

- human bipedalism. In Corruccini RS, Ciochon RL (eds), *Integrative Paths to the Past: Paleontological Advances in Honor of F. Clark Howell*, pp 269–284. Englewood Cliffs: Prentice Hall.
- 30 Sutherland DH, Olshen R, Cooper L, Woo SLY (1980) The development of mature gait. *J Bone Joint Surg* 62A:336–353.
- 31 Steudel K (n.d.) Limb morphology, bipedal gait and the energetics of hominid locomotion. *Am J Phys Anthropol*, in press.
- 32 Cavagna GA, Heglund NC, Taylor CR (1977) Mechanical work in terrestrial locomotion: Two basic mechanisms for minimizing energy expenditure. *Am J Physiol* 233:R243–R261.
- 33 Lovejoy CO (1981) The origin of man. *Science* 211:2441–2450.
- 34 Stern JT Jr, Susman RL (1983) The locomotor anatomy of *Australopithecus afarensis*. *Am J Phys Anthropol* 60:279–317.
- 35 Janis CM, Wilhelm PB (1993) Were there mammalian pursuit predators in the Tertiary? Dances with wolf avatars. *J Mammal Evol* 1:103–125.
- 36 Klein DR, Meldgaard M, Fancy SG (1987) Factors determining leg length in *Rangifer tarandus*. *J Mammal* 68:642–655.
- 37 Jungers WL (1982) Lucy's limbs: Skeletal allometry and locomotion in *Australopithecus afarensis*. *Nature* 297:676–678.
- 38 Wolpoff MH (1983) Lucy's little legs. *J Hum Evol* 12:443–453.
- 39 Steudel K, Beattie J (n.d.) Does limb length predict the energetic cost of locomotion in mammals? *J Zool* (London), in press.
- 40 Cavanagh PR, Williams KR (1982) The effect of stride length variation on oxygen uptake during distance running. *Med Sci Sports Exer* 14:30–35.
- 41 Cotes JE, Meade F (1960) The energy expenditure and mechanical energy demand in walking. *Ergonomics* 3:97–120.
- 42 Harris M, Steudel K (1993) Hindlimb length correlates in the Carnivora. *Am Zool* 33:74A.
- 43 Garland T Jr, Janis CM (1993) Does metatarsal/femur ratio predict maximal running speed in cursorial mammals? *J Zool* (London) 229:133–151.
- 44 Tsuji JS, Huey RB, Van Berkum FH, Garland T Jr, Shaw RG (1989) Locomotor performance of hatchling fence lizards (*Sceloporus occidentalis*): Quantitative genetics and morphometric correlates. *Evol Ecol* 3:240–252.
- 45 Garland T Jr (1985) Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *amphibolurus nuchalis*. *J Zool* (London) 207:425–439.
- 46 Losos JB (1990) The evolution of form and function: Morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution* 44:1189–1203.
- 47 Garland T Jr (1984) Physiological correlates of locomotor performance in a lizard: An allometric approach. *Am J Physiol* 247:R806–R815.
- 48 Cowan IR, Farquhar GD (1977) Stomatal function in relation to leaf metabolism and environment. *Symp Soc Exp Biol* 31:471–505.
- 49 McHenry HM (1991) Sexual dimorphism in *Australopithecus afarensis*. *J Hum Evol* 20:21–32.
- 50 Post DG (1980) Sexual dimorphism in the anthropoid primates: Some thoughts on causes, correlates, and the relationship to body size, unpublished manuscript.
- 51 Day MH (1977) Locomotor adaptations in man. *Biol Hum Affairs* 42:149–151.
- 52 Ravey M (1978) Bipedalism: An early warning system for Miocene hominoids. *Science* 199:372.
- 53 Wheeler PE (1984) The evolution of bipedality and loss of functional body hair in hominids. *J Hum Evol* 13:91–98.
- 54 Du Brul EL (1962) The general phenomenon of bipedalism. *Am Zool* 2:205–208.
- 55 Jolly CJ (1970) The seed-eaters: A new model of hominid differentiation based on a baboon analogy. *Man* 5:1–26.
- 56 Sinclair ARE, Leakey MD, Norton-Griffiths M (1987) Migration and hominid bipedalism. *Nature* 325:307–308.

© 1994 Wiley-Liss, Inc.

Multiple Dispersals and Modern Human Origins

MARTA MIRAZON LAHR and ROBERT FOLEY

Despite a massive endeavour, the problem of modern human origins not only remains unresolved, but is usually reduced to "Out of Africa" versus multiregional evolution. Not all would agree, but evidence for a single recent origin is accumulating. Here, we want to go beyond this debate and explore within the "Out of Africa" framework an issue that has not been fully addressed: the mechanism by which modern human diversity has developed. We believe there is no clear rubicon of modern *Homo sapiens*, and that multiple dispersals occurred from a morphologically variable population in Africa. Pre-existing African diversity is thus crucial to the way human diversity developed outside Africa. The pattern of diversity—behavioural, linguistic, morphological and genetic—can be interpreted as the result of dispersals, colonisation, differentiation and subsequent dispersals overlaid on former population ranges. The first dispersals would have originated in Africa from where two different geographical routes were possible, one through Ethiopia/Arabia towards South Asia, and one through North Africa/Middle East towards Eurasia.

A model of multiregional evolution was the first comprehensive theory of the evolution of modern humans from their hominid ancestors. Multiregional evolution in the Pleistocene explains both the origins of modern

humans and subsequent regional diversity as resulting from the transformation of archaic hominid groups into modern populations in each part of the world. Modern human features have been superimposed on pre-exist-

ing regional ones. Weidenreich,¹ who first proposed the theory of multiregional evolution, explained regional differences in morphology between modern groups like Asians and Australians as resulting from relatively independent evolution from *Sinanthropus* and *Pithecanthropus*. The early multiregional models suffered from the lack of a mechanism for the maintenance of worldwide parallelisms.^{1,2}

Marta Mirazon Lahr is a fellow of Clare College, Cambridge. Her research focuses on modern human origins and subsequent differentiation. Robert Foley is Director of the Duckworth Laboratory at the University of Cambridge and a Fellow of King's College. He has carried out research into the evolutionary biology of fossil hominids, and he is the author of *Another Unique Species* as well as editor of several books.

Key words: Hominid, colonization, evolution, population diversity

Recently however, Wolpoff and others³⁻⁵ have proposed a modified version of this earlier theory in which gene flow takes a major role. Accordingly, the multiregional model proposes that each modern human regional population arose from archaic regional inhabitants, and that a balance between gene flow and isolation allowed regional differentiation without speciation and the maintenance of grade similarities worldwide.

The "Out of Africa" model is more recent. It is based on fossil evidence for an earlier appearance of modern humans in Africa than elsewhere. Howells⁶ proposed the idea of a single and recent origin as the "Noah's Ark" model. This hypothesis has been elaborated in the last few years by several researchers.⁷⁻¹⁰ This model highlights the discontinuity in the fossil record, suggesting a recent localized origin in Africa, followed by geographical expansion and replacement of archaic populations.

THE EVIDENCE FOR THE ORIGINS OF MODERN HUMANS

In recent years, the application of new dating techniques like electron spin resonance and thermoluminescence to Upper Pleistocene fossils has had a revolutionary effect on late hominid chronology.¹¹⁻¹³ These techniques, which date beyond the range of ¹⁴C, have proven three significant points: that hominids with a modern morphology occurred in the Middle East around 100 ky ago;¹⁴⁻¹⁶ that relatively gracile moderns lived in Africa around 70 ky ago;¹⁷ and that Neanderthal remains in Europe and the Middle East date to 60 to 40 ky ago, postdating early modern forms.^{11,18} Furthermore, the remains from Klasies River Mouth (KRM) in South Africa, presenting a variable but modern morphology,¹⁹ are firmly associated with early last interglacial levels, and therefore are 120/100 ky old.^{20,21}

This new chronology has also affected the archeological record. Now it is known that technologies based on the production of blades appear relatively late in the record, some 60,000 years after the appearance of morphologically modern people, although there is some evidence of more complex behavior in a Middle Stone Age

tradition (the Howieson's Poort) between 85 and 60 ky in South Africa.²²⁻²⁴ The first archeological assemblages that present blade tools are found around the Mediterranean.²⁵ In North Africa, there is evidence of a pre-Aurignacian tradition,²⁶ while early upper Paleolithic assemblages have been identified in Boker Tachtit, Israel, and Ksar Akil, Lebanon, between 47 and 38 ky ago.^{27,28} The Aurignacian seems to have spread rapidly through Europe as seen at 43 kya in Bulgaria (Bacho Kiro)²⁹ and at 40 kya in Spain (L'Abreda, El Castillo).³⁰⁻³² Associated with this geographical expansion process of Aurignacian peoples through Europe, the terminal Neanderthal industries, including the Chatelperronian, Szeletian, and Uluzzian, have been interpreted as the result of an acculturation process.^{33,34}

To the fossil and archeological record, the molecular evidence should be added. In 1987, Cann and co-workers obtained a phylogenetic tree based on mtDNA in which one branch led solely to Africans and the other branch to Africans and other populations.³⁶ This tree reflected the fact that Africans present the greatest diversity of mtDNA lineages. This could be explained either by a faster rate of mutations in Africans than in the rest of the world or by a longer time during which mutational differences accumulated in this group. Given the lack of evidence from other sources of a faster mutation rate in Africans, the authors deduced that the evolution of modern humans started in Africa and then expanded to the rest of the world.

Since these results were first published, further research has both reinforced and undermined this conclusion. On the one hand, research on the mtDNA diversity of localized groups like the San and Papuans has thrown light on the levels of diversification of recent people.^{36,37} In addition, mounting nuclear genetic evidence points strongly to an African origin of all modern groups.³⁸⁻⁴⁰ On the other hand, Maddison⁴¹ and Templeton⁴² have shown that the statistical procedures for rooting the mtDNA phylogenetic tree and the statistical significance of the single African branch were incorrect. These technical problems are a major drawback in

the technique. Indeed, it apparently is impossible at the moment to prove statistically the branching pattern of mtDNA lineages. However, contrary to what has been claimed,⁴³ these problems do not completely discredit the genetic evidence. The great diversity of African mtDNA lineages remains unchallenged.⁴⁴

Recently, Rogers and Jorde challenged the notion that greatest diversity equates with greatest age and provided an explanation in terms of paleodemography.⁴⁵ They conclude that the mtDNA diversity patterns reflect the fact that Africa held a larger population than other regions throughout the period. Taking these demographic parameters into account, Harpending finds, through pairwise comparisons (mismatch distributions), that there is evidence of a leading wave signal in African samples, suggesting that Africa may have been the source of dispersal of modern humans.⁴⁶ Although it is clear that the mitochondrial data cannot be interpreted as tightly as the original "Eve hypothesis" proposed, the nuclear DNA evidence is increasingly robust and the genetic evidence, overall, strongly supports a recent African origin of modern people.⁴⁷

The evolutionary interpretations of the genetic evidence have been in such extraordinary agreement with the "Out of Africa" model that the two concepts have been interlaced. It is often mistakenly assumed that the main evidence for a single origin of modern humans is genetic and not morphological or chronological. The conclusion that the available evidence strongly supports a recent, single African origin of modern people must follow if one takes into account the following points: the earliest modern people are found in Africa or the Middle East some 60,000 years before they appear in other regions;⁸ different hominids overlap in time and space in the Middle East, Europe, and, probably, East Asia;¹¹ the archeological evidence in Europe points to a distinct replacement of local traditions;^{34,48} the nuclear and mtDNA evidence indicates an African ancestry of all modern humans;³⁸ and there is an apparently strong correlation between recent linguistic differentiation

and genetic differentiation.⁴⁹ In spite of all this, however, if morphological continuity from regional archaic hominids to modern regional populations can indeed be observed in the fossil record, there will still be evidence that multiregional evolution took place.

TESTING THE MODELS

The Multiregional Hypothesis

The basis for the Multiregional model is that we can observe unique regional patterns of morphological continuity across the transition from archaic to modern forms of hominids.^{4,5} This interpretation of continuity makes two assumptions: that such features are indeed regional markers; and that they are not functionally determined.

Three recent studies have independently tackled the problem of regional morphological continuity.^{50–52} Two of these dealt with the regional distribution of features identified as presenting continuity through time among worldwide archaic populations, and therefore, tested their uniquely Asian and Southeast Asian character in the past.^{50,51} The authors of both studies found that these features were common in *Homo erectus* and “archaic” *Homo sapiens* fossils throughout the world, but reached somewhat different conclusions about their role in proving continuity. On the basis of their plesiomorphic character, Groves concluded that these features should not be used as evidence of phylogenetic relationships.⁵⁰ On the other hand, Habgood considered that the combined occurrence of features like supraorbital tori and zygomaxillary tuberosities in Javanese *H. erectus* and Australian aborigines can be used as evidence of morphological continuity.⁵¹ In the third study, Lahr dealt with the regional distribution of features of continuity in recent populations and their relationship to metrical parameters of the skull, testing their uniquely Asian and Australian character in the present and the independence of that character from developmental processes.⁵² Lahr found that of the thirty so-called Asiatic regional traits, twenty-one did indeed have a significant incidence in a particular region of the world. However, only ten of these

traits actually occurred in the geographical area conventionally associated with them. In other words, the regional traits fail to characterize East Asians and, in Australians, do so only in terms of robusticity.^{52,53} Furthermore, this work showed that the development of characteristics such as pronounced tori and ridges occurs regardless of geographical region among both modern and prehistoric populations with large cranial and dental dimensions. Another finding, that the development of a number of facial features depends on the presence of large supraorbital ridges,^{52,53} is particularly relevant in the light of Habgood’s conclusions regarding the combined oc-

A consistent mechanism for the world expansion of modern humans from their original African source has not been proposed. In this regard, the “Out of Africa” model lacks sufficient specificity to account for the regional patterns of modern human diversity and the specifics of both morphological and behavioral evolution over the last 100,000 years.

currence of features of robusticity, which Lahr showed instead to be correlated with each other. The implication is that traits that have been claimed to show links between, for example, Javanese *Homo erectus* and Australian aborigines, are, in fact, evidence of the link between modern Australians and a robust modern ancestor anywhere in the world. The only conclusion to be drawn is that the morphological evidence does not support

a multiregional model of modern human origins.

Two other lines of evidence related to the mechanisms of multiregional evolution also refute the basis of the multiregional model. One, a survey of the fossil evidence of subspeciation in animals with a wide geographical distribution, has shown that multiregional evolution as a mechanism is undocumented except, possibly, in the Javanese rhinoceros, and that the common pattern observed is one of interspecific or intraspecific replacement.⁵⁴ Second, recent assessments by Harpending and co-workers of the demographic density of *Homo erectus* populations suggest that these populations never achieved the critical size to maintain the levels of gene flow necessary for multiregional evolution to occur.^{45,46}

Besides the chronology of the fossils and the genetic evidence for a single origin of modern people, these studies show that the multiregional hypothesis is based on incorrect premises of morphological continuity and demographic patterns. In addition, the recent dating of some of the *H. erectus* fossils of Java⁵⁶ takes the original expansion of *Homo erectus* (and, according to the multiregional model, the origin of regional differentiation) to around 1.8 MA. This early date is far outside of even the most generous confidence limits for the origin of modern mtDNA lineages.

The “Out of Africa” Model

If the basis of the Multiregional model can be discredited, can the “Out of Africa” model be taken as the best explanation for the origins of modern humans? The lines of evidence in support of that model, in terms of the continuity in form from archaic to modern fossils in Africa,¹⁰ the discrepancy between the dates in African/Levantine modern humans and elsewhere, and the genetic data, are all compatible. However, there still are problems with this hypothesis. Those problems relate less to contradictory evidence than to the lack of specificity in both the model and the data. The model has three components, which, to some extent, can be treated independently: a single origin in Africa; a pattern of total replacement involving

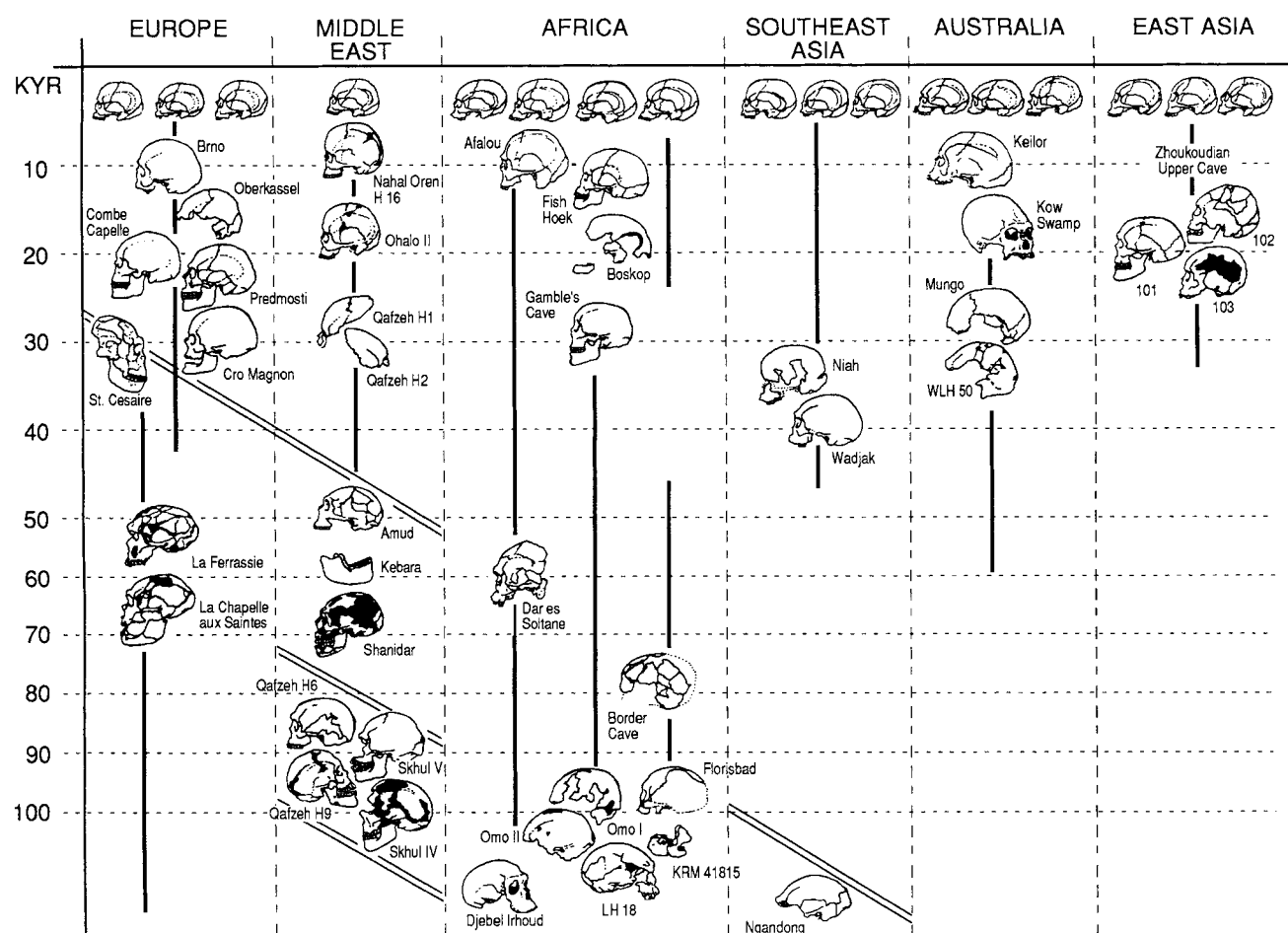


Figure 1. Spatial and temporal distribution of important human fossils in the Upper Pleistocene, together with a representation of present regional cranial variation. Continuous lines represent prehistoric occupation; diagonal double lines represent taxonomic distinctions within a region.

no admixture with other hominid populations; and a mechanism of dispersal across the world. Although current evidence supports a single African origin, the problem of replacement versus admixture remains a major issue. Moreover, a consistent mechanism for the world expansion of modern humans from their original African source has not been proposed. In this regard, the "Out of Africa" model lacks sufficient specificity to account for the regional patterns of modern human diversity and the specifics of both morphological and behavioral evolution over the last 100,000 years.

These problems highlight the need to develop more precise ideas about the origins of diversity. A theory of modern human origins has to be able to explain not only the appearance of modern people, but the origin of the diversity of modern populations.

THE EVIDENCE FOR THE ORIGINS OF HUMAN DIVERSITY

Human diversity refers to the biological and technological differences among modern populations today and in the recent past. Although many people consider the biological diversity of present-day humans to be vast, genetic studies show that it is very limited when compared to that of chimpanzees.⁵⁶⁻⁵⁹ Modern humans are in fact an extraordinarily homogeneous species.⁴⁵ Nevertheless, differences in their morphology, genetics, and archeology are apparent for as long as there is evidence of modern people. It is the evolutionary origin of these differences from a recent common ancestor that we seek to explore. It is clear, and must be stressed, that there has been interbreeding between modern groups throughout the period, and that gene flow was one mechanism of change, although some

subdivision of gene pools must have occurred in order for populations to have acquired and established their differences.

In order to investigate the origins of diversity, three points should be taken into account: first, that only scant evidence is available for the first part of the period; second, that at the point at which there is a record of modern people in various parts of the world, these populations are already different from each other; and third, that diversity increases with time, i.e., people become increasingly more different between wide geographical distances. Therefore, two sets of evidence are important, the patterns of diversity among the first occupants of each region for which there are records and the subsequent pattern of differentiation of each of these groups. Moreover, any theoretical model that attempts to explain the evolutionary process that

created this diversity has to encompass a mechanism that would explain how modern people appeared in various regions, how these peoples acquired their early differentiation, and how they expanded and differentiated to produce modern levels of diversity. Clearly, the available data are not sufficient to answer all the relevant questions, especially those pertaining to differentiation. However, enough evidence has accumulated from diverse disciplines and groups of scholars to give us insight into how this process might have occurred.

The Modern Regional Populations

The point of origin of modern humans within Africa is unclear, but a case can be made for East Africa on the grounds that the earliest transitional forms (Omo) are found there.¹⁰ Furthermore, East Africa, with its diverse habitat and potential for isolation, has been a major source of evolutionary novelty.⁶⁰ Geographical expansion probably led to the early differentiation of populations, as is suggested by the diversity of Middle Stone Age traditions.^{61,62} The early modern fossils of Skhul and Qafzeh in the Middle East should be considered as an extension of North African populations, for they are accompanied by African faunas, at least in Qafzeh,⁶³ and do not seem to have expanded any further at this time.⁶⁴ Outside Africa, modern humans appeared at different regions at different times,¹³ first in Australia and Asia, then later in Europe. Although this may be partly an artifact of a poor fossil record, some of these temporal patterns have remained relatively stable as new dates have been obtained in the last few years.

The evidence from different regions of the world after the appearance of modern humans is highly variable, both spatially and temporally, but vast (Fig. 1). We do not presume to cover it here, but we will outline certain chronological, morphological, and archeological aspects that are relevant to the process of diversification of peoples.

Africa

About 100 ky ago, there were modern humans in East Africa (Omo),⁹

North Africa/Middle East (Skhul, Qafzeh),⁶⁵ and South Africa.^{66,67} In North Africa, the early moderns may have remained restricted to the area for a long period. There is no evidence supporting further expansion from the Middle East at this stage. In addition, biogeographic data show a movement of Palearctic faunas in the Levant between Stages 5 and 4 (70–60 ky).⁶⁴ It is possible that descendants of this early modern population developed the Aterian Middle Palaeolithic industry in North Africa, which shows certain derived characteristics.^{68,69}

It is not yet possible to determine whether the Southeast Asian population around 40 ky ago is the result of long-term differentiation of people present in the area for 20 to 30 ky, represents part of the widespread expansion of peoples from North Africa or the Middle East after 45,000 years ago, or a mixture of both. The evidence suggests that the first hypothesis is correct.

There is climatic,^{70,71} faunal, and archeological⁷² evidence of biogeographic movements across the Sahara around 50 ky ago. The lack of substantial fossil material from this time in this area precludes interpretations of the effect of gene flow from sub-Saharan Africa on North African populations, which eventually developed into the robust Mesolithic groups of Afalou, Taforalt, and Mechta.⁷³ In sub-Saharan Africa, the evidence after the first modern fossils, (Omo, KRM, Border Cave) is scant.

In South Africa, there is continuity

of Middle Stone Age traditions until around 40 ky, after which date the area seems to have been essentially uninhabited until the Late Stone Age around 20 ky.⁴⁸ Genetic mtDNA and Y-chromosome studies have shown that the San and Pygmies are distinct, which suggests their early differentiation from other populations.^{36,74,75} The main characteristic of these groups was a trend toward extreme gracilization. It is possible that this small body size adaptation allowed later colonization of the rainforests of western Africa. The close linguistic and genetic affinities of east and southern African hunter-gatherer populations⁷⁶ may be the result of subsequent movements. Within Africa, and superimposed on the early population patterns, are the recent expansions of farming communities, speakers of the Niger-Kordofanian languages, and from western Asia to North Africa, speakers of the Afro-Asiatic languages.

Australia and Island Melanesia

The first record of people in Australia is archeological. Roberts and colleagues recently obtained artifacts showing a relatively unsophisticated stone tool technology based on flakes dated to around 60 ky.^{78,79} This technology, together with elaborate bone tools and art, characterized most of the subsequent Australian prehistory.⁸⁰ Around 40 ky ago, the number and geographical distribution of archeological sites in Australia increased sharply. At this moment, it is not known whether there was continuous occupation from 60 ky with a demographic expansion around 40 ky, or whether the large number of sites at 40 ky reflects a flow of people into Australia from outside. The archeological data suggest that Australian populations remained relatively isolated until very recent times, when microlithic tools and the dingo were introduced.⁸⁰ The first fossil evidence in Australia was found in the southeast, at the sites of Mungo and the Willandra Lakes system.^{81,82} These fossils show remarkable variation in relation to the level of robusticity they present, the crania ranging from very gracile to more robusticity than most modern ones, past or present.⁸³ They

also show morphological features that clearly link them to recent Australian aborigines.^{84,85} Most craniometric studies show the Australo-Melanesian population as that most closely related to African groups.^{85–88} Therefore, a pattern of early colonization followed by relative isolation may be represented in Melanesia by the level of differences in mtDNA lineages among Papuan tribes³⁶ and of the comparatively high incidence of plesiomorphic archeological⁸⁹ and skeletal⁵² traits.

Eastern Asia

In eastern Asia, the archeological and paleontological record for the first half of the Upper Pleistocene is very poor. The first fossil evidence of modern people in Southeast Asia dates to around 40 ky ago (Niah, Wadjak, Tabon).⁹⁰ The Southeast Asian population of the late Pleistocene and its modern descendants can be identified cranially⁹¹ and dentally (Sundadonts).⁹² The range of this population reached beyond Southeast Asia into southern China, Japan (then connected to the mainland), and eventually Polynesia.^{93,94} In eastern Asia, the best known early modern fossils are those of Zhoukoudian Upper Cave. These fossils were first described as showing such variation as to resemble three different populations, Chinese, Eskimo, and Melanesian.⁹⁵ Recent northeastern Asians show a derived morphology, represented by the "Mongoloid" features of facial flatness and Sinodonty.^{93,94,96–98} Turner has recognized Sinodont characteristics in the Upper Cave Zhoukoudian remains.⁹⁹ However, other authors have found that these fossils are not closely related to recent Asians,¹⁰⁰ which implies a relatively late appearance of the typical Mongoloid morphology. Holocene human remains with Mongoloid features are found in a wide area, from Eastern Siberia (where Turner identified a sharp east-west boundary in the incidence of Sinodonty in the region of Lake Baikal⁹⁹), Mongolia, Korea, Japan, and the Americas. In Japan, the prehistoric Jomonese and recent Ainu, who show Sundadonty⁹⁹ and are cranially isolated from recent Japanese and Chinese,^{91,96,97} must be survivors of the population before the Sinodont expansion.

It is not known how the Southeast Asian population represented by fossils like Niah and Tabon relates to the earliest Southeast Asian population from which Australians and New Guineans derive. It is not yet possible to determine whether the Southeast Asian population around 40 ky ago is the result of long-term differentiation of people present in the area for 20 to 30 ky, represents part of the widespread expansion of peoples from North Africa or the Middle East after 45,000 years ago, or a mixture of both.

We propose a model to explain the diversity and disparity of the paleoanthropological data in the Upper Pleistocene based on the concept of geographical expansions and dispersals. This model is based on a single-origin hypothesis, followed by multiple dispersals out of Africa through two rather independent routes, then subsequent expansions and dispersals from secondary geographical sources.

The evidence suggests that the first hypothesis is correct: current Southeast Asian populations are closer, both genetically³⁸ and archeologically,⁸⁹ to Australo-Melanesians than either is to Eurasians and Indians. Turner has proposed that East Asians derive from a southeast Asian source.⁹³ Cranial,^{84,85,91,96–98,101–103} dental,⁹² archeological,⁸⁹ and mtDNA¹⁰⁴ evidence further suggest that Southeast, East, and Northeast Asians are closely related, presenting a tight Mongoloid complex independent of Eurasia and

India. However, nuclear genetic studies by Cavalli-Sforza¹⁰⁵ show that Northeast Asian (Japanese, Korean, Mongolian) and Amerindian populations are closer to Eurasians than to southern Chinese and Southeast Asians. A possible explanation for these differences is that the nuclear genetic patterns reflect invasions into northeastern Asia by Siberian peoples of Eurasian origin, either in the late Pleistocene, as indicated by archeological evidence,^{106–110} or recently by peoples speaking the Altaic languages.⁷⁷

There is also the question of Amerindian affinities. If the Americas were colonized early (40 to 20 kya^{111–113}), the first inhabitants would have been derived from the less specialized Asian populations, whereas if they were colonized late (15 to 10 kya¹¹⁴), the first inhabitants would have been derived from relatively specialized East Asian groups. Evidence of a more robust and less specialized Asian morphology within the Americas has been suggested for Holocene remains^{115,116} and for marginal native American groups (Fueguians, Patagonians).¹¹⁷ On the other hand, Turner's finding that all Amerindian remains present a homogeneous Sinodont dental pattern⁹⁶ supports a recent migration into the New World (although his sample does not include southernmost South American groups). This hypothesis has been supported by genetic and linguistic data.¹¹⁴ However, other genetic evidence shows that the timing and source of Amerindian differentiation is still unclear.¹¹⁸

Northern, Southern, and Western Asia

This area is not a unit in biogeographical terms. The area of the Middle East was at times an extension of African faunal distributions and at other times an extension of Eurasian ones.⁶⁴ The population history of the Middle East is complex. After the first appearance of modern humans in the last interglacial, the area was occupied by an archaic population with European Neanderthal affinities (Kebara, Amud).¹¹⁹ Technologically, there is no clear distinction between the early modern and archaic populations; both are accompanied by Middle Paleolithic industries. Between 50–40 ky,

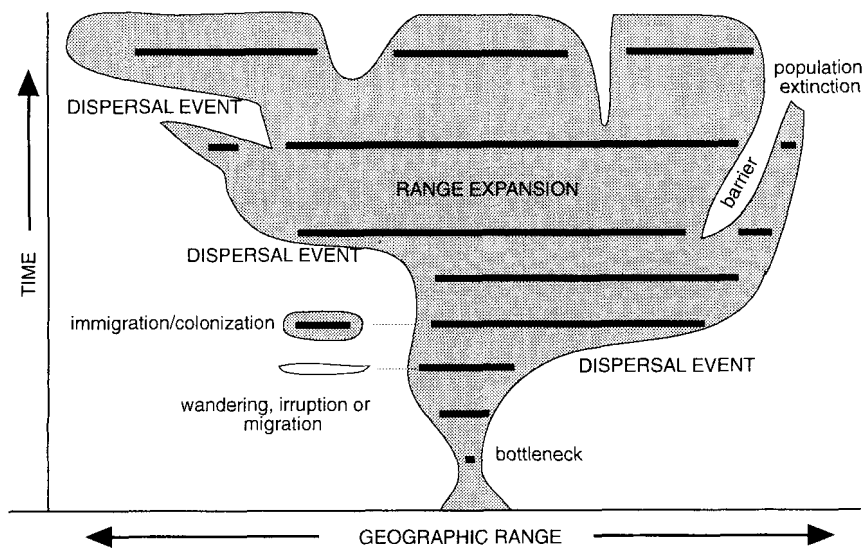


Figure 2. Schematic representation of the geographical expansion of a species through time, showing localized origins, unsuccessful events, successful dispersal events, population isolation through the development of barriers, and superimposition of later dispersal events on the range of previous expansions. Adapted from Tchernov.¹³⁰

the first technologies recognized as early Upper Paleolithic are found at Boker Tachtit and Ksar Akil, the latter associated with a modern human skeleton.^{27,28} The subsequent pattern in the Middle East is one of continuity, from a robust modern Upper Paleolithic population (Qafzeh I and II, Ohalo), to the Natufian pre-agriculturalists, to the first Neolithic farmers.

The paleoanthropology of the last 100 ky in the Indian subcontinent is virtually unknown. The first evidence of modern humans is found relatively late (28 ky) in Sri Lanka,²⁰ and most probably is not representative of the first population that occupied the area. This skeleton is accompanied by a stone tool industry similar to that of the European Upper Paleolithic.

In Northern Asian and Siberia, the archeological record indicates a date of first occupation between 35 and 20 ky by modern people manufacturing Upper Paleolithic-like stone tools.^{48,121}

Europe

During most of the Upper Pleistocene, Europe was occupied by a Neanderthal population. The last known Neanderthals in Europe are those of St. Césaire in France (36 ky)¹²² and Zafarraya in Spain.¹²³ European Neanderthals were typically associated with Mousterian industries.³⁴ In St. Césaire and other similarly late sites,

the technology is Chatelperronian,¹²⁴ a Middle Paleolithic industry with elements similar to the Upper Paleolithic. Once considered as evidence of technological continuity between Neanderthals and modern humans in Europe, the Chatelperronian, being contemporaneous with the earliest Aurignacian sites, is currently interpreted as resulting from acculturation.^{33,34} Similar interpretations apply to industries like the Szeletian of Eastern Europe or the Ulluzzian of Italy. The first evidence of modern humans in Europe is mainly archeological, and is related to the spread of Aurignacian sites. The majority of cases of Upper Paleolithic fossils date to later periods and are accompanied by subsequent industries. These populations were robust and had larger crania¹²⁵ than more recent people, and, in many cases, were distinct from recent Europeans.^{126,127}

Superimposed on these paleolithic populations are the dispersals of agriculture-related peoples in the early Holocene.¹²⁸ Modern Europeans are cranially the most homogeneous of regional human populations.⁵² If the model proposed by Renfrew is correct, and these agriculturalists brought with them a branch of the Indo-European family of languages,⁷⁷ then the Basques and Lapps must represent surviving Palaeolithic groups.¹²⁸

Multiple Dispersals as a Model for the Origins of Human Diversity

These patterns of differentiation suggest that modern populations changed at different rates during the Upper Pleistocene, depending on levels of gene flow and demographic pressures, and that geographical dispersal and expansion were main components of the process of differentiation. The "Out of Africa" model implies that it is dispersal beyond Africa that is critical. This ignores two things: the first is that because Africa itself is more than one third of the habitable Old World, dispersals within Africa are equally important; the second is that dispersal and divergence within Africa would lead to variable populations leaving Africa at different times and possibly by different routes. This means that the levels of differentiation in the populations colonizing the other continents were probably already high.

Beyond the original routes out of Africa, the data also point to a complex process of population differentiation involving the incomplete superimposition of dispersing populations on previously existing ones. In morphological terms, the temporal and spatial variation in the presence of common features suggests that modern humans differentiated, acquiring and losing traits in a stepwise manner, reducing at each step the communality of modern cranial traits.⁵² The archeological remains also show uneven development of technologies during the Upper Pleistocene and the appearance of technological innovations at particular temporal and geographic points, suggesting a generally localized process of differentiation. Further, the genetic data available from contemporaneous populations show that degrees of differentiation and admixture vary markedly, some populations being the result of very recent expansions and differentiation and others being the result of previous expansions that may or may not have come into recent contact with other populations.⁴⁴ Therefore, the evolutionary origin of present populations may be extraordinarily varied. At this point, however, the evidence is only tentative. In east-

ern Asian and Australia, for example, we may be sampling three populations that resulted from three distinct dispersals. A population like the Australians may be the descendant of a group who left Africa between 100 and 60 ky, and hence present a high degree of morphological continuity with early and more robust moderns. A population like the Southeast Asians may be the result of long-term tropical differentiation in the area and geographical expansion. Differing amounts of gene flow, together with the effects of the break-up of the Sunda land mass, could account for the varying levels of distinctness of groups like the Andaman Islanders, Philipinos, and others. A population like the present east Asians may be the result of a relatively recent adaptation, having undergone its own geographical expansion that included the Americas. Therefore, it is possible to see differentiation followed by population growth and dispersal as the mechanism of expansion of modern humans out of Africa and as the mechanism of development of subsequent regional populations.

THE MULTIPLE DISPERSALS MODEL

We have seen that the morphological basis of the multiregional model is incorrect. That fact, together with the chronological, archeological, and genetic evidence, indicates that the alternative single-origin explanation is more compatible with the available data. However, we have also seen that although the "Out of Africa" hypothesis explains the origins of modern humans from an archaic source, the model lacks a mechanism to explain the origins of human diversity. We propose a model to explain the diversity and disparity of the paleoanthropological data in the Upper Pleistocene based on the concept of geographical expansions and dispersals. This model is based on a single-origin hypothesis, followed by multiple dispersals out of Africa through two rather independent routes, then subsequent expansions and dispersals from secondary geographical sources.

A Mechanism: Dispersals and Evolutionary Change

Biogeographical comparisons suggest that the appearance of evolution-

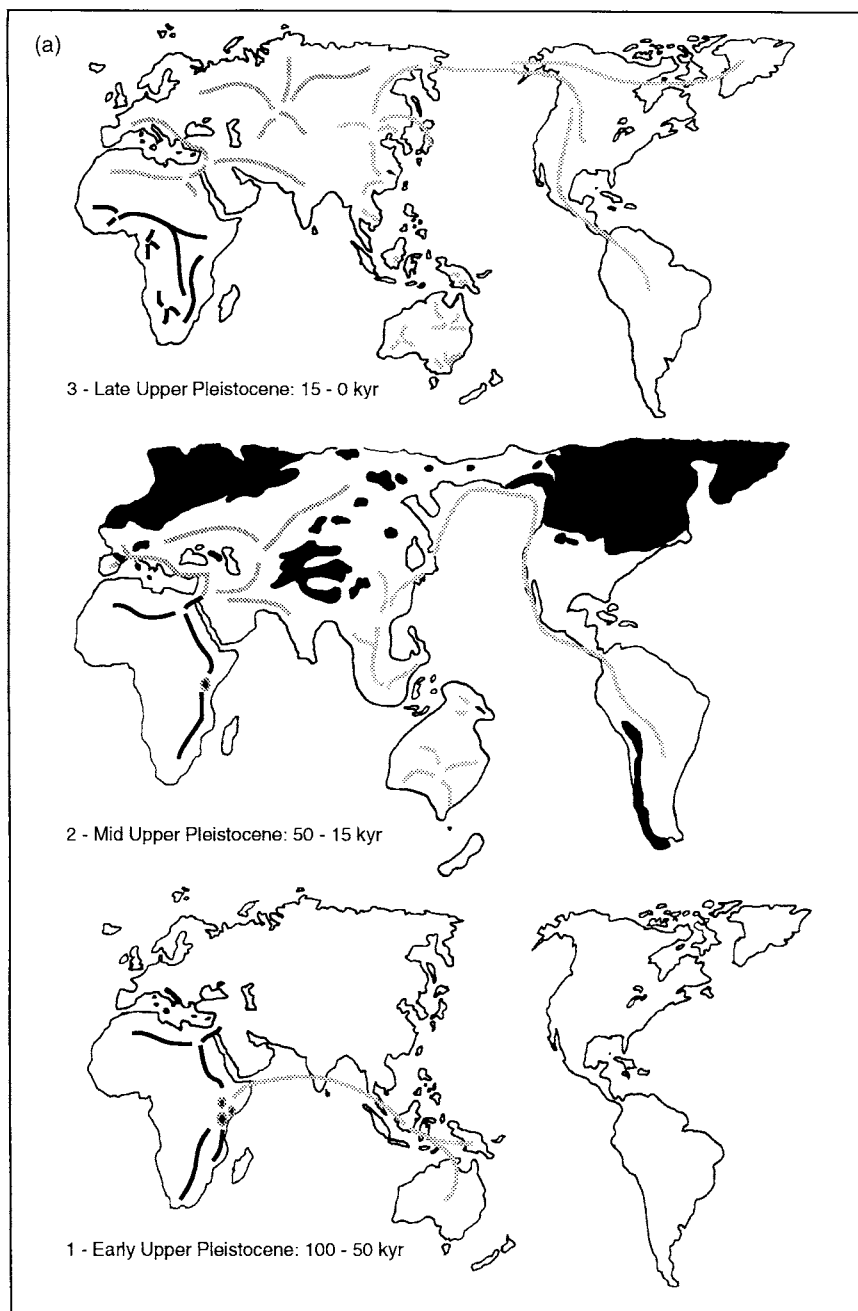


Figure 3. Two views of the pattern of modern human divergence and dispersal according to the multiple dispersals model. (a) Possible Pleistocene dispersals: 1) In the early Upper Pleistocene (100–50 ky) there are dispersals within and out of Africa of early robust forms of modern humans; 2) The mid-Upper Pleistocene (50–15 ky) is the scene of world glaciations and the dispersals within southeast Asia and of Eurasian Upper Palaeolithic populations; and 3) In the late Upper Pleistocene (15–0 ky), we see the recent dispersals, some associated with agricultural expansions, that have been superimposed on the Palaeolithic human distribution.

ary novelty tends to occur in small areas and that successful populations can expand explosively, or at least relatively rapidly, from these centers of origins^{129,130} (Fig. 2). This seems to be the case with well-documented paleontological events, as well as histori-

cal ones involving humans and other species.^{131–133} The process begins with dispersals into new regions and if colonization is successful, the available habitats of the colonized region would be occupied. Range expansion then takes place. Through time, this

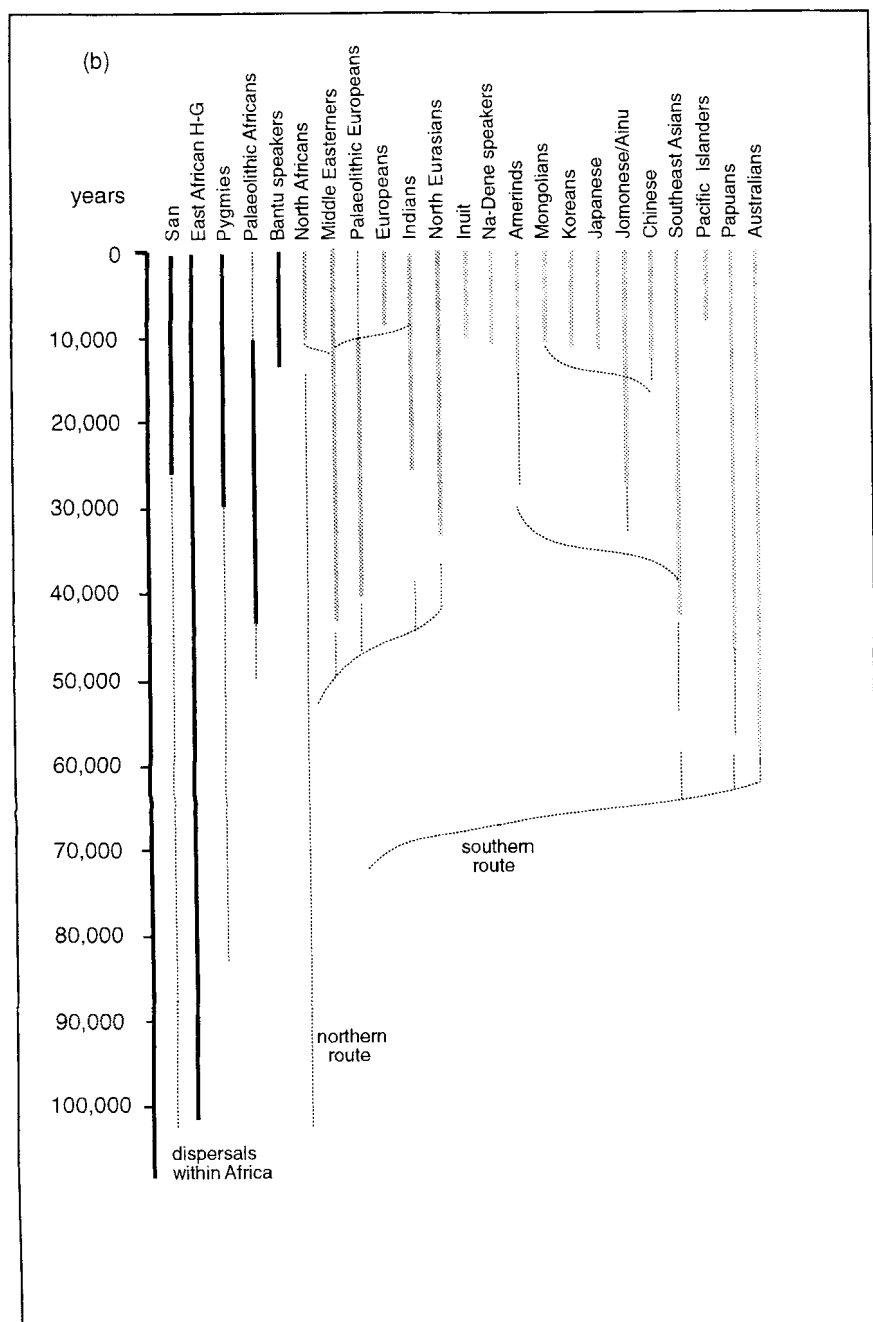


Figure 3. (b) The implied time depth of the main populations of living *Homo sapiens*.

would be followed by differentiation as the population breaks up due to the appearance of barriers. Further dispersals would be superimposed on this pattern, resulting in a complex palimpsest of relic and recent populations. Range expansion, migrations, dispersals, colonizations, and differential survival of populations are the norms of evolutionary biogeography.¹³⁰⁻¹³⁴ Furthermore, even if only a small proportion of invaders establish

themselves,¹³⁴ they can be spectacularly successful. The mechanisms involved in the displacement of local populations by invading groups may be diverse, ranging from adaptive superiority, disease, habitat disturbance and destruction, and differential reproductive rates.¹³⁴ The processes of displacement ensuing from the expansion of modern human populations may have ranged from nonexistent (total interbreeding of local and incom-

ing populations) to complete, either directly, through factors like disease, or indirectly, through the competition for resources and differential reproduction or demography. If such dispersal events occurred frequently during the later Pleistocene and were the primary mechanisms by which the human population diversified, then the mosaic of modern human diversity can be seen as the product of several events of differing geographical extent occurring over 100,000 years. This process would account for the pattern of modern human variability as a consequence of differential ancestral morphology occurring in successive dispersals followed by local adaptation. According to this view, Africa is unique only as the original source of populations, whereas the diversification process involved varied geographical foci, both African and non-African. Where modern populations were already present, dispersals would have acted as a primary mechanism of gene flow.

A Pattern: Routes of Dispersal and Levels of Differentiation

Traditionally, it has been assumed that expansions out of Africa occurred through the narrow corridor of north-eastern Africa and the Middle East, a northern route. This assumption carries two implications. First, the direction of movement was across a major desert towards the Middle East, an area that certainly was populated at the time. Therefore, movement would have been strongly constrained by climatic conditions and competition with other hominids. Second, that there was morphological and genetic unity in the expanding population at any one time. However, another route of dispersal, through the Horn of Africa towards the Arabian Peninsula, a southern route, has been used by animals in the past. Use of this route by expanding early moderns has also been suggested^{49,60} (Fig. 3).

How would the existence of two different routes out of Africa affect the subsequent diversity of modern humans? Three main aspects of the expansion process would be affected. First, the climatic conditions necessary for northward expansion are very strict—faunal dispersals across the

Sahara occurred during short episodes of fast deglaciation, during which wet conditions prevailed in most of northern Africa. These strict climatic constraints would not have acted on populations expanding eastward toward Asia from East Africa. Second, the circum-Mediterranean area was certainly occupied by hominid populations during the last 200 ky. Hence, any movement into this region would imply competition with other groups. Although hominids were present throughout southern and eastern Asia in the late Pleistocene, the sizes and densities of populations may have been highly variable. The third and, perhaps, the most important aspect is that as hominids took different routes at different times, it is likely that the African source populations also differed from each other.

How does the available data fit the hypothesis of different routes of expansion? A northern faunal route of dispersal into the Nile Valley and across northern Africa has been intermittently used since the Miocene, and the Levantine corridor was alternatively occupied by Afro-Arabian or Palearctic elements.⁶⁴ As Tchernov^{63,64} has argued, the paleoanthropological evidence suggests that an early modern population took an inland route to north Africa and the Middle East during the hypsithermal phase of the last interglacial.^{70,135–137} However, this population, represented by the Skhul and Qafzeh fossils, seems to have faced a competitive or geographical barrier to further expansion at that stage. The main expansion of modern humans out of Africa through the Levantine corridor occurred around 45 ky,⁴⁸ but this event postdates the first occupation in Australia.^{78,79} Furthermore, the morphological and archaeological features of Middle Eastern and European population of 40 ky ago precludes them from the ancestry of many Australian fossils. If, however, another population, already genetically separated from other modern groups, expanded out of East Africa toward the Indian subcontinent at any time between 100 and 50 kya, this could explain some of the marked differences in morphology and technological traditions at the point of the first appearance of regional popula-

tions and the relatively early dates for the occupation of Australia.

Is the hypothesis of differentiation in Africa of populations ancestral to regional groups consistent with the available evidence? One way of interpreting the differences between regional modern populations when they appear in the archeological record is that these differences, in fact, reflect various levels of admixture between modern people and local archaic populations. Although it is commonly stated that there are two models of modern human origins, others have been proposed, such as the Afro-European Sapiens Hypothesis^{138,139} and the Assimilation Hypothesis.^{140,141} Both of these hypotheses are largely concerned with the level of genetic admixture between dispersing African populations and indigenous populations, especially European Neanderthals. They differ, however, in the amount of gene flow considered to have taken place. The Afro-European Sapiens model sees archaic genes persisting in a modern gene pool, whereas the Assimilation Hypothesis sees modern genes imposed on an archaic gene pool. The difference is therefore one of relative contribution. However, the absence of consistently transitional fossils throughout the world¹⁰ argues against gene flow as the main process in the geographical expansion of modern morphology, making the Assimilation Hypothesis as unlikely as the multiregional model. Although some hybridization between modern humans and archaic populations might have occurred, it is not clear that the morphological features considered to reflect continuity between Neanderthals and early Upper Paleolithic Europeans (generally measures of robusticity, as is the case for the claimed similarities between Australians and *Homo erectus*), are relevant phylogenetic markers. Furthermore, the mtDNA data show that no widely divergent lineage that could be attributed to Neanderthal descent has ever been sampled. The possibility of finding such a lineage remains, at least theoretically, until all people have been sampled, but its absence in the thousands of individuals studied so far indicates that even if such interbreeding took place, it did not have signifi-

cant magnitude. This conclusion is further supported by recent research by Waddle using matrix correlation of Eurafrikan fossils.¹⁴²

Another way of explaining the original diversity of regional populations is that these populations were already different at the time they left Africa. In this case, a certain amount of prior differentiation and population subdivision would have taken place prior to expansion. There is little fossil data to support or refute this idea. Between 130 and 60 ky ago in Africa, there are fossils from south, east, and north Africa, but these are very few, localized, and early. The groups in these three regions do show marked population differences, and indicate an even earlier date for the first appearance of a common morphology. They are also technologically diverse, although all present what are called Middle Stone Age or Middle Paleolithic stone tools. Therefore, both the fossil and archeological evidence tentatively suggests African diversification at this time. However, genetic evidence obtained by Harpending and co-workers strongly supports the idea of diversification of populations prior to geographical expansion, a model they have called the Weak Garden of Eden.^{45,46,143} Their interpretation of mtDNA diversity through pairwise distributions indicates that modern humans underwent a bottleneck around 100 ky, that this bottleneck was followed by population subdivision and relative isolation of these diverse modern groups, and that demographic geographical expansion occurred between 70 and 40 ky, the youngest being that of Europeans. Therefore, molecular data show that a large amount of population differentiation occurred prior to expansion.

CONCLUSIONS

Although we believe that a recent single origin is the evolutionarily correct explanation for the appearance of *Homo sapiens*, we suggest that the "Out of Africa" model does not explain the temporal and geographical patterns of diversification observed in the Upper Pleistocene. The theoretical explanation of human diversity that best accounts for data on the dates of first occupation, morphological variation,

and technological innovations involves multiple dispersal events. These dispersals would have taken different routes out of Africa, as well as different routes and directions from other subsequent non-African sources. The varying order and geographical extent of the early dispersals from Africa are proposed to explain the different times at which various regions of the world were first occupied. The incomplete geographical extent of subsequent dispersals is proposed to explain the persistence of relic populations as new populations were superimposed on the range of earlier groups. Finally, high levels of isolation, especially in tropical areas, are proposed to explain the differing rates of morphological, genetic, and technological change through time between long-standing adaptations and very recent colonizations.

Modern humans originated from a recent single evolutionary event, whereas modern human diversity is the result of multiple evolutionary events brought about by multiple geographical dispersals. Much remains to be done to document these various dispersals and their morphological, archeological, and genetic correlates. However, we also need to investigate further the possibility that one principal difference between modern humans and archaic hominids lay not in any major cognitive difference or any single edge of advantage, but simply in the social and ecological potential of modern humans to disperse at higher rates than could archaic hominids.

We are not naive or optimistic enough to suppose that this paper will end the debate between the multiregional and "Out of Africa" theories. We hope nonetheless, that by more fully developing the mechanisms for the evolution of modern human diversity and by emphasizing the importance of pre-existing variability at the origins of modern humans, albeit within Africa, rather than worldwide, we have at least brought something new to this discussion.

ACKNOWLEDGMENTS

We thank J. Fleagle for the invitation to write this paper, as well as C. Gamble, W.W. Howells, F. Lahr, and C. Stringer for commenting on an earlier

version of it. Thanks also to R. Klein and six anonymous referees for their reviews. All errors that remain are our own. Special thanks to B. Arensburg, H. Harpending, R. Haydenblit, J. Nichols, and K. Robson Brown for stimulating discussions on the subject of modern human differentiation and to F. Lahr for his help with the figures. Financial support to MML was provided by CNPq, (Brazil), the Leaky Trust, and the CARE Foundation.

REFERENCES

- Weidenreich F (1943) The skull of *Sinanthropus pekinensis*: A comparative study of a primitive hominid skull. *Palarontol Sinica* N. S., No. 10.
- Coon CS (1962) *The Origin of Races*. New York: Knopf.
- Thorne A, Wolpoff MH (1981) Regional continuity in Australasian Pleistocene hominid evolution. *Am J Phys Anthropol* 55:337-349.
- Wolpoff MH, Wu XZ, Thorne A (1984) Modern *Homo sapiens* origins: A general theory of hominid evolution involving the fossil evidence from East Asia. In Smith FH, Spencer F (eds), *The Origin of Modern Humans: A World Survey of the Fossil Evidence*, pp 411-483. New York: Alan R. Liss.
- Frayer DW, Wolpoff MH, Thorne AG, Smith FH, Pope GG (1993) Theories of modern human origins: The palaeontological test. *Am Anthropol* 95:14-50.
- Howells WW (1976) Explaining modern man: Evolutionists versus migrationists. *J Hum Evol* 5:477-495.
- Stringer CB (1989) The origin of modern humans: A comparison of the European and non-European evidence. In Mellars P, Stringer CB (eds) *The Human Revolution*, pp 232-244. Edinburgh: Edinburgh University Press.
- Stringer CB (1993) Reconstructing recent human evolution. In Aitken MJ, Stringer CB, Mellars PA (eds) *The Origin of Modern Humans and the Impact of Chronometric Dating*, pp 179-195. Princeton: Princeton University Press.
- Stringer CB, Hublin JJ, Vandermeersch B (1984) The origin of anatomically modern humans in Western Europe. In Smith FH, Spencer F (eds) *The Origin of Modern Humans: A World Survey of the Fossil Evidence*, pp 51-135. New York: Alan R. Liss.
- Stringer CB, Andrews P (1988) Genetic and fossil evidence for the origin of modern humans. *Science* 239: 1263-1268.
- Grun R, Stringer CB (1991) Electron spin resonance dating and the evolution of modern humans. *Archaeometry* 33:153-199.
- Aitken MJ, Stringer CB, Mellars PA (eds) (1993) *The Origin of Modern Humans and the Impact of Chronometric Dating*. Princeton: Princeton University Press.
- Foley RA, Lahr MM (1992) Beyond "Out of Africa": Reassessing the origins of *Homo sapiens*. *J Hum Evol* 22:523-529.
- Valladas H, Reyss JL, Valladas G, Bar-Yosef O, Vandermeersch B (1988) Thermoluminescence dating of Mousterian "Proto-Cro-Magnon" remains from Israel and the origin of modern man. *Nature* 331:614-616.
- Szwarcz HP, Grun R, Vandermeersch B, Bar-Yosef O, Valladas H, Tchernov E (1988) ESR dates for the hominid burial site of Qafzeh in Israel. *J Hum Evol* 17:733-737.
- Stringer CB, Grun R, Szwarcz HP, Goldberg P (1989) ESR dates for the hominid burial site of Skhul in Israel. *Nature* 338:756-758.
- Grun R, Beaumont PB, Stringer CB (1990) ESR dating evidence for early modern humans at Border Cave in South Africa. *Nature* 334:537-539.
- Valladas H, Joron JL, Valladas G, Arensburg B, Bar-Yosef O, Belfer-Cohen A, Goldberg P, Laville H, Meignen L, Rak Y, Tchernov E, Tillier AM, Vandermeersch B (1987) Thermoluminescence dates for the Neanderthal burial site at Kebara in Israel. *Nature* 330:159-160.
- Rightmire P, Deacon HJ (1991) Comparative studies of late Pleistocene human remains from Klasies River Mouth, South Africa. *J Hum Evol* 20:131-156.
- Deacon HJ (1989) Late Pleistocene palaeoecology and archaeology in the southern Cape, South Africa. In Mellars P, Stringer CB (eds) *The Human Revolution*, pp 547-564. Edinburgh: Edinburgh University Press.
- Singer R, Wymer J (1982) *The Middle Stone Age at Klasies River Mouth in South Africa*. Chicago: University of Chicago Press.
- Brooks AS, Yellen JE (1989) An archaeological perspective on the African origins of modern humans. *Am J Phys Anthropol* 78:197.
- Clark JD (1982) The transition from Lower to Middle Palaeolithic in the African continent. In Ronen A (ed) *The Transition from Lower to Middle Palaeolithic and the Origin of Modern Man*, pp 235-255. Oxford: BAR Int Series 151.
- Deacon HJ, Schuurman R (1992) The origins of modern people: The evidence from Klasies River. In Brauer G, Smith FH (eds) *Continuity or Replacement? Controversies in Homo sapiens Evolution*, pp 121-129. Rotterdam: Balkema.
- Gowlett JAJ (1987) The coming of modern man. *Antiquity* 61:210-219.
- McBurney CBM (1967) *Haua Fteah and the Stone Age of the Southeast Mediterranean*. Cambridge: Cambridge University Press.
- Marks AE (1990) The Middle and Upper Palaeolithic of the Near east and the Nile Valley: The problem of cultural transformations. In Mellars P (ed) *The Emergence of Modern Humans*, pp 56-80. Ithaca: Cornell University Press.
- Bergman CA, Stringer CB (1989) Fifty years after: Egbert, an early Upper Palaeolithic juvenile from Ksar Akil, Lebanon. *Paleorient* 15:99-111.
- Smith FH (1984) Fossil hominids from the Upper Pleistocene of central Europe and the origin of modern Europeans. In Smith FH, Spencer F (eds) *The Origin of Modern Humans: A World Survey of the Fossil Evidence*, pp 137-209. New York: Alan R. Liss.
- Bischoff JL, Soler N, Maroto J, Julia R (1989) Abrupt Mousterian/Aurignacian boundary at c 40 ka bp: Accelerator 14C dates from l'Abreda Cave (Catalunia, Spain). *J Archeol Sci* 16:563-576.
- Cabrera V, Bischoff JL (1989) Accelerator 14C dates for early Upper Palaeolithic (Basal Aurignacian) at El Castillo Cave (Spain). *J Archeol Sci* 16:577-584.
- Straus LG (1989) Age of the modern Europeans. *Nature* 342:476-477.
- Mellars P (1991) Cognitive changes and the emergence of modern humans in Europe. *J Cambridge Archeol* 1:63-76.
- Mellars P (1993) Archaeology and the population-dispersal hypothesis of modern human origins in Europe. In Aitken MJ, Stringer CB, Mellars PA (eds) *The Origin of Modern Humans and the Impact of Chronometric Dating*, pp 196-216. Princeton: Princeton University Press.

- 35 Cann RL, Stoneking M, Wilson AC (1987) Mitochondrial DNA and human evolution. *Nature* 325:31–36.
- 36 Vigilant L, Stoneking M, Harpending H, Hawkes K, Wilson A (1989) African populations and the evolution of human mtDNA. *Science* 253:1503–1507.
- 37 Stoneking M, Jorde LB, Bhatia K, Wilson AI (1990) Geographic variation in human mitochondrial DNA from Papua New Guinea. *Genetics* 124:717–733.
- 38 Wainscoat JS, Hill AVS, Boyce AL, Flint J, Hernandez M, Thein SL, Old JM, Lynch JR, Falusi AG, Weatherall DJ, Clegg JB (1986) Evolutionary relationships of human populations from an analysis of nuclear DNA polymorphisms. *Nature* 319: 491–493.
- 39 Mountain J, Lin AA, Bowcock M, Cavalli-Sforza LL (1993) Evolution of modern humans: Evidence from nuclear DNA polymorphisms. In Aitken MJ, Stringer CB, Mellars PA (eds) *The Origin of Modern Humans and the Impact of Chronometric Dating*, pp 69–83. Princeton: Princeton University Press.
- 40 Tishkoff SA, Kidd KK (1994) Evidence for stability of a highly variable short tandem repeat polymorphism during recent human evolution. *Am J Phys Anthropol Suppl* 18:195.
- 41 Templeton AR (1992) Humans origins and analysis of mitochondrial DNA sequences. *Science* 255:737.
- 42 Maddison DR (1991) African origin of human mitochondrial DNA reexamined. *Syst Zool* 40:355–363.
- 43 Wolpoff MH, Thorne A (1991) The case against Eve. *New Scientist*, 22 June:37–41.
- 44 Stoneking M, Sherry ST, Redd AJ, Vigilant L (1993) New approaches to dating suggest a recent age for the human mtDNA ancestor. In Aitken MJ, Stringer CB, Mellars PA (eds) *The Origin of Modern Humans and the Impact of Chronometric Dating*, pp 167–175. Princeton: Princeton University Press.
- 45 Rogers AR, Jorde LB (n.d.) *Genetic Evidence on Modern Human Origins*.
- 46 Harpending H, Sherry ST, Rogers AR, Stoneking M (1993) The genetic structure of ancient human populations. *Curr Anthropol* 34:483–496.
- 47 Stoneking M (1993) DNA and recent human evolution. *Evol Anthropol* 2:60–73.
- 48 Klein RG (1992) The archaeology of modern human origins. *Evol Anthropol* 1:5–14.
- 49 Cavalli-Sforza LL, Piazza A, Menozzi P, Mountain J (1988) Reconstruction of human evolution: Bringing together genetic, archaeological and linguistic data. *Proc Nat Acad Sci* 85:6002–6006.
- 50 Groves CP (1989) A regional approach to the problem of the origin of modern humans in Australasia. In Mellars P, Stringer CB (eds) *The Human Revolution*, pp 274–285. Edinburgh: Edinburgh University Press.
- 51 Habgood PJ (1989) The origin of anatomically modern humans in Australasia. In Mellars P, Stringer CB (eds) *The Human Revolution*, pp 245–273. Edinburgh: Edinburgh University Press.
- 52 Lahr MM (1992) The origins of modern humans: A test of the Multiregional hypothesis. PhD dissertation, University of Cambridge.
- 53 Lahr MM (1994) The Multiregional Model of modern human origins: A reassessment of its morphological basis. *J Hum Evol* 26:23–56.
- 54 Groves CP (1992) How old are subspecies? A tiger's eye-view of human evolution. *Perspect Hum Biol* 2/ Archaeol Oceania 27:153–160.
- 55 Swisher CC III, Curtis GH, Jacob T, Getty AG, Suprijo A, Widiasmoro (1994) Age of the earliest known hominids in Java, Indonesia. *Science* 263:1118–1121.
- 56 Li WH, Sadler LA (1991) Low nucleotide diversity in man. *Genetics* 129:513–523.
- 57 Ferris S, Brown W, Davidson W, Wilson A (1981) Extensive polymorphism in the mitochondrial DNA of apes. *Proc Nat Acad Sci USA* 78:6319–6323.
- 58 Kocher T, Wilson A (1991) Sequence evolution of mitochondrial DNA in humans and chimpanzees: Control region and a protein-coding region. In Osawa S, Honjo T (eds) *Evolution of Life: Fossils, Molecules and Culture*, pp 391–413. New York: Springer-Verlag.
- 59 Wilson A, Cann R, Carr S, George M, Gyllenstein U, Helm-Bychowski K, Higuchi R, Palumbi S, Prager E, Sage R, Stoneking M (1985) Mitochondrial DNA and two perspectives on evolutionary genetics. *Biol J Linnean Soc* 26:375–400.
- 60 Kingdon J (1993) *Self-Made Man and His Undoing*. London: Simon & Schuster.
- 61 Masao FT (1992) The Middle Stone Age with reference to Tanzania. In Brauer G, Smith FH (eds) *Continuity or Replacement? Controversies in Homo sapiens Evolution*, pp 99–109. Rotterdam: Balkema.
- 62 Clark JD (1993) African and Asian perspective on the origins of modern humans. In Aitken MJ, Stringer CB, Mellars P (eds) *The Origin of Modern Humans and the Impact of Chronometric Data*, pp 201–215. Princeton: Princeton University Press.
- 63 Tchernov E (1992) Biochronology, paleoecology and dispersal events of hominids in the southern Levant. In Akazawa T, Aoki K, Kimura T (eds) *The Evolution and Dispersal of Modern Humans in Asia*, pp 149–188. Tokyo: Hokusen-sha.
- 64 Tchernov E (1992) Eurasian-African biotic exchanges through the Levantine corridor during the Neogene and Quaternary. *Cour Fors Senck* 153:103–123.
- 65 Vandermeersch B (1989) The evolution of modern humans: Recent evidence from Southwest Asia. In Mellars P, Stringer CB (eds) *The Human Revolution*, pp 155–164. Edinburgh: Edinburgh University Press.
- 66 Deacon HJ (1993) Southern Africa and modern human origins. In Aitken MJ, Stringer CB, Mellars P (eds) *The Origin of Modern Humans and the Impact of Chronometric Dating*, pp 177–183. Princeton: Princeton University Press.
- 67 Rightmire GP, Deacon HJ (1991) Comparative studies of late Pleistocene human remains from Klasies River Mouth, South Africa. *J Hum Evol* 20:131–156.
- 68 Close AE, Wendorf F (1990) North Africa at 18,000 BP. In Gamble C, Soffer O (eds) *The World at 18,000 BP, Vol 2*, pp 41–57. London: Unwin.
- 69 Debenath A, Raynal JP, Roche J, Texier JP, Ferembach D (1986) Stratigraphie, habitat, typologie et devenir de l'Aterien marocain: Données recentes. *L'Anthropol* 90:233–246.
- 70 Petit-Marie N (1989) Interglacial environments in presently hyperarid Sahara: Paleoclimatic implications. In Leinen M, Sarntheim M (eds) *Paleoclimatology and Paleometeorology: Modern and Past Patterns of Global Atmospheric Transport*, pp 637–661. London: Kluwer Ac Press.
- 71 Fontes JC, Gasse F (1989) On the ages of humid and late Pleistocene phases in North Africa: Remarks on "Late Quaternary climatic reconstruction for the Maghreb (North Africa)" by P Rogon. *Pal Pal* 70:393–398.
- 72 Wendorf F, Schild R, Siad R, Haynes CV, Gautier A, Kobusiewicz M (1976) The prehistory of the Egyptian Sahara. *Science* 193:103–114.
- 73 Brauer G, Rimbach KW (1990) Late archaic and modern *Homo sapiens* from Europe, Africa and southwest Asia: Craniometric comparisons and phylogenetic implications. *J Hum Evol* 19:789–807.
- 74 Lucotte G (1992) African pygmies have the more ancestral gene pool in studies for Y-chromosome DNA haplotypes. In Brauer G, Smith FH (eds) *Continuity or Replacement? Controversies in Homo sapiens Evolution*, pp 75–81. Rotterdam: Balkema.
- 75 Stine OC, Dover GH, Zhu D, Smith KD (1992) The evolution of two west African populations. *J Mol Evol* 34:336–344.
- 76 Ruhlen M (1990) An overview of genetic classification. In Hawkins JA, Gell-Mann M (eds) *The Evolution of Human Languages*, pp 1–27. Addison-Wesley.
- 77 Renfrew C (1991) Before Babel: Speculation on the origins of linguistic diversity. *Cambridge Archeol J* 1:3–23.
- 78 Roberts RG, Jones R, Smith MA (1990) Thermoluminescence dating of a 50,000 year old human occupation site in northern Australia. *Nature* 345:153–156.
- 79 Roberts RG, Spooner N (1992) Luminescence dating of early occupation sites in northern Australia. Paper presented at the conference "Australia Day" University of Cambridge.
- 80 Kirk RL (1981) *Aboriginal Man Adapting*. Oxford: Oxford University Press.
- 81 Thorne AG (1977) Separation or reconciliation? Biological clues to the development of Australian society. In Allen J (ed) *Sunda and Sahul: Prehistoric Studies in Southeast Asia, Melanesia, and Australia*, pp 187–204. London: Academic Press.
- 82 Thorne AG (1984) Australia's human origins: How many sources? *Am J Phys Anthropol* 63:227.
- 83 Habgood PJ (1985) The origin of the Australian Aborigines: An alternative approach and view. In Tobias PV (ed) *Human Evolution: Past, Present and Future*, pp 367–380. New York: Alan R. Liss.
- 84 Pietrusewsky M (1984) *Metric and Non-Metric Cranial Variation in Australian Populations Compared with Populations from the Pacific and Asia*. Canberra: Australian Inst. Aboriginal Studies.
- 85 Howells WW (1989) *Skull shapes and the map*. Papers Peabody Museum, Arch Ethnol, vol 79, Cambridge: Harvard University Press.
- 86 Hedges SB, Kumar S, Tamura K, Stoneking M (1991) Comment on "Human origins and analysis of mitochondrial DNA sequences" by JA Templeton. *Science* 255:737–739.
- 87 Vigilant L, Stoneking M, Harpending H, Hawkes K, Wilson A (1991) African populations and the evolution of human mitochondrial DNA. *Science* 253:1503–1507.
- 88 Wright RVS (1992) Correlation between cranial form and geography in *Homo sapiens*: CRANID. A computer program for forensic and other applications. *Perspect Hum Biol* 2/Arch Oceania 27:128–134.
- 89 Pope GG (1988) Recent advances in Far Eastern palaeoanthropology. *Ann Rev Anthropol* 17:43–77.
- 90 Jones R (1989) East of Wallace's Line: Issues and problems in the colonization of the Australian continent. In Mellars P, Stringer CB (eds) *The Human Revolution*, pp 743–782. Edinburgh: Edinburgh University Press.
- 91 Brace CL, Brace ML, Dodo Y, Leonard WR, Li Y, Shao XQ, Sangvichien S, Zhang Z (1990) Micronesians, Asians, Thais and relations: A craniofacial and odontometric perspective. *Micronesia, Suppl* 2:323–348.

- 92** Turner CG II (1987) Late Pleistocene and Holocene population history of East Asian based on dental variation. *Am J Phys Anthropol* 73:305–321.
- 93** Turner CG II (1990) The major features of Sundadonty and Sinodonty, including suggestions about East Asian microevolution, population history and late Pleistocene relationships with Australian Aborigines. *Am J Phys Anthropol* 82:295–317.
- 94** Turner CG II (1990) Origin and affinity of the people of Guam: A dental anthropological assessment. *Micronesia, Suppl* 2:403–416.
- 95** Weidenreich F (1939) On the earliest representatives of modern mankind recovered on the soil of East Asia. *Peking Nat Hist Bull* 13:205–224.
- 96** Brace CL, Brace ML, Leonard WR (1989) Reflections on the face of Japan: A multivariate and odontometric perspective. *Am J Phys Anthropol* 78:93–113.
- 97** Howells WW (1984) Prehistoric human remains from China. In Schwidetzky I (ed) *Rassengeschichte der Menschheit*, pp 29–38. Munich: R.O. Verlag.
- 98** Howells WW (1986) Physical anthropology of the prehistoric Japanese. In Pearson RJ (ed) *Windows on the Japanese Past: Studies in Archaeology and Prehistory*, pp 85–99. Ann Arbor: Michigan Center for Japanese Studies.
- 99** Turner CG II (1985) The dental search for Native American origins. In Kirk R, Szathmari E (eds) *Out of Asia: Peopling of the Americas and the Pacific*, pp 31–78. Canberra: Journal of Pacific History.
- 100** Kamminga J, Wright RVS (1989) The Upper Cave at Zhoukoudian and the origins of the Mongoloids. *J Hum Evol* 17:739–767.
- 101** Hanihara K (1985) Origins and affinities of the Japanese as viewed from cranial measurements. In Kirk R, Szathmari E (eds) *Out of Asia. Peopling of the Americas and the Pacific*, pp 105–112. Canberra: Journal of Pacific History.
- 102** Pietrusewsky M (1990) Craniofacial variation in Australasian and Pacific populations. *Am J Phys Anthropol* 82:319–340.
- 103** Pietrusewsky M, Li Y, Shao X, Nguyen QQ (1992) Modern and near modern populations of Asia and the Pacific: A multivariate craniometric interpretation. In Akazawa T, Aoki K, Kimura T (eds) *The Evolution and Dispersal of Modern Humans in Asia*, pp 531–558. Tokyo: Hokusensha.
- 104** Ballinger SW, Schurr TG, Torroni A, Gan YY, Hodge JA, Hassan K, Chen KH, Wallace DC (1992) Southeast Asian mitochondrial DNA analysis reveals genetic continuity of ancient Mongoloid migrations. *Genetics* 130:139–152.
- 105** Cavalli-Sforza LL, Menozzi P, Piazza A (1992) Genetic history and geography of Asia. In Akazawa T, Aoki K, Kimura T (eds) *The Evolution and Dispersal of Modern Humans in Asia*, pp 613–623. Tokyo: Hokusensha Publ Co.
- 106** Bellwood P (1990) From late Pleistocene to early Holocene in Sundaland. In Gamble G, Soffer O (eds) *The World at 18,000 BP, Vol 2*, pp 155–163. London: Unwin Hyman.
- 107** Chen C, Olsen JW (1990) China at the last glacial maximum. In Soffer O, Gamble C (eds) *The World at 18,000 BP, Vol 1*, pp 276–295. London: Unwin Hyman.
- 108** Jia L, Huang W (1985) The late Palaeolithic of China. In Wu R, Olsen JW (eds) *Palaeoanthropology and Palaeolithic Archaeology in the People's Republic of China*, pp 211–223. Orlando: Academic Press.
- 109** Olsen JW (1987) Recent developments in the Upper Pleistocene prehistory of China. In Soffer O (ed) *The Pleistocene Old World: Regional Perspectives*, pp 135–146. New York: Plenum.
- 110** Reynolds TEG, Kaner SC (1990) Japan and Korea at 18,000 BP. In Soffer O, Gamble C (eds) *The World at 18,000 BP, Vol 1*, pp 296–311. London: Unwin Hyman.
- 111** Dillehay TD, Collins MB (1988) Early cultural evidence from Monte Verde in Chile. *Nature* 332:150–152.
- 112** Gruhn R (1987) On the settlement of the Americas: South American evidence for an expanded time frame. *Curr Anthropol* 28:363–365.
- 113** Delibrias G, Guidon N (1986) L'abri Toca do Boqueirao da sitio da Pedra Furada. *L'Anthropol* 90:307–316.
- 114** Greenberg J, Turner CG II, Zegura S (1986) The settlement of the Americas: A comparison of the linguistics, dental and genetic evidence. *Curr Anthropol* 27:477–497.
- 115** Steele DG, Powell JF (1992) Peopling of the Americas: Paleobiological evidence. *Hum Biol* 64:303–336.
- 116** Neves WA, Pucciarelli HM (1991) Morphological affinities of the first Americans: An exploratory analysis based on early South American human remains. *J Hum Evol* 21:261–273.
- 117** Lahr MM (1993) Patterns of modern human diversification: Implications for Amerindian origins. Paper presented at the XIII ICAEJ, Mexico, Aug. 1993.
- 118** Szathmari EJE (1993) Genetics of aboriginal North Americans. *Evol Anthropol* 1:202–220.
- 119** Bar-Yosef O (1993) The role of western Asian in modern human origins. In Aitken MJ, Stringer CB, Mellars PA (eds) *The Origin of Modern Humans and the Impact of Chronometric Dating*, pp 132–147. Princeton: Princeton University Press.
- 120** Kennedy KAR, Deraniyagala SU (1989) Fossil remains of 28,000 year old hominids from Sri Lanka. *Curr Anthropol* 30:394–399.
- 121** Morlan RE (1987) The Pleistocene archaeology of Beringia. In Nitecki MH, Nitecki DV (eds) *The Evolution of Human Hunting*, pp 267–307. New York: Plenum.
- 122** Mercier N, Valladas H, Joron JL, Reyss JL, Leveque F, Vandermeersch B (1991) Thermoluminescence dating of the late Neanderthal remains from Saint-Cesaire. *Nature* 351:737–739.
- 123** Hublin JJ (pers. comm.)
- 124** Leveque F, Vandermeersch B (1981) Le neanderthalien de Saint-Cesaire. *Recherche* 12:242–244.
- 125** Kidder JH, Jantz RL, Smith FH (1992) Defining modern humans: A multivariate approach. In Brauer G, Smith FH (eds) *Continuity or Replacement? Controversies in Homo sapiens Evolution*, pp 157–177. Rotterdam: Balkema.
- 126** van Vark GN (1990) A study of European Upper Palaeolithic crania. *Fysisch-Antropol Mededelingen* 2:7–15.
- 127** van Vark GN, Bilsborough A, Henke W (1992) Affinities of European Upper Palaeolithic *Homo sapiens* and later human evolution. *J Hum Evol* 23:401–417.
- 128** Cavalli-Sforza LL (1991) Genes, people and languages. *Sci Am*, November.
- 129** Foley RA (1989) The ecological conditions of speciation: A comparative approach to the origins of anatomically modern humans. In Mellars P, Stringer CB (eds) *The Human Revolution*, pp 298–320. Edinburgh: Edinburgh University Press.
- 130** Tchernov E (1992) Dispersal: A suggestion for a common usage of this term. *Cour Fors Senck* 153:21–25.
- 131** Groves RH, Burdon JJ (1986) *Ecology of Biological Invasions*, Cambridge: Cambridge University Press.
- 132** Gray AJ, Crawley MJ, Edwards PJ (eds) (1987) *Colonization, Succession and Stability*. Oxford: Blackwell Scientific.
- 133** Hengeveld R (1989) *Dynamics of Biological Invasions*. London: Chapman & Hall.
- 134** Lodge DM (1993) Biological invasions: Lessons for ecology. *TREE* 8:133–137.
- 135** Causse C, Conrad G, Fontes JC, Gasse F, Gibert E, Kassir A (1988) Ledernier "Humide" Pleistocene du Sahara nord-occidental daterait de 80–100,000 ans. *C R Acad Sci Paris, t 306, Serie II*:1459–1464.
- 136** Causse C, Coque R, Fontes JC, Gasse F, Gibert E, Ben Ouezdou H, Zouari K (1989) Two high levels of continental waters in the southern Tunisian chotts at about 90 and 150 ka. *Geology* 17:922–925.
- 137** Gaven C, Hillaire-Marcel C, Petit-Marie N (1981) A Pleistocene lacustrine episode in southeastern Libya. *Nature* 290:131–133.
- 138** Brauer G (1984) The "Afro-European sapiens hypothesis" and hominid evolution in East Asia during the late Middle and Upper Pleistocene. *Cour Fors Senck* 69:145–165.
- 139** Brauer G (1992) L'hypothese africaine de l'origine des hommes modernes. In Hublin JJ, Tillier AM (eds) *Aux Origines d'Homo sapiens*, pp 181–215. Paris: Presses Université de France.
- 140** Smith FH (1992) The role of continuity in modern human origins. In Brauer G, Smith FH (eds) *Continuity or Replacement? Controversies in Homo sapiens Evolution*, pp 145–156. Rotterdam: Balkema.
- 141** Smith FH, Simek JF, Harrill MS (1989) Geographical variation in supraorbital torus reduction during the later Pleistocene (c 80,000–15,000 B.P.). In Mellars P, Stringer CB (eds) *The Human Revolution*, pp 172–193. Edinburgh: Edinburgh University Press.
- 142** Waddle DM (1994) Matrix correlation tests support a single origin for modern humans. *Nature* 368:452–454.
- 143** Sherry ST, Rogers AR, Harpending H, Soodyall H, Jenkins T, Stoneking M (n.d.) Mismatch distributions of mtDNA reveal recent human population expansions. *Hum Biol*. in press.