Genetic and Fossil Evidence for the Origin of Modern Humans

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The origin of living *Homo sapiens* has once again been the subject of much debate. Genetic data on present human population relationships and data from the Pleistocene fossil hominid record are used to compare two contrasting models for the origin of modern humans. Both genetics and paleontology support a recent African origin for modern humans rather than a long period of multiregional evolution accompanied by gene flow.

After a period of relative neglect, increasing attention is being given to the biological and behavioral changes that led to the evolution of *Homo sapiens*, the last major event in human evolution (*1–4*). We examine two opposing models proposed to explain the origin of *Homo sapiens* and compare their compatibility with recent reviews of genetic (*5*) and paleontological (*6*) data. These two models are not the only ones currently under discussion, but it is likely that one or other reflects the predominant mode of *Homo sapiens* evolution. Comparison of these two extreme models should allow the clearest tests for the models from existing data, tests which are not feasible for several other proposed models.

The two competing models for recent human evolution have been termed "regional continuity" (multiregional origins) and "Noah's Ark" (single origin) (*7*). In the multiregional model (*8–10*), recent human variation is seen as the product of the early and middle Pleistocene radiation of *Homo erectus* from Africa. Thereafter, local differentiation led to the establishment of regional populations which successively evolved through a series of evolutionary grades to produce modern humans in different areas of the world. In contrast to Coon's version of this model in which the local lineages evolved independently (*11*), the role of gene flow in maintaining grade similarities and preventing speciation is emphasized now, along with the development and persistence of regional features in morphology, particularly in peripheral areas (the "center and edge" corollary).

According to the multiregional model, some regional ("racial") features are considered to have preceded the appearance of the *Homo sapiens* morphology and to have been carried over from local *Homo erectus* ancestors. The exact manner of establishment of "modern" features in any area has depended on gene flow, local selection, and drift. The appearance of *Homo sapiens* was thus primarily the result of a continuation of long-term trends in human evolution, and it has occurred mainly through the re-sorting of the same genetic material under the action of selection, rather than by the evolution and radiation of novel genetic material and morphologies. Thus some advocates of this model have suggested that there have been no speciation events during the last 1.5 million years of human evolution and that hominids usually referred to *Homo erectus* might instead be allocated to *Homo sapiens* (*9*).

In contrast, the single origin model assumes that there was a relatively recent common ancestral population for *Homo sapiens* which already displayed most of the anatomical characters shared by living people. Proponents of this model have proposed Africa as the probable continent of origin of *Homo sapiens*, with an origin for the species during the early part of the late Pleistocene, followed by an initiation of African regional differentiation, subsequent radiation from Africa, and final establishment of modern regional characteristics outside Africa (*6, 12, 13*). A single origin minimizes the amount of parallel evolution required to produce the widespread appearance of *Homo sapiens* characteristics (*6, 14*). Cladistic versions of the model are based on the identification of a suite of derived features characterizing *Homo sapiens* and the recognition of these characters should be possible at an earlier date in the area of origin of the species (that is, Africa) than elsewhere (*6, 15*).

In Table 1, predictions from the two models of *Homo sapiens* origins about geographic patterning, about the establishment of *Homo sapiens*, and about the role of selective and behavioral factors (the last of which we will not discuss in detail here) are summarized. Throughout this article the use of the term *Homo sapiens* will be restricted to anatomically modern humans, following recent proposals (*16*). A summary of suggested shared derived characteristics of *Homo sapiens* (*15*) includes the following. (i) All living humans are characterized by a gracile skeleton compared with that of other species of the genus *Homo*, and this is reflected in features such as long bone shape and shaft thickness, depth or extent of muscle insertions, and the relatively thin bone of the cranial walls and mandibular body; (ii) the cranium is voluminous (but no more so than in Neanderthals), and, like the brain it contains, is typically relatively short, high, and domed; (iii) the supraorbital torus and external cranial buttressing are considerably reduced or absent; (iv) the dentition and supporting architecture are reduced in size; (v) perhaps related to these last differences, the face in *Homo sapiens* is orthognathous (tucked well under the anterior cranium); and (vi) a mental eminence is present on the mandible from a young age. Beyond such morphologically derived characters of *Homo sapiens*, there are also suggested novelties in ontogeny and in behavioral and ecological adaptations (*17–19*).

Geographic Patterning and Regional Continuity

The patterns of regional genetic variation predicted by the two models are quite distinct. The multiregional model predicts that the same kinds of evolutionary changes occurred across the major

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continents, with local populations evolving gradually into *Homo sapiens*. This provided continuity of genes through time, whereas gene flow maintained continuity through time and space. However, local differences in drift, selection, and access to gene flow should have ensured that no universal patterns of *Homo sapiens* origins emerged. Restricted gene flow at the peripheries of the populated world allowed greater differentiation and stabilization of gene pools and morphology there, in comparison with central areas. Any central area might be expected to show most within-population variation, but the least differentiation, as a result of multidirectional gene flow. Each region should have displayed a distinctive, but essentially gradual, transition from local ancestral populations to modern humans, with a persistence of regional features. Transitional (mosaic) fossils should be common, with a wide geographic distribution, and no particular temporal restriction. However, multidirectional gene flow at the center of the species range should have allowed earlier establishment of combinations of *Homo sapiens* characters there than in any single peripheral region.

The model of a recent African origin, on the contrary, predicts different patterns of variation comparing African populations and those from elsewhere. Variation should be greatest within African populations (based on their earlier divergence, and assuming predominantly neutral genetic change), and they should be sharply distinguished in gene frequencies from non-African populations. Transitional fossils would not occur outside the African area of origin, and population replacement would represent the mode of establishment of *Homo sapiens* in other areas. The earliest record of *Homo sapiens* fossils should occur in the continent of origin of the species (Africa), and the youngest records at the peripheries of the radiation. Population relationships in Europe, Asia, and Australasia would approximate those of the Holocene only in the later Pleistocene.

Modern Genetic Data

The human species shows great morphological variation. However, in contrast to this, genetic variation between human populations is low overall. Genetic distances based on electrophoretic analyses of proteins are small in comparison with those found in other hominoids (*20*). There is also relatively little protein variation between human populations. As much as 84% of protein polymorphism in human populations results from variation among individuals within populations, a further 6% represents genetic divergence associated with nationality, and only 10% varies between human "racial" groups (*21*). Thus differences between populations are small when compared with differences within populations.

Analyses of mitochondrial DNA (mtDNA) show similarly low variation between geographically distant human populations. The mean pairwise difference between human populations based on mapping of mtDNA by restriction nucleases is 0.3%. The nearest approach to this low figure in any other hominoid yet studied is for a single subspecies of gorilla, in which the mean mitochondrial sequence difference is about twice this figure, whereas the two subspecies of orangutan differ by as much as 5% (*22*). This remarkable difference in magnitude of population divergence in the globally distributed human species is an excellent illustration of the low level of geographic differentiation in *Homo sapiens*. Moreover, while each hominoid species has diverged into numerous mtDNA lineages (the two most divergent individuals differ by five sites in gorillas and 12 each in chimpanzees and orangutans), the two most divergent humans (again obtained from a large and globally distributed sample) differ by only two sites (*22*).

Sequencing of both mtDNA and nuclear DNA for human populations suggest that interpopulation divergences are relatively low in comparison with intrapopulation divergences (*23, 24*). For mtDNA, percentage sequence divergence within sub-Saharan African populations is 0.47%; this compares with a range of divergence figures between African and other human populations of 0.40% to 0.45%. Interestingly, when the interpopulation distances are corrected for this intrapopulation variation they become very small, with a mean value of 0.04%, less than 15% of the mean within-population variation. Furthermore, there is little evidence that peripheral populations are always the most differentiated because samples from the peripheral areas of Europe, the Americas, and Australasia often appear similar to each other. Contrary to the multiregional model but consistent with the recent African origin model, when many different genetic data are examined, it is only the African periphery that consistently appears most differentiated from the others, and these populations, although not "central," are the most diverse.

The greater genetic diversity among sub-Saharan African popula-

Table 1. Theoretical predictions from models of *Homo sapiens* evolution.

Aspect	Multiregional evolution	Recent African evolution
1) Geographic patterning of human evolution	Continuity of pattern from middle Pleistocene to present	Continuity of pattern only from late Pleistocene appearance of *H. sapiens* to present
	Interpopulation differences are high, greatest between each peripheral area	Interpopulation differences relatively low, greatest between African and non-African populations
	Intrapopulation variation greatest at center of human range	Intrapopulation variation greatest in African populations
2) Regional continuity and the establishment of *Homo sapiens*	Transitional fossils widespread	Transitional fossils restricted to Africa, population replacement elsewhere
	Modern regional characters of high antiquity at peripheries	Modern regional characters of low antiquity at peripheries (except Africa)
	No consistent temporal pattern of appearance of *Homo sapiens* characters between areas	Phased establishment of *Homo sapiens* suite of characters: (i) Africa, (ii) S.W. Asia, (iii) other areas
3) Selective and behavioral factors involved in the origin of *Homo sapiens*	Factors varied and widespread, perhaps related to technology; local behavioral continuity expected	Factors special and localized in Africa; behavioral discontinuities expected outside Africa

tions may indicate a longer period of separation of populations within Africa (*23–25*) than elsewhere. Restriction mapping of mtDNA has shown that pairs of African populations are some 50% more genetically distinct from each other than are any other pairs of populations (*23, 25*). If mtDNA changes are assumed to accumulate at a steady rate, genealogical trees constructed by minimizing genetic changes (through maximum parsimony analysis) distinguish two main branches. One leads exclusively to a number of African (or African origin) individuals, whereas the other leads to all other individuals of African or non-African origin. Dates for the branching points of the tree can be estimated from rates of mtDNA evolution in other organisms. This gives a date for the origin of the mtDNA of *Homo sapiens* at between 140,000 and 290,000 years ago, assuming constant rates of change at 2 to 4% per nucleotide site per million years. This rate has been claimed to be too high because it implies a human–African ape split at only 1.4 to 2.8 million years ago (*26, 27*), but this last calibration is erroneous (*28*), and the rate appears reasonable when tested against archeological data on known colonization events (*29*). The initial mtDNA split was found between Africans and others, followed by progressively younger calibrated ages for specific Asian, Australian, New Guinea, and European mtDNA types, respectively (*23, 25, 29*).

However, by contrast, trees produced from the mtDNA genetic distances show a small but consistent African–New Guinea initial link where both groups have long branch lengths (*27*), and the results of a smaller analysis of human mtDNA variation have been interpreted to show an Asian rather than African root (*30*). Nevertheless, earlier surveys of a small sample of mtDNA showed Africans to possess both the highest mtDNA variability and the highest between-population variability of the displacement loop in a noncoding region of mtDNA (*31*). Moreover, the claim of an Asian mtDNA root has been challenged through a re-analysis of the data by midpoint rooting to produce an African root instead (*25*), and the use of mtDNA genetic distances to construct trees has been criticized (*28*).

Expectations of a gradual and regular increase in human variation through time are based on the assumption that such variation is selectively neutral. Natural selection could either increase or decrease the rate of accumulation of variations in populations (*32*). Any excess of variation maintained by selection could lead to an overestimate of time since the last common ancestor shared with other populations, while any selective removal of variation could affect conclusions about the presence of bottlenecks during evolution. However, predictions of allele frequencies based on the neutral model are largely consistent with the actual distributions for mtDNA (*33*), so that for the human mtDNA system, at least, the assumption of neutrality does appear approximately valid. Departures from the neutral model that do occur can be explained by the effects of population expansion during the last 10,000 years.

Patterns of genetic differences in nuclear DNA are generally similar to those of mtDNA. In the beta-globulin cluster, African populations share a haplotype not found in other populations, whereas the non-African populations share a limited number of haplotypes not present in Africans (*34*). More recent work (*35*) links a population of Canadian Indians to Eurasian populations, further extending the split between African and non-African populations, and a separate study (*36*) confirms the presence of the common African haplotype in Bantu-speaking South Africans (*24, 34*). Moreover, there is a similar pattern of genetic diversity in the alpha-globin gene cluster (*35*), with African populations showing striking similarities in frequencies of common polymorphisms. Eurasian populations are similar to each other (although Melanesians differ, perhaps through founder effect), but the separation of African and non-African patterns is again clear. These nuclear DNA patterns accord much better with the recent African origin model than with the multiregional model, as does research on Y-chromosome DNA, where an African root for modern human variation is most parsimonious (*37*).

One line of genetic evidence that is more ambivalent in its implications is that of genetic distances, as we have already found in the case of mtDNA. Genetic distances calculated from blood groups show a close "caucasoid"-"mongoloid" relationship (as expected from the recent African origin model), but a smaller distance between "caucasoids" and "negroids" than between the latter and "mongoloids" (*38*). This points to a closer African-European than African-Asian relationship. Protein analyses, however, show a consistent split between "negroids" and the other groups, in accordance with most results from mtDNA and nuclear DNA. There may be stronger selection on blood group types, and there is a less clear relationship between blood group phenotype and nucleotide sequence. Since the body of data from protein systems is also larger, the results from protein analyses are probably the most relevant here, and support the recent African origin model. These have been used to calibrate divergence times (again assuming selective neutrality and absence of gene flow) of about 110,000 years ago for the African–non-African split and about 41,000 years for the European-Asian split (*38*).

Regarding the role of gene flow, although this can prevent increasing genetic differentiation between adjacent populations [although not necessarily prevent speciation (*32*)], it seems improbable that it could prevent increasing differentiation in a very widely distributed species over long periods of time. It has recently been calculated that for human populations with a density of 0.1 per square mile and a gene flow of 5% per generation (20 to 25 years), it might take 400,000 years for the spread of an advantageous gene from South Africa to China, and this does not take into account geographical, environmental, social, or possible specific barriers to gene flow (*39*). This is strong evidence against the multiregional model, unless it is assumed that selection maintained a low genetic differentiation among populations or that there was an extraordinary (and quite unrealistic) level of gene flow.

Paleontological Data

In the middle Pleistocene, regional populations of early *Homo* are represented at fossil sites in Europe by early Neanderthals (for example, at Swanscombe in England, Biache in France, and Ehringsdorf in the German Democratic Republic) (*15, 40*), in the Far East by evolved *Homo erectus* (for example, at Zhoukoudian and Hexian in China) (*9*), and in Indonesia by the poorly dated Ngandong (Java) material (*9, 41*). In southern Africa, specimens such as the skull from Broken Hill (Zambia) show similarities to other African fossils to the north (for example, at Bodo in Ethiopia), and to pre-Neanderthal or earliest Neanderthal material in Europe (for example, those from Arago, France, and Petralona, Greece) (*15, 42–44*). As a result, indigenous features in southern African middle Pleistocene fossils are more difficult to identify (*45*).

Comparing the patterns of variation in the fossil samples through time contradicts the expectations of the multiregional model because of marked changes in pattern and diversity. Prior to Neanderthal differentiation (>230,000 years ago), a basic west-east division of middle Pleistocene hominids can be recognized, as Asian late *Homo erectus* fossils are most distinct from those of Europe and Africa (*12, 41, 44*). Such a pattern is not consistent with the multiregional model, since a closer relationship between Eurasian populations might be expected, either from assuming a common Eurasian *Homo erectus* founding population with continuing morphological clines,

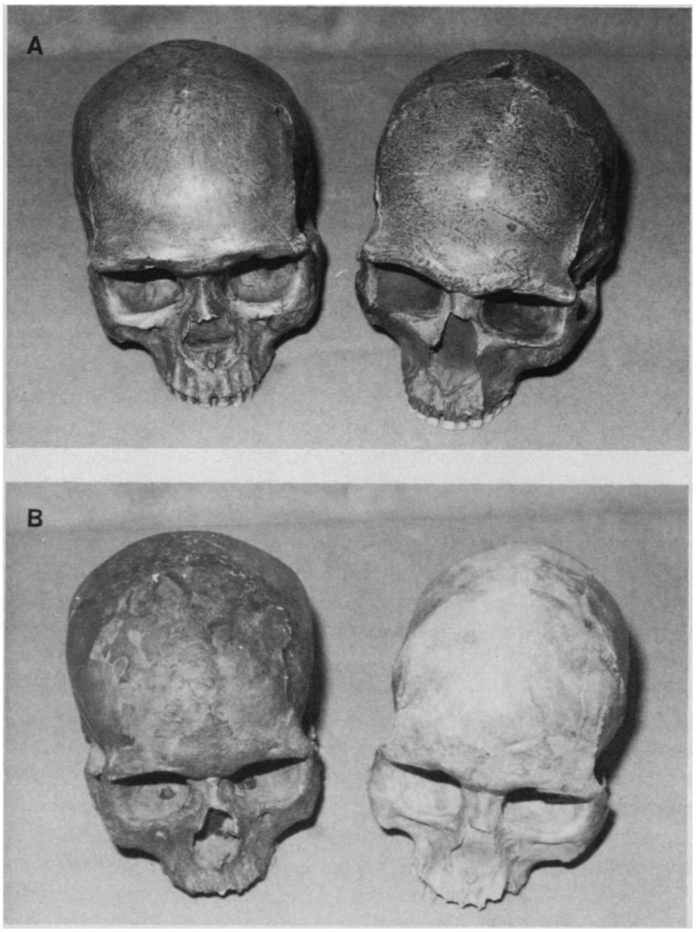

Fig. 1. Comparisons of late Pleistocene *Homo sapiens* crania from Czechoslovakia and China. (**A**) Casts of male crania from Predmostí (right) and Zhoukoudian Upper Cave. (**B**) Assumed female crania from Mladeč (left) and Zhoukoudian Upper Cave. Under the multiregional model, the marked morphological and metrical similarities of these geographically distant crania are explained as the result of parallel evolution from distinct middle Pleistocene ancestors, together with gene flow. From the recent African origin model, the similarities are explained by descent from a common ancestral population that had originated in Africa during the early part of the late Pleistocene.

or from the projection of recent genetic relationships back to the middle Pleistocene.

Moreover, late middle to late Pleistocene fossils from China (for example, Yinkou and Dali) show a change from the middle Pleistocene pattern, through a greater resemblance to European and African middle Pleistocene hominids and a greater contrast with their supposed local ancestors (*46, 47*). Despite such contrasts, these same fossils are said to display transitional features between local *Homo erectus* and *Homo sapiens* populations, and have mainly been interpreted in terms of regional continuity (*9, 46*), although detailed comparative analyses of the best specimens have yet to be published. In addition, there are no very informative fossils known to derive from the critical time period (50,000 to 100,000 years ago) immediately preceding the local first appearance of *Homo sapiens*. For Australasia, there is a complete lack of fossil evidence from the early part of the late Pleistocene period (unless the Ngandong hominids date from that time). The only credible morphological intermediate between middle Pleistocene Indonesian hominids and late Pleistocene Australians (but not the Mungo and Keilor specimens) is the Willandra Lakes WLH-50 cranium (*10, 48*), but this fossil is probably no older than the Mungo specimens and has not yet been well described. Furthermore, its thick cranial vault may reflect pathology rather than homology with that of *Homo erectus* (*49*).

The first appearance of *Homo sapiens* raises further problems for the multiregional model. Despite arguments to the contrary (*10, 50*), present evidence shows that Africa and the adjacent area of the Levant have the earliest known *Homo sapiens* fossils (*51, 52*). Furthermore, Europe, the Far East, and Australasia appear to have a relatively late first known appearance of *Homo sapiens* compared with southwest Asia and Africa, and for Europe at least, a relatively late survival of other forms of *Homo*. There is a dramatic change of pattern at the appearance of *Homo sapiens*, with a reduction in skeletal variation compared with the greater diversity present in the middle and early part of the late Pleistocene (Fig. 1). Multivariate distance studies show relatively compact groupings for living and fossil *Homo sapiens*, compared with the greater differences found from and between earlier hominids (*53–55*). The reasons for these apparent changes in pattern may be disputed, but since the multiregional model posits a consistent pattern for human population relationships through the middle and late Pleistocene, with a consequent maintenance or increase in levels of variation, such departures from the expected pattern need to be explained.

There is also an absence of evidence for morphological clines immediately prior to the global appearance of *Homo sapiens*. Neanderthals of Europe are present in western Asia and as far east as Uzbekistan (*56*), but there is little evidence of Neanderthal-derived characters in the Far East and Australasia (*9, 12, 18, 41, 44, 55*), nor in Africa (*13, 14, 18, 42, 43, 45, 55, 56*). Neither, from the same sources, is there much morphological evidence of gene flow in reverse directions into Europe prior to the appearance of *Homo sapiens*. It is only with the emergence of *Homo sapiens* that "African" morphological characters (including primitive characters lost in the Neanderthal lineage, and derived characters which were already present in Africa) appear in Eurasia (*6, 12, 13, 15, 55–57*). As already indicated, this suggests there was a remarkable change in pattern at the appearance of *Homo sapiens*, when "modern" derived characters became distributed globally during a period of perhaps 60,000 years.

Although Europe and southwest Asia have the most complete fossil record for this period, there is an absence of Neanderthal–modern *Homo sapiens* transitional fossils in either area. Not only are such transitional forms lacking, but recent dating evidence suggests that true *Homo sapiens* was present in the Levant before Neanderthals, some 60,000 years prior to the last Neanderthals in western Europe (*15, 52*). There is little or no continuity of genuine regional features, for the most distinctive and well-established characteristics of Neanderthals are poorly represented or absent in contemporaneous or immediately succeeding *Homo sapiens* fossils (*6, 12, 15, 18, 55–58*), although there are undoubtedly shared primitive characters, such as relatively larger brows and teeth compared with modern Europeans (*58–61*), and homoplasies found elsewhere, such as protruding occipital regions (*62, 63*). The African record is sparser and covers a much greater area, yet "intermediate" fossils have been recognized from sites such as Florisbad (South Africa), Ngaloba (Tanzania), Omo Kibish (Ethiopia), and Djebel Irhoud (Morocco). Here, at least, there is general agreement about regional continuity between earlier fossils and those of *Homo sapiens* (*6, 12–14, 18, 42, 43, 57, 64, 65*).

As predicted by the recent African origin model, early *Homo sapiens* fossils from Africa and western Eurasia are morphologically rather similar, when due allowance is made for the fact that the earliest European *Homo sapiens* fossils (such as those from Cro-Magnon, Stetten, and Mladeč) are younger than those from southwest Asia (Qafzeh and Skhūl) and Africa (Klasies, Omo-Kibish 1, Dar-es-Soltane 5, and perhaps Border Cave) (*6, 12, 13, 15, 57, 65*).

Furthermore, late Pleistocene North African *Homo sapiens* fossils combine local regional features with those found in early *Homo sapiens* samples in Eurasia, showing that many supposed regional features in Europe, Asia, and Australia were at that time part of the normal range of variation in African *Homo sapiens* (*62*). Some of the east Asian and Australian early *Homo sapiens* fossils (such as the Liujiang, Upper Cave Zhoukoudian, Mungo, and Keilor specimens) are also more similar to those of western Eurasia than might be expected from the multiregional evolution model (Fig. 1) (*6, 12, 13, 57, 66*). However, other Australian fossil evidence poses serious problems for both models through its high level of cranial variation, which appears to be larger than that observed for any other comparable area or time span (*8–10*).

The high variation displayed in late Pleistocene and early Holocene samples in Australia would not be expected at a periphery of the human range under the multiregional model, nor in early *Homo sapiens* fossils outside Africa under the recent African origin model. Furthermore, some of the fossil samples display supposed features of regional continuity while others do not. Most of the features claimed to link the Willandra Lakes WLH-50 and Kow Swamp hominids with Indonesian *Homo erectus* clearly also occur in early *Homo* or *Homo sapiens* fossils from elsewhere (*48, 67*), and there are also losses of Indonesian-derived characters which must be accounted for under the multiregional model (*41, 44, 68*). But even if the claimed regional characteristics are disregarded as irrelevant to the establishment of an Indonesian *Homo erectus*–Australian *Homo sapiens* lineage, there is still a remarkable Pleistocene cranial variation to be explained, with some Australian early *Homo sapiens* fossils looking decidedly more "archaic" than their counterparts from elsewhere.

In order to account for such variation, some proponents of the multiregional model have argued that two separate founding populations must have colonized Australia (*9, 10*). A relatively gracile group (for example, Mungo and Keilor) originated in Asia, whereas the more robust population (for example, some of the Kow Swamp specimens and WLH-50) derived from Indonesian *Homo erectus*. However, genetic data give no indication of the heterogeneity that would be expected in modern Australasians from such a model (*23–25, 29, 30, 34, 35, 38*). Distinct regional features are claimed to exist in the two groups, but there are no suggested mechanisms for maintaining such a long-term coexistence of separate Australian populations.

From the recent African origin model, the first Australasian *Homo sapiens* should have been no more archaic than Eurasian early *Homo sapiens*. If the Niah Cave (Borneo) and Mungo and Keilor fossils can be taken as representative of the first *Homo sapiens* in the area, this is indeed true. However, if accurate dating can establish that more robust populations were also present at an early date, this would need to be explained. Perhaps Australia was a special case where local differentiation, cultural practices, or pathologies led in some cases to apparent evolutionary reversals (*6, 49, 69*). Alternatively, the initial radiation of *Homo sapiens* from Africa may have been by populations which retained primitive characters in features such as frontal bone form and cranial robusticity, but this would require some parallelism in the subsequent loss of such primitive characters in areas apart from Australia. A third option would be to argue for more than one founding population for Eurasian *Homo sapiens*, but this would be inconsistent with genetic data, as well as again introducing further homoplasy into the recent African origin model.

Concluding Remarks

Our review of recent genetic evidence on evolutionary processes in human evolution favors the model of a recent African origin for *Homo sapiens*. Several geneticists who previously favored a primary "Eurafrican"-Asian split in human populations now favor an African-Eurasian split instead (*70*), and many different genetic systems illustrate the distinctiveness and greater internal diversity of sub-Saharan African populations. Under the assumption of selective neutrality and regularity of change, this must indicate a greater age for African *Homo sapiens* evolution. There is some evidence of unexpectedly large differentiation in certain non-African populations, but such exceptions are uncommon and offer no particular support to the alternative model of multiregional evolution. Although precise calibration of events in human evolution from genetic data is still problematic, variation in mitochondrial and nuclear DNA indicates a recent origin for *Homo sapiens* and gives no support to an antiquity for peripheral human populations on the order of 750,000 years ago, as would be required for an area such as Australasia under the multiregional model.

Paleontological data in the middle Pleistocene do not match with the expectations of the multiregional model, nor with extrapolations of modern genetic data back into the past. Although the recent African origin model does not provide any particular predictions for middle Pleistocene data, growing evidence of an early appearance of *Homo sapiens* during the late Pleistocene in Africa and the Levant, coupled with a late persistence of Neanderthals in western Europe, provide excellent support for it. Evidence that *Homo sapiens* was present in the Levant before an appearance in more peripheral areas of Eurasia is also consistent with a dispersal event from Africa by way of southwest Asia. Arguments continue about the extent of gene flow between *Homo sapiens* and other forms of *Homo*, but it is possible that these will be settled from more genetic data rather than through the fossil record. This is particularly the case in the Far East and Australasia, where the sparse fossil record from the early part of the late Pleistocene prevents a resolution of arguments about local continuity, compounded by the confusing diversity of late Pleistocene Australasians. The fact that "colonization" events in Europe and Australasia can be calibrated at about the same antiquity from the genetic evidence might be taken to support either an early Pleistocene dispersal (multiregional model) or a late Pleistocene one (recent African origin). However, there is growing evidence for a recent replacement event in western Eurasia, and the considerable genetic similarities of European and Australasian populations in several recent studies also indicate a closer evolutionary relationship than would be expected through common ancestry and continuing gene flow over more than 500,000 years and 12,000 kilometers under Pleistocene conditions (*71*).

Although we feel that an African origin for *Homo sapiens* is highly probable, the exact time, place and mode of origin of the species cannot yet be determined. The presence of *Homo sapiens* fossils in the early part of the late Pleistocene at both the southern tip of Africa (*51*) and in the Levant (*52*) means that a southern African origin as recent as 100,000 years ago is unlikely. The origin of the species must have been more ancient, and, as we have seen, plausible precursor populations are sampled at sites in northern, eastern, and southern Africa. Given the recently determined age of the Qafzeh *Homo sapiens* fossils (*52*), even the adjacent area of the Levant cannot be excluded as a possible source area for *Homo sapiens*. However, it appears that only the genetic divergence and diversity of sub-Saharan African populations now reflect an age appropriate for the species origin, presumably because areas of northern Africa and the Levant have been exposed to extensive subsequent gene flow from Eurasian populations, particularly in historic times.

In the next decade we will see important developments in the study of the origins of modern human variation. We can expect significant discoveries of fossil hominids to continue, and these are particularly required from the early late Pleistocene of the Far East and Australasia. Further study of the existing fossil and archeological records will provide new hypotheses about modern human origins that can be tested by future discoveries and the growing body of genetic data. New dating techniques may be developed that will help to calibrate events in human evolution more accurately, and radiocarbon accelerator dating should become a standard technique for directly dating the appearance of *Homo sapiens* in the fossil record of areas colonized during the last 50,000 years. Finally, we can expect a great deal of new genetic data, and much discussion on how best to analyze these and make them relevant to the subject of the origin of *Homo sapiens*. Improved communication between paleoanthropologists and geneticists should allow researchers in the latter field to make an increasingly important contribution to debate about our origins. As has proved to be the case in the study of hominid origins, paleoanthropologists who ignore the increasing wealth of genetic data on human population relationships will do so at their peril.

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