbad, Eliye Springs, and Guomde would be representatives of this population in sub-Saharan Africa, while those of Djebel Irhoud in North Africa, Tabun D in the Middle East, and the diverse group of Atapuerca Sima de los Huesos (currently dated to ~300 Ka, but this date is under revision [Stringer, 1995]), Pontnewydd, and Ehringsdorf in Europe (the only remains dated to stage 7 [Blackwell and Schwarcz, 1986; Green, 1984]) would represent descendants from this dispersal episode. These remains, which we have called *Homo helmei* (Foley and Lahr, 1997), share a number of features that have long made their taxonomic affinities ambiguous, including a level of encephalization not observed in the earlier mid-Middle Pleistocene hominids (Ruff et al., 1997)⁵ (Fig. 6). We would expect increasing specialization and decreasing diversity in Europe from 250 to 100 Ka (stage 6), when the Neanderthal morphological pattern is selectively fixed, as

Fig. 4. Palaeoclimatic information for the last 1,000,000 years as derived from deep-sea cores and a tentative terrestrial correlation. Sub-Saharan faunas, which dispersed across large areas as savanna habitats expanded during early phases of interglacials, could have reached the Levant at the end of stages 19 (~790 Ka), 12 (~408 Ka), 10 (~336 Ka), 8 (~145 Ka), and 6 (~128 Ka). These expansions and their association with palaeoanthropological remains are recorded in the Levantine sequence for the end of stages 12 and 6, but those of stages 19 and 8 are indicated by faunal and archaeological evidence in Europe. (Oxygen isotope data from N. Shackleton.)

⁵The species name *Homo helmei* as used here differs in composition from that of Stringer (1996b) by specifically including both African and European hominids of stages 8, 7, and 6 associated with mode 3 technologies. The remains from Sima de los Huesos, Atapuerca, do not have associated archaeology and are thus only tentatively included in the group. Similarly, the fossil of Reilingen, Germany, which has been interpreted as showing Neanderthal features, has no stratigraphic association (Dean et al., 1994).

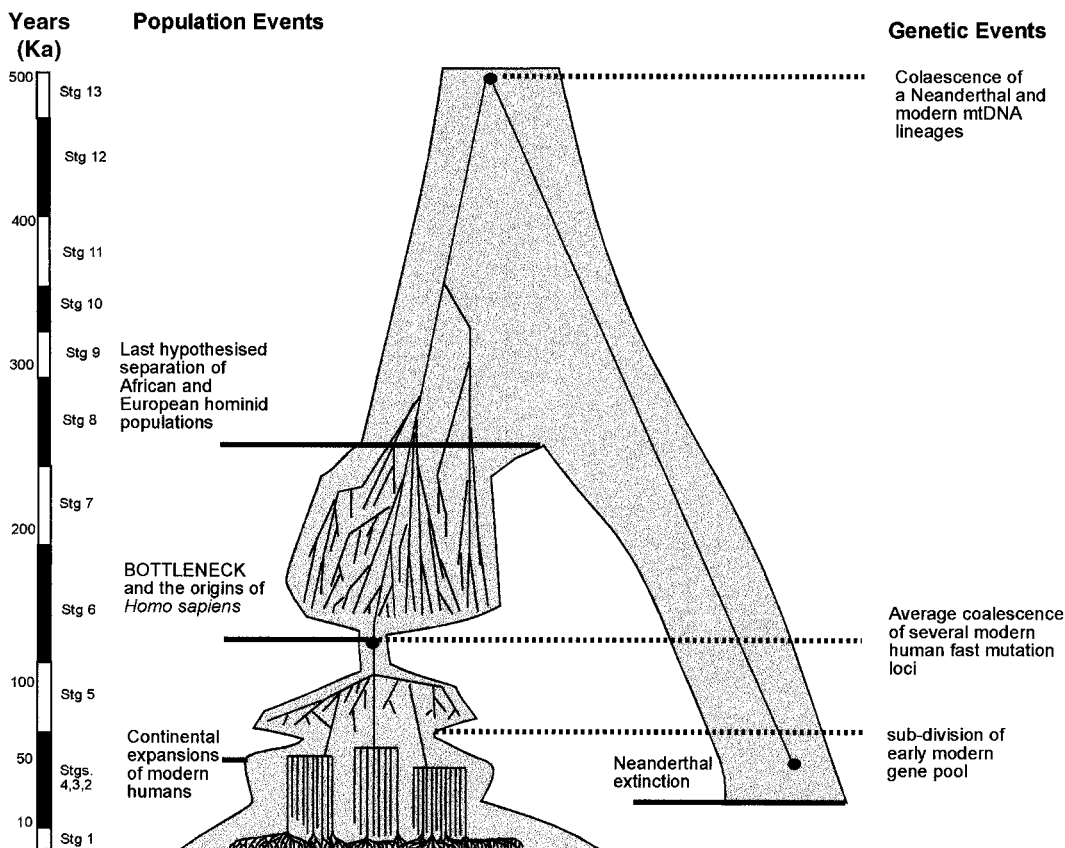


Fig. 5. Schematic representation of the relationship between the population history of humans and Neanderthals and mtDNA genealogy highlighting the likelihood that the time of mtDNA coalescence between a Neanderthal and modern lineages preceded population vicariance, whereas the time of coalescence of human mtDNA, Y-chromosome loci, and microsatellites could coincide with the demographic bottleneck that separated early modern humans from late archaic African hominids.

seen in fossils like Biache, La Chaise-Suard, La Chaise-Bourgeois-Delauney, Krapina, and Saccopastore. As it is hypothesized that fossils like Eliye Springs and Florisbad are more closely related to the European specimens from stage 7 than the earlier European sample (Petralona, Arago, Versteeszöllos, Bilzingsleben, Mauer, Steinheim, Swanscombe), the "Neanderthal" features observed in some of the latter remains (e.g., the face of Arago 21, features of the Arago 2 mandible, features of the Swanscombe occipital (undated but associated with Acheulean [Barton & Stringer, 1997]), and the facial prognathism of Atapuerca Sima de los Huecos AT-5 [Arsuaga et al., 1993]) would represent homoplastic specializations occurring as adaptations to periglacial European condi-

tions. If persistence of Acheulean traditions is an indication that earlier Middle Pleistocene populations did not disappear from Europe during stages 7 and 6, the likelihood, character, and degree of interaction among *H. heidelbergensis* and this later archaic hominid population becomes an interesting evolutionary problem. Finally, behaviorally Neanderthals should share more with the African descendants of Florisbad, including anatomically modern humans, than they do with the early Middle Pleistocene hominids associated with mode 2 technologies and thus the claims for derived behavior among them are far less anomalous.

Recent discussions have focused on the relationship between the evolution of modern humans and the extinction of Neander-

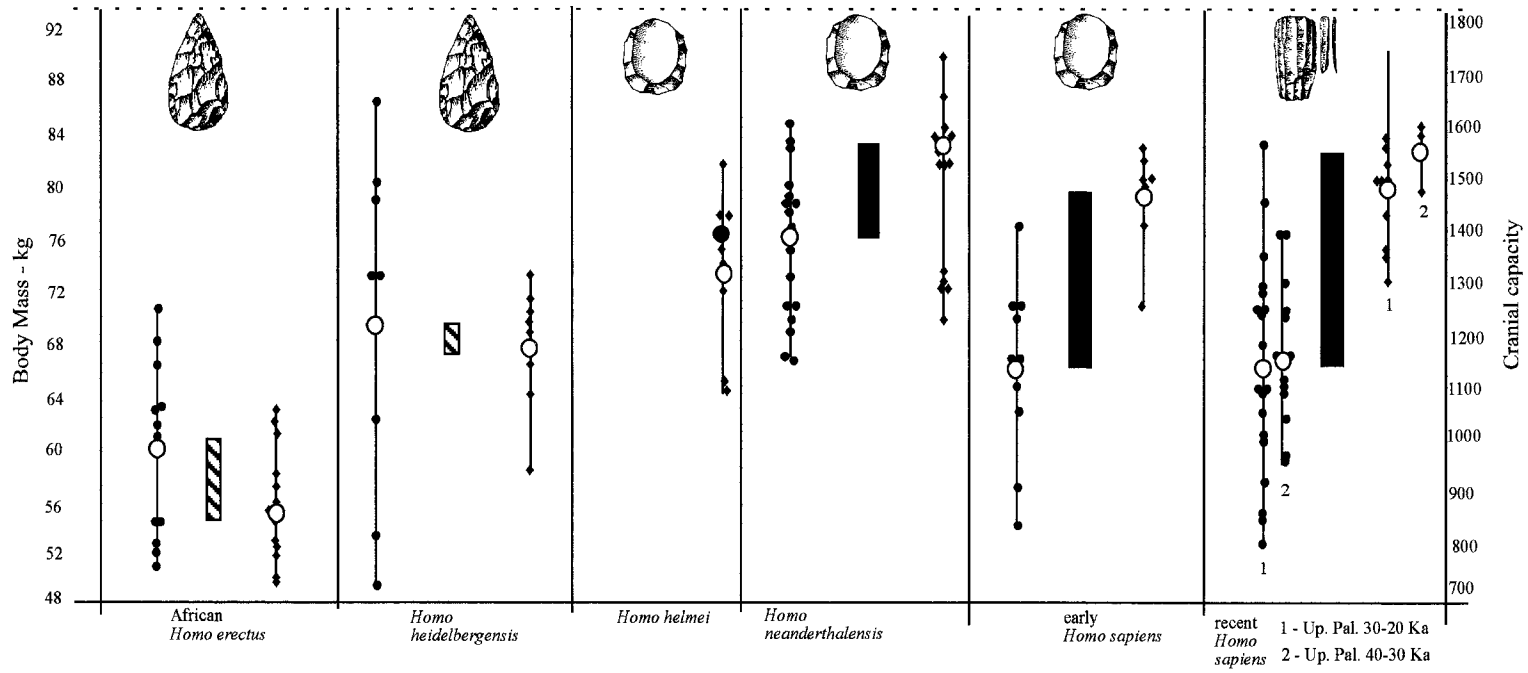


Fig. 6. Variation in body mass and cranial capacity in African and European *Homo*. For each group of fossils, here clustered as *H. erectus*, *H. heidelbergensis*, *H. helmei*, *H. neanderthalensis*, early *H. sapiens*, and recent *H. sapiens*, the estimated body mass (in kilograms) is plotted on the left and the measured or estimated cranial capacity (in cubic centimeters) on the right (data from Ruff et al., 1997 [www.nature.com]). Encephalization quotients (EQs) were not calculated given the paucity of associated cranial and postcranial remains, particularly for the Middle Pleistocene remains, but the relation between average body mass and average cranial capacity is represented by the thicker bar. However, the range and mean of body mass and cranial capacity in the various groups clearly shows the increased brain volumes observed in the late Middle Pleistocene specimens (here grouped as *H. helmei* in terms of their association to mode 3 archaeological remains) in relation to earlier hominids. The relatively larger body mass of Neanderthals in relation to modern humans (early and recent) results in their comparative smaller encephalization (Ruff et al., 1997).

thals. However, in evolutionary terms, Neanderthal extinction is not the outcome of the evolution of modern humans, which had occurred some 100,000 years before in another continent, but of the dispersal of a particular regional population of humans with powerful biological and technological advantages. The extinction of Neanderthals represents the extinction of one among many regional populations that competed for space and resources, although, as they represented the latest surviving nonmodern hominids, it affected global levels of hominid diversity to a greater extent than most. On the other hand, the evolutionary geography of African and European Middle Pleistocene hominids suggests an intimate relationship not between the evolution of modern humans and Neanderthal extinction but between the origins of both modern human and Neanderthal lineages.

Ancestral bottlenecks and the establishment of modern humans outside sub-Saharan Africa

Modern human genetic diversity is, relative to that of a closely related species like *Pan*, very small. This has been interpreted as the result of a recent loss of variability—a demographic bottleneck (see discussion above). Although human populations differ in their levels of diversity (Africans being more diverse than others in fast mutation loci), all humans share this overall lack of diversity in relation to other species, implying that the main demographic bottleneck occurred in the population ancestral to all living humans. On the basis of the relationship between diversity, ancestral population size, and mutation rates, the approximate size of the effective ancestral population during the bottleneck has been estimated as >10,000 individuals (Bowcock et al., 1991; Brown, 1980; Haigh and Maynard Smith, 1972; Harpending et al., 1993; Jones, 1986; Hammer, 1995; Nei and Graur, 1984; Maynard Smith, 1990; Rogers and Jorde, 1995; Takahata et al., 1995; Wills, 1990). Other calculations have led to the suggestion that over the long term (the last 1 million years), the lineage ancestral to modern humans in Africa fluctuated between 100,000 and 40,000 individuals (Sherry et al., 1997; Takahata et al., 1995), and so the bottleneck

would have represented a reduction of between 75–90%. Recent studies using pairwise comparisons of mtDNA differences in human populations have suggested that the distributions of these differences at a population level reflect the effect of very significant demographic expansions between 70 and 50 Ka (Di Rienzo and Wilson, 1991; Harpending et al., 1993; Rogers, 1995; Rogers and Harpending, 1992; Rogers and Jorde, 1995; Watson et al., 1997). The different relative position of the peak of these distributions between and within populations further suggests that the ancestral population had subdivided into those ancestral to Africans, Asians, and Europeans before the expansions took place (Harpending et al., 1993; Rogers and Jorde, 1995).

Although a bottleneck is a demographic event, it has both spatial and temporal components that may strongly affect the outcome. These can be phrased in terms of three questions. First, did the bottleneck in human history reflect a population reduction into a number of small breeding populations or a reduction into a single breeding group? Second, how can we explain the population subdivision and relative isolation of the populations ancestral to Africans, Asians, and Europeans before the demographic expansions reflected in the mismatch results? And third, are the differences between large modern human clusters the result of the long-term effects of small population size or of subsequent bottlenecks that affected the proportion of shared ancestral diversity?

Spatial structure of the ancestral population. The first question, that of the structure of the population during the bottleneck, can be formulated into two hypotheses. Both hypotheses imply demographic vicariance but differ regarding the number of late Middle Pleistocene hominid populations that survived such a period of population contraction. In the first case, the sub-Saharan African hominid population would have divided into several geographical groups, some of which would have become extinct while others survived. The summed effective population size of all those separate populations that survived would have totaled less than ~10,000 people (i.e., each

subdivided population would have been very small) (Fig. 7, bottom). Rogers and Jorde (1995) estimated that if the ancestral population was structured, the sum of all groups could not have been more than approximately 4,000–5,000 genetic ancestors. In this model, survivorship would have been due partly to the area occupied by each reduced group and its resource potential and partly to the evolutionary response of each group to the selective pressures posed by stringent conditions as well as the interaction of these with the novelties introduced by genetic drift. As more than one of these small groups would have survived to the present, the duration of the bottleneck becomes important for estimating the process of drift in originating interpopulation diversity. If this hypothesis were correct, observed palaeoanthropological African diversity between 200 and 100 Ka could represent true ancestral diversity.

The second hypothesis would postulate that of all the hominid populations in sub-Saharan Africa undergoing contraction at the time, only one survived (Fig. 7, top). However, this one group would have been larger, composed of >10,000 genetic ancestors in continuous genetic exchange. Again, survivorship would have been related to the interaction between the size of different populations and the potential of different African environments for supporting small hominid groups during a period of loss of larger-scale ranges and social networks, but in this case the model suggests an effect of minimum population sizes in population extinction. The duration of the bottleneck becomes important for estimating the effects of drift in the ancestral population, the outcomes of which would be shared by all living humans. Although new selective pressures would have accompanied the process that caused the bottleneck in the first place, the overall environmental component would have been maintained, as differentiation would have taken place over the range of the parental group. If this hypothesis were correct, archaeological and hominid fossil diversity in Africa between 200 and 100 Ka would not represent ancestral diversity but rather the diversity of several small distinct populations, each under the effects of drift and local

selective pressures, but only one of which was ancestral to present *Homo sapiens*.

The two hypotheses lead to very different interpretations of the African 200 to 100 Ka hominid fossil record, but they also point to different implications for the shared loss of genetic diversity observed in living humans. Recent simulations by A. Rogers show that population subdivision, with its generation of interpopulation differences, prevents the loss of diversity even during a major demographic bottleneck (in these simulations, with subdivision into three groups, the change from $\theta = 1,000$ to $\theta = 1$ (where $\theta = 2N\mu$ [N = effective population size and μ = mutation rate]) results in almost no diversity loss (mean pairwise differences (mpd) change from 158.61 to 124.26), while the change from $\theta = 1000$ to $\theta = 1$ with survivorship of a single group results in the loss of 70% of the group's diversity (mpd = 47.23) [Ambrose, 1998; Rogers, personal communication]). These simulations strongly suggest that only one geographical population survived this period of population contraction and that hominid African diversity in the late Middle Pleistocene does not represent true ancestral variability but that of a number of groups, most of which later became extinct. Only one, and perhaps or even probably one not yet palaeontologically sampled, is directly ancestral.

If the correct model for a bottleneck is that of a single surviving population, then infra-African archaeological and palaeontological variability becomes significant. Unfortunately, the fossil sample for most of the period concerned (stage 6) is nonexistent (from the very end of the period, all with dates approximating 130 Ka, there are the fossils of Omo Kibish, Ethiopia, and the cranium from Singa, Sudan, and the late archaic fossil of Ngaloba, Tanzania). Therefore, an assessment of hominid morphological variability during the latest African Middle Pleistocene is restricted to an indication that by the very end of the period early modern humans had evolved in at least northeastern sub-Saharan Africa, with the possibility that late archaic groups were still present. Archaeological diversity should be more informative, as several Middle Stone Age (MSA) sites are known. However, chronological resolution is poor for much of

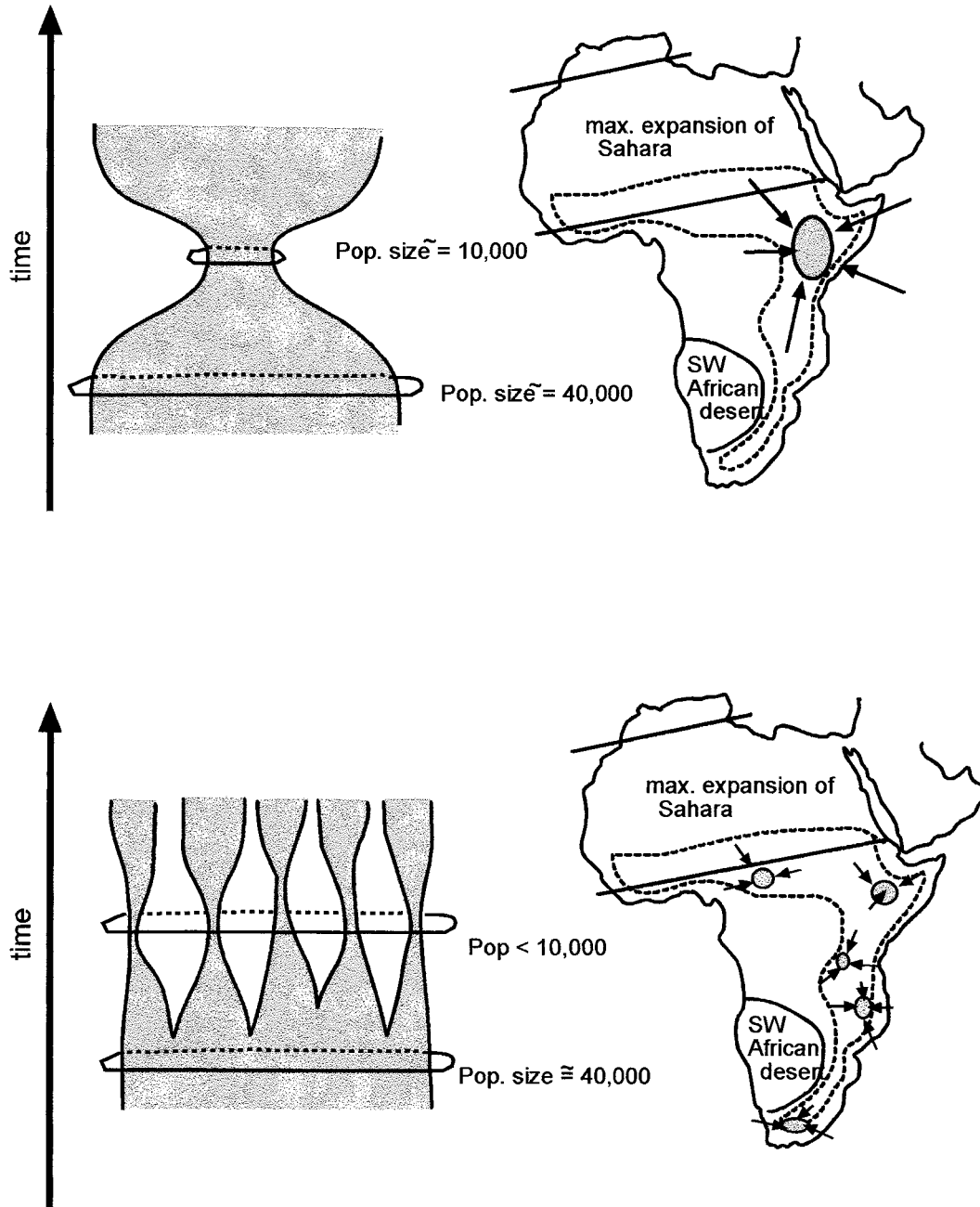


Fig. 7. Schematic representation of the two hypotheses of population structure during an extreme bottleneck discussed in the text. **Top:** Population contraction results in the survival of a single refugium, which would have contained approximately 10,000 genetic ancestors. **Bottom:** Population contraction results in a number of refugia, which would have contained less than 10,000 genetic ancestors (calculated as <4,300 people in all by Rogers and Jorde [1995]).

this time. What we know of the African Middle Stone Age (mode 3) is that it appears around 250 Ka and possibly somewhat earlier, from which time it is found in a number of sites—in the late Acheulian Victoria West tradition of Kenya and in Florisbad, southern Africa, where it is associated with a late archaic fossil recently dated to ~250 Ka (Grün et al., 1996). In Kapthurin, Kenya, one of the few Middle Pleistocene sites with a radiometrically known sequence, the time ~250 Ka coincides with the disappearance of typical Acheulian (McBrearty et al., 1996). Those areas in sub-Saharan Africa where there is the early appearance of mode 3 techniques were characterized by the overall substitution of Acheulian industries generally (McBurney, 1960; Phillipson, 1985). There is only one site that has been securely dated to stage 6—the Gademotta Formation in Ethiopia, where early prepared core artefacts (M3) have been dated to 180 Ka (Wendorf and Schild, 1974). By the last interglacial (stage 5e), great diversification and regionalization of the stone tool assemblages, broadly within what may be described as variants of the MSA, is observed throughout Africa—the Howieson's Poort in southern Africa, the Bambatan in Zambia, the Mumba tradition in Eastern Africa, the Sebilian along the Upper Nile, the Lupemban in western Africa, the Aterian of the Maghreb and Sahara, and the pre-Aurignacian of Lybia (Allsworth-Jones, 1993; Clark, 1992; Deacon, 1989; McBurney, 1960; Vignard, 1923). All these show, besides regionalization, certain technological innovations like blades, small backed blades, tanged points, and harpoons but within a mode 3 context and are consistent with the expansion of early modern humans within Africa at this time (see discussion below). We are left with an almost complete lack of palaeoanthropological evidence that can be attributed with certainty to stage 6. This picture might change as more sites are found and dated. On the other hand, it may be that the lack of stage 6 MSA sites, the disappearance of the African Acheulian (in contrast to what is observed in Europe), and the later expansion and diversification of the African MSA in stage 5 reflect the population contraction seen in the genetic data, from which only

one relatively large population, with novel biology and behavior, survived and expanded at the onset of the last interglacial.

Population structure prior to Upper Pleistocene expansions. Using empirically obtained values of diversity, these computer simulations raise another issue. The loss of variability through an ancestral bottleneck in a single breeding population would be very large but not as large as that actually observed in and inferred from living humans. Results broadly concordant with empirically derived human mpds are obtained only by simulating various histories that include the effects of later subdivision during the small size phase and secondary bottlenecks (Ambrose, 1998).⁶ The issue of secondary bottlenecks brings us to the second question posed above: how the populations ancestral to Africans, Asians, and Europeans became subdivided before the demographic expansions reflected in the mismatch results took place. In order to answer this question, we must consider the temporal and spatial context of the events involved to integrate the genetic and palaeoanthropological evidence.

The genetic evidence reviewed above indicate that a number of fast mutating genes, like mtDNA and Y chromosome microsatellite loci, show coalescent times between 180 and 120 Ka, 154,000 for nuclear gene haplotypes (CD4, DM PLAT) (Tishkoff et al., 1997), 130,000–170,000 for global mtDNA (Wallace et al., 1997), 185,000 for nine sites on the Y chromosome (Hammer et al., 1997), and $112,000 \pm 34,000$ to $123,000 \pm 39,000$ for 18 microsatellite markers on the Y chromosome [Pandya et al., 1997]), as well as ages derived from Alu insertion polymorphisms ($137,000 \pm 15,000$ [Stoneking, 1997]). The key question is what this congruity of coalescent times means in terms of population history. With regard to the Neander-

⁶The simulations performed by Rogers give the outcome of three scenarios. One of these posits that after the original loss of diversity the population subdivides into three and then expands from $\theta + 1$ to $\theta + 1,000$ without further bottlenecks; the resulting mpd = 13.36. The second possibility is a secondary bottleneck after the subdivided population expands from $\theta = 1$ to $\theta = 1,000$, resulting in an mpd of 11.4. Finally, the last scenario would have only one population surviving the secondary bottleneck, resulting in an mpd of 9.3 (Ambrose, 1998; Rogers, personal communication).

thals, it was argued that the time of coalescence of a given gene must precede population divergence by x generations (Krings et al., 1997), an unknown number of generations that disassociates the time of coalescence of a single gene from population parameters. However, as the number of loci considered is increased, there will be an increasing probability that their combined history reflects population history (Avice and Wollenberg, 1997). Therefore, the relative contemporaneity of coalescent events between 180 and 120 Ka may be taken to reflect the probabilistic effect of a concomitant loss of lineage diversity in various systems associated with demographic contraction and therefore a broad parameter of when the ancestral bottleneck occurred. This period corresponds to a glacial phase, peaking around 130 Ka (stage 6). In ecological terms, population contraction reflects a response to conditions that lead to deaths outnumbering births. In the absence of catastrophes, the conditions that alter a birth-death ratio in a population are mainly ecological (reduced food availability), which can also lead to social mechanisms associated with intergroup competition (warfare). In equatorial regions, the ecological conditions that lead to food scarcity and increased competition are related to periods of aridity, which occurred as part of the effects of higher latitude continental glaciation. Therefore, the ecological evidence is consistent with the genetic estimates that the population ancestral to humans suffered a demographic bottleneck during stage 6, possibly culminating at the maximum glacial ~130,000 years, from which only one geographical refugium survived. Using the lowest recorded hunter-gatherer density (for the !Kung, two individuals per 100 km² [Kelly, 1995]), we find this ancestral population would have ranged over an area of at least 700 × 700 km (approximately the size of Kenya).⁷

These considerations of the genetic evidence in the context of palaeoclimatic patterns lead to the conclusion that the bottleneck at the base of modern human ancestry

lies in stage 6, the same time that the Neanderthals seem to have been evolving as a distinctive population. The timing of the ancestral bottleneck is also consistent with the available evidence on the morphological evolution of humans. If only one population survived the ancestral bottleneck, then changes that occurred in this group would be shared by all humans. *Homo sapiens* crania share a morphological pattern that differentiates them from archaic hominids, the characteristics that make a skull modern. The definition of modern humans is in itself a controversial question (Brown, 1987; Day and Stringer, 1991; Kidder et al., 1992; Smith, 1994; Wolpoff, 1986), as the differences acquired by human populations under allopatric conditions in the Upper Pleistocene mean that the proportion of features shared by all recent humans is small (Lahr, 1996). Nevertheless, modern humans are characterized by a certain cranial shape (high vault in relation to vault length and breadth), short facial height (secondarily changed to a certain extent in recent Mongoloids), a number of basicranial traits, a change of shape in supraorbital superstructures, and a chin on the mandible. This morphological combination appears first in the fossils of Omo Kibish from Ethiopia, dated to approximately 130 Ka, and, from the perspective of the genetic data discussed above, would have been the result both of selection acting on a decreasing population living with increasingly scarce resources and of the effects of drift once population size decreased significantly.

Modern humans also share behavioral traits not observed in the archaeological record of archaic hominids, even Neanderthals. These are related to flexibility, inventiveness, and perception of self (be it group-self or individual-self). The first is reflected in the much broader use of raw materials (bone, antler, shell, ivory, etc.), the second in the innovative solutions for practical problems (blades, tanged points, composite tools, boats, bows and arrows, etc.), and the third in art and ornamentation. The difficulty arises in that these are mainly expressed tens of thousands of years after the first appearance of morphologically modern humans. This time lag has been interpreted as an indication that the earliest African *Homo*

⁷This area would correspond to ~10,000 individuals, which represent more closely effective rather than census size, and consequently an under-estimation of the area occupied by the population.

sapiens were modern morphologically but not behaviorally (Klein, 1992, 1995).

This discrepancy should be considered in three perspectives. The first is that there are many aspects of modern human cognition and thought that are clearly under strong genetic control and are universal. Language, with its deeply embedded syntax and uniform pattern of development, is one (Pinker, 1994). Since both genetics and palaeoanthropology indicate the early subdivision of the modern human gene pool into populations that later colonized different parts of the world, it should be inferred that the capacity for modern syntactical language must have been present in the very earliest modern humans. Were it to have spread by later gene flow, the genetic structure of human populations would have been very different. It has also been argued that social and planning aspects of the actual modern human dispersals out of Africa, which included the use of watercraft, represent evidence of the universal human capacity to speak (Noble and Davidson, 1996). The second is that the earliest modern groups do show a number of novel behavioral traits—the persistent exploitation of certain marine resources, the first evidence of novel practical solutions (blades in the Howieson's Poort tradition of southern Africa (Deacon, 1989; Klein, 1994), tanged elements in the Aterian (Clark, 1993; McBurney, 1960; Wendorf et al., 1990), microliths in sites in the Nile Valley (McBurney, 1967), barbed points and harpoons at the Katanda sites in the Semliki Valley in Zaire [Brooks et al., 1995; Yellen et al., 1995]), and the earliest evidence of the use of ochre. These would imply that the biological cognitive changes that underlie shared human behavior had already taken place. Finally, while the biological basis for modern human behavior would be in place early, its material expression would vary in relation to local social and ecological conditions, such as differing combinations of individual mental attributes, social structure, technological pressure, and intra- and intergroup competition. The more intense expressions of modern human complexity found in the later dispersals of populations across both Africa and Eurasia would thus be the outcome of particular demographic and socioecological histories rather

than fundamental biological shifts and innovations.

Secondary bottlenecks and the differentiation of human populations. Studies of the pairwise differences in mtDNA within (mismatch distributions) and between (intermatch distributions) human populations indicate that human populations divided into at least three groups that later expanded severalfold, known as the Weak Garden of Eden Hypothesis. The subdivision would have taken place around 100 Ka, and populations would have remained small until the expansions between 70 and 50 Ka (Harpending et al., 1993; Rogers and Jorde, 1995; Sherry et al., 1994). The integration of the palaeoanthropological evidence into this model poses an interesting question. The beginning of the last interglacial ~125 Ka (stage 5) was characterized by a period of markedly increased rainfall, which resulted in the expansion of the range of equatorial forests and that of savannas over previous deserts. At this time, the range of African faunas reached northern Africa and the Middle East, as shown by the presence of sub-Saharan African species, including modern humans, in the Levantine sites of Skhul and Qafzeh (Grün and Stringer, 1991; Stringer et al., 1989; Tchernov, 1992a; Valladas et al., 1988; Vandermeersch, 1982) and of modern humans in southern Africa (Die Kelders 1, Equus Cave, Klasies River Mouth, Sea Harvest, and the somewhat later Border Cave [Deacon, 1989; Grine and Klein, 1993; Grine et al., 1991; Klein, 1994; Morris, 1992; Rightmire and Deacon, 1991; Singer and Wymer, 1982]) and the Maghreb, as shown by the fossil of Dar es-Soltan associated with the Aterian (Hublin, 1993; Wendorf et al., 1991, 1993). All these early modern specimens show the changes in skeletal proportions and craniofacial and superstructural shape that characterize *Homo sapiens* while still retaining some plesiomorphic traits and skeletal robusticity to a larger extent than is observed in most recent populations (Churchill et al., 1996; Lahr, 1996; Lahr and Wright, 1996; Pfeiffer and Zehr, 1996; Stringer, 1992). If this geographical expansion represented an early demographic expansion of humans, then the pooled mis-

match and intermatch distributions should coincide instead of the intermatch leading the mismatch waves, as is observed. This raises the issue of how to interpret demographically the early geographical expansion of humans observed in the fossil record.

Two hypotheses can be proposed to account for the fact that this early expansion of humans is not observed in the mean number of pairwise genetic differences within recent human groups. The first is that the last interglacial expansion of modern humans was genetically insignificant in comparison to the scale of the demographic expansions around 70 to 50 Ka (estimated to have been at least 100-fold [Rogers and Jorde, 1995]) and thus invisible in genetic terms. Expansions are the result of either an increase in population as available resources expand or a change in the mode of exploitation that allows either more individuals to survive in the same environment or to colonize new ones. In the case of the early humans of the last interglacial, the palaeoclimatic information regarding the expansion of habitats, together with the absence of a change in exploiting capabilities (as shown by the stability in the archaeological Middle Stone Age/Middle Palaeolithic record), suggests that there was no major change in subsistence strategies and that this early geographical expansion resulted from the expansion of the environments being exploited. By extrapolating from a modeled reconstruction of African environments 8,000 years ago (Adams and Faure, unpublished manuscript) to those of 125 Ka and assuming that early humans could have occupied areas of savanna and tropical grasslands at a relatively low hunter-gatherer density (5/100 km²) and areas of thorn-scrub woodlands at a slightly smaller density (4/100 km²), we reach a conservative estimate of ~500,000 individuals as the size of the population that could have ranged over the area available during early phases of the interglacial represented by stage 5 (with the smallest values for ethnographic hunter-gatherers (2/100 km²), the number of predicted individuals during the beginning of the last interglacial in Africa would be ~225,000). However, Rogers and Jorde (1995) estimate that the effective size of the

subdivided modern population after the bottleneck was less than 66,000 (divided into at least three populations of ~20,000 individuals each), while the postexpansion population must have been composed of more than 300,000 adults. Therefore, either the population estimates for occupation of early interglacial African environments are wrong by an order of magnitude (implying that MSA human populations could not achieve even the lowest densities of recent hunter-gatherers or that there were very significant gaps in the hominid distribution) or the hypothesis that this event should be insignificant in terms of diversity is not supported.

The second hypothesis to explain why the early interglacial expansion of modern humans is not represented in the genetic data is that, once conditions deteriorated and populations could not maintain the expanded range, peripheral groups contracted in size and became extinct at various points in the subsequent tens of thousands of years. Therefore, the increased diversity that would have been generated by the demographic expansion at this time was subsequently lost through secondary bottlenecks and is not represented in the mismatch data of living groups. Among the fossil populations of early modern humans from the last interglacial, several seem to have subsequently become extinct. In the Middle East, the early modern population is replaced by Neanderthals after 70 Ka (Bar-Yosef, 1993). In northwestern Africa, the Aterian MSA tradition (associated with the modern fossil of Dar es-Soltan [Hublin, 1993]) seems to have disappeared before the appearance of the Iberomaurusian in the area 22 Ka (Klein, 1995). In southernmost Africa, the earliest modern humans associated with the Howieson's Poort MSA tradition also seem to have suffered a considerable reduction around 60 Ka, when the area becomes virtually depopulated (Klein, 1992, 1994). However, not all of the peripheral populations would have become extinct. The later expansion in parts of Eurasia of modern humans with Upper Palaeolithic technology around 50 Ka is likely to have been derived from one of these peripheral populations. Its location is a matter of debate; while the earliest Upper Pal-

aeolithic tools are found in southwest Asia, an area previously occupied by Neanderthals, the source area could lie equally in northeast Africa, the Arabian peninsula, or even across towards Iran and northwest India. Other surviving peripheral populations may have been in north Africa as well as central and eastern Africa that would have given rise to African and Asian groups. Therefore, the subdivision of the early modern human gene pool would have resulted from this process of early expansion followed by fragmentation as early interglacial habitats contracted and barriers like the Sahara desert formed again. The extinction of several of these early populations, together with a possible reduction of those that survived, would explain why the early expansion of modern humans throughout Africa did not leave a signature in the mismatch distribution of mtDNA pairwise differences of living groups.

It should be noticed, however, that it could well be a combination of the expectations of both hypotheses that approximates the events in stage 5. It is likely that several of the early modern localized populations that were formed within Africa after the expansion 125 Ka became subsequently extinct. However, it has also been suggested that these early modern humans, associated with Middle Stone Age industries, could not support demographic densities similar to more recent hunter-gatherers, associated with the Later Stone Age, in the same area (Klein and Cruz-Urbe, 1996). Therefore, it could be that the population estimates using recent hunter-gatherer densities are indeed gross overestimations, a fact that would only increase the probability of group extinction and reduction explored by the second hypothesis above.

Therefore, the best interpretation of the palaeoanthropological and genetic evidence of the early history of our species would suggest that the ancestors of humans underwent a population bottleneck sometime during stage 6 (200 to 130 Ka) that reduced them to a single population of >10,000 genetic ancestors; that around 125 Ka this early human population underwent a demographic expansion that led to the occupation of a savanna belt along 10–15° latitude as

well as northern and southern Africa; that subsequent population contraction and extinction led to the establishment of a number of regional-local populations within sub-Saharan and northern Africa and further loss of diversity; and that these localized human populations remained separate for some 50,000 years before new expansions occurred. In other words, the ancestors of Europeans and Asians lived in Africa for some 50,000 before they dispersed.

Human diversity within and out of Africa. This model for the early history of modern human evolution would explain several aspects of the palaeoanthropological record of humans outside Africa (Lahr and Foley, 1994). First, it explains the differences in morphology observed at the time of the first appearance of modern regional world populations as resulting from inter-population differences acquired during the phase in which populations were already subdivided and still small (i.e., the features of the main human races would have been defined by a combination of ancestral African diversity and diversity accumulated during allopatric conditions because of reduced population sizes, evolutionarily frozen by the expansion events). Second, it accounts for the archaeological diversity observed, as it proposes the derivation of the southern Asian industries directly from African mode 3 technologies, while the Upper Palaeolithic would have resulted from a localized northeasternmost African development, which came to have a major impact in the dispersal of the population throughout Eurasia. Third, it would explain the early occupation of Australia through the dispersal of an eastern African population along the southern Asian coast at a time when the Levantine corridor was closed to African groups (60 to 50 Ka, as suggested by the sites of Malakunanja and Nawabilla [Roberts et al., 1994]). The latter has recently received genetic support from studies of Alu insertion polymorphisms that show that Australian aborigines are as distant to the ancestral source as recent Africans (Stoneking et al., 1997). Finally, this model in its broader context explains both the evolution of modern humans and their sister clade, the Neanderthals, within the context of a general theo-

retical framework rather than the result of a unique event.

DISCUSSION AND CONCLUSIONS

This paper set out to explore a single origin of modern humans in the context of evolutionary theory, in particular the way in which the principles of evolutionary geography can be applied to the evolution to an animal lineage, and through this provide the basis for formulating hypotheses about phylogenetic patterns.

Three broader theoretical issues in evolutionary theory were raised in the introduction: the need to account for changes in diversity through origin thresholds, the need for demographically based models of population diversification, and the need to consider the effects of geography in interpreting evolutionary change. In this final section, we will use the discussions presented above to address these points.

Dispersals of modern humans

This paper has derived two primary conclusions about the role of dispersals in modern human evolution and origins. The first of these is that dispersals are one of the primary evolutionary mechanisms, the means by which successful species adapt and expand as their native habitats expand and break through into new environments and adaptive plateaus. The second is that the dispersal events underlying human diversity are detached from the processes leading to the origins of the species. The latter occurred during stage 6, while the former are primarily associated with stages 5, 4, and 3. Furthermore, we have seen that there are underlying biogeographical reasons, contingent upon the nature of glacial cycles, which result in hominid dispersals being predominantly from Africa and that such dispersals have occurred.

The primary underlying basis for this pattern is that populations are expanding as the habitat in which they can survive expands and that, for climatic reasons, this occurs first in Africa during an interglacial. However, the question should be posed whether there are specific behavioral factors that led to the success of the dispersals of modern humans. At this stage, it is impos-

sible to give any form of definitive answer, but a number of possibilities may be proposed. The first of these is that if there is a dispersal based on a fundamentally new and different cognitive capacity (such as language or symbolic thought), then this would be the original stage 5 dispersals. Dispersals occurring after the fragmentation of the population after the last interglacial would be population-specific and therefore could not be based on fundamental biological change such as language. Second, the early dispersals in stage 5 and those occurring before stage 3 along the southern coast of Asia may well have been specifically coastal and involved the use of certain marine resources, particularly shellfish (fish and birds apparently not being exploited [Klein and Cruz-Urbe, 1996]). Aquatic specializations may have provided a predictable resource base that, combined with a tendency to overexploit easily obtainable resources and the ability to move on, led to rapid population spread without major demographic expansion. Third, the dispersal that is best documented, that of the Upper Palaeolithic across Eurasia and the Mediterranean, is of specific interest because it appears to occur against the grain of climatic change. Therefore, it may well be a dispersal associated with either social or technological innovations that gave the populations a major advantage. Large group size and social networks may be proposed for the former, the bow and arrow for the latter. And finally, it should not be forgotten that the present interglacial has seen a very large scale pattern of dispersals associated primarily with agriculture—dispersals that, as occurred in stage 5, have radically altered the pattern of human diversity.

Diversity through time

The reconstruction of the evolutionary history of humans has traditionally been focused on events—the point of separation of modern and archaic hominids, the point of origin of morphologically and behaviorally modern humans, the point of expansion of humans out of Africa. However, these events are not evolutionarily discrete but rather represent the outcome of demographic processes that affected the levels of population

diversity in ways that allow us to identify them. We have argued that the contraction of African populations and their subsequent expansion and dispersal into Eurasia have evolutionary precedents and are to be expected as part of the biogeographical changes of glacial cycles. This offers an interpretation for the different evolutionary trajectories of African and European populations. African hominids would have repeatedly undergone periods of population contraction during arid phases—bottlenecks which would have combined the effects of rapid change through genetic drift and of selection for energetically more efficient bodies and more efficient technologies as resources became scarce. These changes, which would represent either an increase in diversity within a period if several fragmented populations survived or a loss of diversity if extinction of most groups took place, would be frozen and magnified by the subsequent population expansion during the early phases of interglacials. It would be these diverse populations that reached the Mediterranean, taking with them the biological and behavioral innovations acquired in the preceding tens of thousands of years. Within Europe, the processes would have been different. Once allopatric conditions in relation to African hominids were established at the onset of glacial climates, European hominids would be under the pressure of directional selection leading towards morphological specializations that improved survivorship in periglacial habitats. Directional selection reduces diversity in that it attempts to move the population close to a new adaptive peak and therefore a level of homogenization reflected morphologically in the fixation of apomorphic traits.

Evolution within the modern human lineage can also be expressed in terms of changing levels of diversity. The stringency of the period preceding the ancestral bottleneck has to be measured by the effect it had on population survivorship. By implication, we may infer that the selective pressure for energetic economy and efficiency acting on these African populations was very strong, as must have been the effects of drift as population numbers fell. Therefore, the population ancestral to all humans became both

different and, for a short period of time, homogeneous. Why is it difficult to establish thresholds between successive hominid groups in Africa? One possible answer to this question is that morphological change in Middle Pleistocene Africa was strongly influenced by periods of significant genetic drift altering the combination of preexisting traits, while the selective pressure directed toward survivorship under scarce resources would have favored the evolution of behavioral and cognitive novelties not reflected morphologically.

However, the ancestral modern population was not homogeneous for long, as population expansion, subdivision, and contraction subsequently took place. Depending on the balance of ancestral polymorphisms throughout the range of the ancestral population prior to subdivision, the pattern of synapomorphism among subdivided groups may have been very different. In the case of modern human differentiation, early fragmentation of the ancestral population led to the establishment of at least three groups that, during a long period of population isolation and relatively small size, changed both the level and pattern of ancestral variability in different ways. It is thus that groups like the Australians seem to have retained a larger proportion of ancestral traits than others and that Europeans and Asians show directional changes towards new morphotypes, while Pleistocene Africans show the effects of large interpopulation differences. This is hardly surprising; although gene flow has played a significant part in homogenizing the human population over the last ten thousand years, for most of our species history it has been survival in particular environments as relatively small populations that would have been the principal selective pressure. The evolution of the human species may thus be universal, but it is made up of a myriad of local histories.

Extinction

In the course of the debate on modern human origins, there has been considerable emphasis on the idea of competing species and the subsequent extinction of some of these. The framework adopted here has

placed the emphasis on populations rather than species, as these are the units in which differentiation and novelty will occur. We have been able to track the history of the species in terms of populations that have expanded and contracted, and the genetic structure and the palaeontological record are the product of these multiple events. What has emerged is a picture of small hominid populations becoming extinct and the subsequent history of the species as the result of only one or a small number of populations surviving and expanding. This implies that population-level extinctions may have been an important part of our evolutionary history. This is not just a question of different species and of archaics vs. moderns but of both modern and nonmodern populations, both African and non-African. The models discussed here have imputed that pre-Neanderthal European populations, archaic and modern African groups, and early modern humans (Skhul/Qafzeh, southern African) as well as the Neanderthals themselves all became extinct. These are likely to be just a sample. Our evolutionary history, even in the last 100,000 years, is likely to have been structured as much by extinction as by innovation.

This has implications for considering diversity. First, the diversity of modern humans today is likely to be just a subset of *Homo sapiens* diversity that could have been sampled across the last 100,000 years. Second, patterns of diversity, particularly the relationship between inter- and intrapopulation diversity, are likely to have varied considerably over time. Third, the fact that populations may have become extinct, either literally or as distinct units identifiable culturally or genetically, suggests that we need to know more about the dynamics of population interactions over the long term and in particular how boundaries are formed, maintained, and lost.

Microevolutionary events

We have argued that human evolution, like the evolution of other animal lineages, has been largely governed by microevolutionary mechanisms and therefore that demographically-based patterns should be sought. However, the demography of populations in

time and space forms the basis for changes that lead to speciation. Defining palaeontological species is dependent upon the concept of species used and the interpretation of the significance of the differences between populations observed. Under the constraint of being unable to test reproductive isolation between fossil populations, many palaeontologists use the evolutionary species concept developed by Simpson (1950), in which a species is a population with an independent evolutionary trajectory. On the basis of this, several authors raise the differences between lower and Middle Pleistocene archaic hominids and between Neanderthals and modern humans to specific level, resulting in four Pleistocene species of *Homo*—*H. erectus*, *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens*. We have introduced a population intermediate between African and European *H. heidelbergensis* and the Neanderthal and modern populations of the early Upper Pleistocene, for which we have resurrected the name *H. helmei* (Foley and Lahr, 1997). This population would have differentiated in Africa during a glacial-arid episode between 300 and 250 Ka, primarily reflected in the evolution of behavioral traits.

Whether *H. helmei* represents a biological species (*sensu* Mayr, 1963) or not is not the center of the argument. In reality, whether any of these larger-brained late Pleistocene hominids represented a biological species that could not interbreed with others is questionable. The key point is what biological and behavioral heritage the individuals within each of these groups shared that allowed them to undergo assortative mating and to compete as social units with other hominid groups for space and resources.

Role of geography in recent human evolutionary history

Darwin's greatest difficulty was to convince his readers that the effect of small-scale mechanisms could explain the incredible magnitude of evolutionary change. This remains the most challenging aspect of evolutionary studies, and accordingly large-scale contingent and punctuated events are commonly proposed instead. Catastrophic explanations can account for drastic change, and, given their sudden nature, their effects

are rarely represented in geological scale. Recently, Ambrose (1998) has proposed that the secondary bottlenecks in the populations ancestral to Africans, Asians, and Europeans were related to the effects of the volcanic winter resulting from the eruption of the Toba volcano 70 Ka. The Toba Volcano did erupt 70 Ka, and, as argued by Rampino and Self (1993), it may have been the largest volcanic eruption in the last 100,000 years. Nevertheless, however attractive such a catastrophic explanation, we cannot confirm it or refute it at present. We would argue that alternative explanations, relying on the processes that generate change in evolutionary time—natural selection, genetic drift, mutations, and gene flow—can account for the evolution of human populations. The discussions above have attempted to show how strong geographic and demographic mechanisms can be in explaining evolutionary patterns, even when the outcome of these is as extraordinary as human diversity.

Finally, we have argued that the model of a recent African origin of modern humans is empirically strong and have tried to show how, when treated as the complex evolution of populations in time and space, it is consistent with current thinking on evolutionary theory. Such theory emphasizes small-scale demographic processes and allopatry as the appropriate scale and dispersals and contractions as the primary demographic mechanisms underlying both differentiation and diversity. We have referred to the combination of a microevolutionary perspective and the spatial considerations as evolutionary geography and have found it a useful means for integrating genetic and palaeoanthropological data and for bringing together biological processes and historical context. Much of the debate about modern human origins has foundered on the lack of integration of different approaches. We would hope that a greater emphasis on the broader theoretical underpinnings, and in particular populations rather than species and microevolution rather than macroevolution, of a single origin and multiple dispersals model will open the way for new questions to be addressed.

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