

DAVID W. FRAYER

University of Kansas

MILFORD H. WOLPOFF

University of Michigan, Ann Arbor

ALAN G. THORNE

Australian National University

FRED H. SMITH

Northern Illinois University

GEOFFREY G. POPE

William Paterson College

Theories of Modern Human Origins: The Paleontological Test

IN A FIELD OFTEN ACCUSED of being unable to settle controversies or resolve competing hypotheses, the recent proposal based on interpretations of mitochondrial DNA (mtDNA) allows for the unambiguous testing of two models about the origin of modern *Homo sapiens*. These are the total replacement (“Eve”) and the continuity (multiregional evolution) models, both of which have clearly definable, completely different predictions about the pattern of past evolution, as well as different expectations about the distribution of certain grade (modernizing) and clade (regional, such as African, North Asian, etc.) features in the human fossil record. Since proponents of both views recognize that the fossil record is real, and the two competing interpretations of prehistory have non-overlapping predictions about the modern human origins, specific aspects of each model can be weighed against the fossil record for potential refutation. Here, fossils are not used to develop interpretations of the human evolutionary pattern, a thankless task whose success is very sensitive to the completeness of the fossil record. Instead, limited conflicting predictions of these two models can be addressed from a circumscribed data set, which the fossil record clearly provides. Unlike an earlier controversy between the genetic and fossil reconstruction of the past concerning the timing of the split between humans and chimpanzees, the current debate about the origin of modern *Homo sapiens* is represented by a much more extensive fossil record, spanning a reasonably well dated time period and supplemented by extensive archeological data.

Using the prehistoric skeletal data of Australasia (Southeast Asia and Australia), North Asia, Europe, Africa, and the Levant, we test the conflicting predictions of these two models by evaluating evidence for the existence of transitional samples and the persistence of morphological and metric features over time and space. While many previous and some current models about the later aspects of human evolution are riddled with untestable or non-excluding hypotheses, the differences between the “Eve” and the multiregional evolution models are so profound it is impossible for both to be correct. These differences in theoretical expectations relate to the requirements of the Eve theory that a single source of all contemporary mtDNA variation exists and that this source is derived exclusively from a relatively recent African female (Eve). In this article we review the predictions of the Eve and the multiregional evolution models and test these against the human fossil record from the Old World. In addition, we will show that, while an extreme replacement interpretation is unsupported, the mtDNA data can be reconciled with the fossil record within the context of multiregional evolution.

Two Theories of Modern Human Origins

The genesis of this debate goes back to the later writings of F. Weidenreich and the earliest formulations of W. W. Howells, then and now perhaps his best-known antagonist. Weidenreich (1939, 1943, 1946) contended that human evolution was best understood as a network of interconnected populations that retained regional continuity in at least some geographic areas. Each of the four major evolutionary centers of his polycentric model retained differences on the racial level and could be directly related to the races of today (Weidenreich 1943). At the same time, there was significant gene flow across regions and the human species retained its unity. For instance, in summarizing Australasian evolution, Weidenreich wrote:

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

Weidenreich concluded that a significant aspect of the skeletal morphology of aboriginal Australians was to be found in their regional antecedents, but never regarded this as a unique ancestral-descendant relation. He illustrated this evolutionary pattern as something like a trellis (Figure 1), with the main vertical lines representing the centers of evolution, and diagonal and horizontal connections between them reflecting the patterns of genetic interchange (Weidenreich 1946:30).

From Howells's earliest publications (1942), it is clear that he did not accept the polycentric theory. After Weidenreich's death the model was misinterpreted in an illustration that reproduced the vertical lines of descent but did not retain the diagonal lines of gene exchange—transforming it into the “candelabra” theory (Howells 1959:236). This was misattributed to Weidenreich, and Howells characterized the theory as one in which “[h]uman evolution progressed in each corner of the world, *essentially apart* from what was happening in the other corners” (1959:235, emphasis added). Howells asked of this theory, how could one explain the independent evolution of four major races? His answer was:

Weidenreich has at least four different evolving human varieties, living far apart, moving ahead by fits and starts, producing their own special peculiarities of form. . . . Yet these four careers at last converged to produce the same kind of man everywhere. And all, miraculously enough, breasted the tape at the same time. [1959:235]

Howells discounted the theory because he could provide no answer as to how this could have happened, unless by some kind of evolutionary miracle. This should not be surprising, because the four independent converging lines were not components of the polycentric theory, but of Howells's misinterpretation of Weidenreich's theory. Ironically, in his modification of Weidenreich's polycentrism, Coon (1962) accepted the precept of independent lines of evolution, and this developed into an extreme theory of independent modern human origins in different regions of the world—a theory that was manifestly *not* Weidenreich's. Among human paleontologists, the extreme parallelism suggested by Coon (1962), where each of the major divisions of living humanity were subspecies (or races) of *Homo sapiens*, has been widely and, in our view, correctly rejected. Yet Howells's misinterpretation has long outlived the original polycentric theory, as authors such as Klein (1989) and Lewin (1991) persist in illustrating multiregional evolution as main vertical lines of descent without any linkages through genic exchanges. In reporting that the model (as he misconstrues it) could not work, Lewin (1991) cites the geneticist Rouhani (1989), who asserts that the model could not work, and we concur with this assessment because Rouhani has also addressed Coon's model of parallel, independent evolution of human races and *not* multiregional evolution.

The combination of Howells's subsequent “Noah's Ark” hypothesis (1976) of a *single recent origin* for living peoples and Protsch's claim (1975) of an *African origin* for all modern

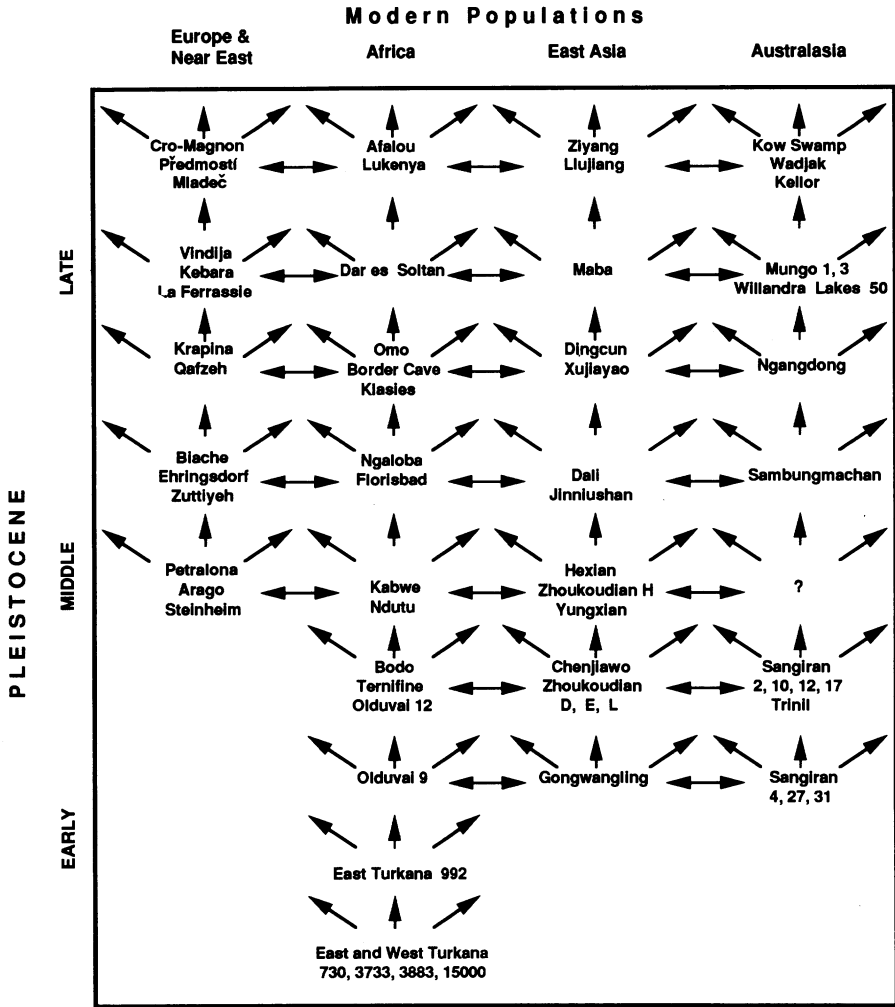


Figure 1
The trellis of multiregional evolution with some key fossils and sites placed in the Old World sequence. Vertical lines signify regional links; diagonal and horizontal lines represent contributions of genic exchange and migration.

humans, developed into the other extreme view: the total replacement by Africans or their descendants as the origin of modern humans. Ultimately, this became the Eve theory, held among paleontologists—most prominently, if not uniquely, by Gould (1987, 1989), Bräuer (1989, but see 1992), and Stringer (1990, 1992; Stringer and Andrews 1988a, 1988b).

Multiregional Evolution

Coon’s parallel evolutionary lines and the Eve theory have one thing in common—they both minimize the importance of genic exchanges (gene flow and migrations) in the evolutionary process. Other prevalent theories, such as the “stages of human evolution,” emphasize genic exchange to the exclusion of geographic variation, treating all of humanity as one panmictic population. Quite different from each of these is a model of evolution that focuses on the importance of long-term geographic variation and posits a crit-

ical role for genic exchange as a driving mechanism underlying the pattern of human evolution. Multiregional evolution (Wolpoff, Wu, and Thorne 1984) envisages a role for both local genetic continuity and genetic exchanges (with or without invasions). The hypothesis began as an explanation for the observations that some of the features distinguishing major human groups, such as Asians, Australian Aborigines, or Europeans, evolved over a long period in approximately the same geographic regions where these traits are found in their highest frequency. This view traces all modern populations back to what was ultimately an African source (but to a time when people lived only there), through a web of ancient lineages whose genetic contributions to the present varied from region to region and from time to time (Weidenreich 1939). Regional variants first became distinct at the geographic edges, a consequence of the colonization events that limited peripheral variability, primarily because of drift and bottlenecks. Regional differences were maintained through a series of balances between (1) genic exchange often but not always from the center toward the peripheries, and (2) selection (for some features) and drift (for others) that may have been more intense at the peripheries but, in any event, tended to be unique from one peripheral area to another (Wolpoff 1989a). This dynamic view of the evolutionary process accounts for how human populations both *developed* and *maintained* regional differences, while at the same time continuing to exchange genes. Thus, selectively advantageous gene frequency changes (and the occasional new allele) could spread rapidly throughout the human range. We find that just as in the world today, where very distinctive populations maintain their physical differences even though they are linked by gene flow, this situation has existed within our lineage ever since humans first spread out of Africa and colonized the Old World.

Multiregional evolution is an explanation about the worldwide pattern of Pleistocene human evolution. A number of different hypotheses of modern human origins fit this model, although of course only one (if any) reflects the reality of what actually took place. We believe the best evidence of the fossil record indicates that modern humans did not have a single origin, or for that matter a number of independent origins, but rather that it was modern human features that originated—at different times and in different places. This model implies that there is no specific morphological rubicon to be crossed to mark the appearance of modern humans. This view also implies that certain features that distinguish some modern groups were developed very early in our history, after the exodus from Africa. It is also important to recognize that not all features common to modern humans emerged at precisely the same time (Thorne 1981; Thorne and Wolpoff 1991; Wolpoff 1989a; Wolpoff and Thorne 1991; Wu 1988; Wu and Wu 1982).

Total Replacement: The Eve Theory

The total replacement theory proposes that modern humans are a new species that arose between 50,000 and 500,000 years ago (Stoneking and Cann 1989), a range often reduced to a date of 200,000 years ago. This represents the polar opposite of Coon's idea of independent lineages by postulating a unique African origin for all modern humans, and ultimately the descent of all races from a single African woman (see Vigilant et al. 1991 for the most recent statement). The theory relies on an interpretation of the genetic data, concluding that over a period as short as 50,000 years there was a complete replacement of all preexisting hunter-gatherers in Africa and the rest of the then-inhabited world.

The impetus for the Eve theory comes from the study of mtDNA. Some biochemists believe that the evolutionary record of this extranuclear organelle can be traced back to a single female, the putative Eve. Wilson's Eve theory (Cann, Stoneking, and Wilson 1987) thereby transformed the "out-of-Africa" explanation first proposed by Protsch (1975) into one of complete and total replacement of indigenous peoples around the inhabited world by "Eve's" descendants (Stringer and Andrews 1988a; Stringer 1990, 1992). According to this genetic interpretation, only mtDNA that can be traced to Eve is

found among living people. How could this be? If Eve's descendants mixed with other peoples as their populations expanded, we would expect to find the remnants of other mtDNA lines, especially outside Africa, where Eve is said to have originated (Cann 1988). This is because it is normal for genetic mixing to occur between invaders and residents, thereby perpetuating and even proliferating the mtDNA of the people being replaced. In modern examples of this kind, paradoxically, wherever major invasions have taken place, the resulting people of mixed descent often show a diminution of the physical features of the original inhabitants, but an expansion of their mtDNA variation. However, the mtDNA of Eve's contemporaries cannot be found among the people of today—only Eve's and that of her female descendants who replaced their contemporaries throughout the Old World is represented (Cann 1987, 1988; Cann, Stoneking, and Wilson 1987). The only credible explanation for the absence of other ancient mtDNA lines in modern humans is that none of the other people who lived in the distant past (or specifically none of their women) mixed with these invaders. Therefore, this mtDNA interpretation requires the assumption that there was no admixture between Eve's descendants and the people they replaced (Cann, Stoneking, and Wilson 1987). It is reasonable, if not necessary, to interpret the "no mixture" assumption to mean that Eve founded a new species, since by definition members of different species cannot have fertile offspring.

While it is not uncommon to find a specific geographic area where one animal species replaced another in a fairly short time period, what is unusual about this claim is the worldwide scope of the rapid replacement, occurring in diverse climates and physical environments. Moreover, this replacement is unlike examples from the animal kingdom, since it involves the worldwide extinction of human hunter-gatherers by other human hunter-gatherers. Even the best-documented case of competitive exclusion in the Hominidae, the replacement of *Australopithecus boisei* by *Homo*, took place over a period of more than one million years, measured by the unequivocal coexistence of at least two different species of hominids.

Points of Agreement

Even though the concepts in multiregional evolution and the Eve theory offer very different interpretations of modern human origins, there are several points on which both sides concur. While there is great controversy about the analytical procedures used to interpret mtDNA variation, both sides agree that genetic variation exists and is important. There is no serious dispute over the techniques that are used to generate data about variation. Both groups also accept the fact that the fossils represent a sampling of the humans living in the past. Beyond these basic admissions, both accept the mtDNA evidence as strong confirmation that all human beings are closely related. Both point to Africa as the original source of humanity, regardless of differences about the length of time over which modern human variation developed. There is agreement that only one mtDNA lineage, with a single origin, is found in the mtDNA of all living humans. And, finally, there is mutual acceptance of the fact that when Eve was supposed to have lived, some 200,000 years ago, there were other people spread all over the Old World, from the tropics to the temperate zones.

Contradictions and the Predictions that Can Resolve Them

In spite of these points of agreement, multiregional evolution and the Eve theory are largely contradictory (Wolpoff and Thorne 1991; Thorne and Wolpoff 1992). The most important consequence of the mtDNA studies is the unavoidable implication that one of the two views of modern human origins must be incorrect. There is no compromise *that incorporates elements of both* because the genetics make it clear that if there was a replacement, it must have been without admixture (Cann, Stoneking, and Wilson 1987). When authors such as Bräuer (1989) embrace the genetic evidence as supporting their position, they cannot validly claim to have an intermediate theory (e.g., Bräuer 1992), since the

geneticists have consistently argued against admixture. Contrary to Bräuer's contentions and Stringer's idea that different human species can have fertile offspring (Stringer and Grün 1991), any evidence of admixture between Eve's descendants and the natives they are said to have replaced entirely contradicts the Eve theory.

The fossils are the direct evidence for human evolution, and their role in the analysis of modern human origin theories is in their unique potential to refute these two models of recent human evolution. Their potential for refutation is high because the evidence for human evolution over the past million years is rich, in both human skeletal material and archeological remains. Unlike genetic data derived from living humans, fossils can be used to test predictions of theories about the past without relying on a long list of assumptions about the neutrality of genetic markers, mutational rates, or other requirements necessary to retrodict the past from current genetic variation. While the role played by mtDNA has been useful in theory formation, theories must be tested and only fossils can provide the basis for refutation. This is because the genetic information, at best, provides a theory of how modern human origins *might have happened* if the assumptions used in interpreting the genetic data are correct. One theory about the past, however, cannot be used to disprove another. As Stoneking and Cann (1989:24) once wrote, "it should be stressed that the transformation from archaic to modern humans is defined by the fossil and archeological evidence." Yet, more recently, Cann has argued that the fossils are of limited utility in reconstructing the past and that "fossils cannot be interpreted objectively" (Wilson and Cann 1992:68). Given the new developments in the mtDNA interpretations, this is an ironic statement. Moreover, we contend that those who would discard the remnants of the very past they seek to understand are in the position of historians who begin their study of a historical event by discarding all that was written when the event took place. Our attempt here is not to choose which data source is the better (in contrast with Wilson and Cann 1992), but is to synthesize as much as possible about what we know of modern human origins and test the fossil record against specific theoretical predictions.

In this context, we take the Eve theory as the null hypothesis. We propose here to examine five major predictions that are unique to the Eve theory and that diametrically oppose predictions drawn from multiregional evolution. We will use samples taken from the extensive record of human fossil remains and archeological sites to test both models, but will focus on the issue of whether the Eve theory can be refuted.

If the Eve theory is correct, a number of predictions distinguish it from multiregional evolution.

1. In a complete replacement of one worldwide human hunter-gatherer species by another, species change must have been highly competitive. If the present is any guide to the past, this replacement ranged from uneasy coexistence to violent extermination of the resident archaic groups by the new species. Moreover, we would expect the complete replacement to have involved a technological advantage at least as dramatic as the European expansions of the past several hundred years. These seldom *completely* replaced the native populations, even though in some cases this was the intent. We predict that there should be evidence of a spreading technological advantage in the archeological record that accounts at least in part for the replacement.

2. The evidence of the earliest modern people should be found in Africa. This is in accordance with the Eve theorists, coming from both the genetic (Cann, Stoneking, and Wilson 1987) and the paleontological (Stringer and Andrews 1988a) perspective.

3. Everywhere outside Africa the earliest modern humans should resemble these African ancestors and not the local people who lived there first. Here, we are testing the Stringer and Andrews (1988a) contention that modern people develop African features first in their continent of origin and then these populations spread throughout the world. It is not possible to test Bräuer's recent suggestion that the first moderns were a "less differentiated anatomical form" (1992) because it is not clear what this means. Given the fact that several anatomical definitions of "modern *Homo sapiens*" fail to include all living

people (Wolpoff 1986; P. Brown 1990), the features diagnosing their presence probably cannot be defined if none of them are unique to Africans.

4. There should be no anatomical evidence of mixing between the earliest modern African people and the populations they replaced.

5. In regions outside of Africa there should be no evidence of anatomical continuity spanning the period before and after the replacement event.

Archeological Evidence

For the first prediction we are troubled by a theory that must assume there was a total replacement of the hunter-gatherer populations of 200,000 years ago by another (presumably rapidly expanding) group of hunter-gatherers, because it would have involved the demise of people who had successful long-term occupations and adaptations to many different environments (Jones 1989; Pope 1988, 1992a). For instance, in northern China, Zhoukoudian Locality 1 was inhabited for as long as 500,000 years (Chia 1975; Pope 1992a). These inhabitants formed a succession of closely related peoples (Chiu et al. 1973; Wu and Lin 1983) with local cultural adaptations, such as traditional knowledge of the resource base and seasonal use of the environment. Yet, if the Eve theory is correct, we must assume that these successfully adapted natives were overrun by African invaders, who, in spite of their origin in a very different habitat, were somehow more successfully adapted both here and in every other inhabited environment. For these reasons we would expect the earliest modern humans to evince an adaptive and demographic advantage over the natives they replaced. In the quincentenary of the discovery of America by Europeans, we are reminded of the many hunter-gatherer groups that survived in both North and South America after the arrival of Europeans. These invaders came not only in large numbers, but with a collection of lethal diseases and an arsenal of technologies vastly more complex and destructive than those of the original inhabitants. This, at the minimum, provides an indication of what we might expect to find in the archeological record of modern human origins, if the Eve theory is correct.

The fact is, however, that a model of technological superiority is directly at odds with the archeological evidence. For instance, in eastern Asia the persistence through the Pleistocene of distinct, non-Acheulean lithic assemblages provides no evidence for the introduction of novel technology. The unique nature of the Asian Paleolithic record compels one to consider the implications of the fact that six decades of research have failed to show any indication of intrusive cultures or technologies. Artifact types recorded in Asia's earliest Paleolithic assemblages continue into the latest Pleistocene (Pope et al. 1990). If invading Africans replaced local populations, they must have fully adopted the cultures and technologies of the people they replaced, even as their own (presumably superior) cultures vanished without trace.

For these reasons, if a worldwide invasion and complete replacement of all native peoples actually took place, we should expect to find at least some archeological traces of the behaviors that made it successful. But are there any? In western Asia, where some researchers believe the earliest modern humans outside of Africa can be found at the Qafzeh site, there is no indication of an intrusive culture. Indeed, the superb archeological record at Qafzeh shows that these people had the same stone industries; that is, they made the same tool types with the same frequencies, manufactured these tools using the same technology, utilized the same stylized burial customs, hunted the same game, and even used the same butchering procedures as their Neanderthal contemporaries (Bar-Yosef 1987; Shea 1988, 1989; Speth, personal communication, 1991). By any archeological measure yet constructed, the Neanderthals and so-called moderns from Qafzeh participated in the identical culture. Moreover, at the time when Eve's descendants are supposed to have left Africa, there is no evidence for the emergence of any new African stone industry or other local African technology (Lindly and Clark 1990a, 1990b). This incongruity has led Klein (1992) to suggest that the *real* origin of modern humans was in a brain mutation

underlying the appearance of modern human behavior. Should this be the case, there is no anatomical evidence for where and when such a mutation took place, and no particular reason to believe it occurred in Africa.

In all, while the Eve theory clearly predicts certain behavioral consequences, the archeological data as we understand them refute these predictions and we conclude that there is no archeological support for the Eve theory. Perhaps this is why Alan Wilson turned to a different behavioral advantage, asserting in a talk before the American Association for the Advancement of Science that the invasion was successful because Eve and her descendants carried a gene for language ability in their mtDNA (M. Brown 1990). This proposal has failed to gain any kind of acceptance by either paleoanthropologists or geneticists. It directly contradicts the evidence from paleoneurology (Holloway 1983; Falk 1987) and would provide the strongest possible disproof for Wilson's own hypothesis of neutrality for mtDNA evolution.

The remaining predictions of the Eve theory relate to the question of anatomical evidence for abrupt change and the question of whether the earliest recognizably "modern" humans resemble earlier regional populations or Africans. With the fossil evidence known at this time, these questions can be unambiguously resolved by examining the fossil records for various regions of the Old World.

Southeast Asia and Australia

The hominid fossils from Australasia (Indonesia, New Guinea, and Australia), one of the most peripheral areas of long-term Pleistocene occupation, show a clear anatomical sequence (Wolpoff, Wu, and Thorne 1984) uninterrupted by African migrants at any time. This sequence has two important characteristics: (1) large samples that are transitional between the earliest Indonesians and the recent and living Australians, and (2) long-term persistence of certain morphological features that reflect the genetic continuities linking these populations over hundreds of millennia. The distinguishing features of the earliest "Pithecanthropus" remains, dated to about one million years ago, show that these regional characters were already developed at the time the region was first inhabited. Unique to the region, the characteristic features of the ancient Javan people lie in the pattern of their overall cranial robusticity and the detailed morphology of their faces (Pope 1991; Thorne and Wolpoff 1981, 1991; Wolpoff, Wu, and Thorne 1984).

Compared to other contemporary populations, the Javan people (Figure 2) have a *distinctive combination* of cranial features (Habgood 1989a; Thorne and Wolpoff 1981). These include (1) thickened vault bones, (2) a long, flattened frontal squama whose anterior edge merges into (3) strong, continuous browridges forming an almost straight bar of bone across the orbits, (4) a posterior position for the minimum frontal breadth, and (5) a prebregmatic eminence. Facial features can be generally described as involving (6) large projecting faces with (7) massive, rounded cheekbones, especially in the males, facing in an anterolateral direction; (8) postcanine teeth are among the largest to be found anywhere at that time, and while large postcanine teeth can be found in all Pleistocene populations, it is interesting that, holding sex constant, average postcanine tooth size does not change in this clade until the Holocene (Thorne and Wolpoff 1981), making the (9) *pattern of dental reduction* an additional regional feature. Details of the face include (10) a "rolled edge" on the lower margin of the orbits, (11) a distinctive ridge on the cheek at the zygomaxillary suture, and (12) a nasal floor that flows out smoothly onto the face. In the case of this aspect of nasal floor anatomy, other later populations such as some modern Africans also possess the feature. What makes it important here is the fact that it characterizes the Australasian peoples both in the past and today *in combination* with the other features we have found.

The presence of this complex of features distinguishes the fossil Javans from groups in other areas. After all, the humans we have compared belong in the same species, and we can hardly expect that, within species, regional groups can be characterized by single



Figure 2

Australasian craniofacial features: (a) Sangiran 17, (b) Willandra Lakes 50, (c) Border Cave (an African Eve), (d) Kow Swamp 1. The multiregional continuity model recognizes morphological links among a, b, and d attributed to close phylogenetic relationship. In the African Eve model only c can have ancestry to d.

unique features that do not appear elsewhere. That would assume the virtual isolation of human populations and would suggest that the trait's categorization as a variant within a species might be incorrect. To the contrary, it is our expectation that *combinations* of features with differing frequencies diagnose groups in the past, just as they are important in forensic diagnoses of racial identification (Stewart 1979).

This unique combination of regional features of the Javan morphology was stable for at least 700,000 years, while other characteristics continued evolving. The more recent Javan remains have expanded brains that have reached the modern range, but the crania that are known from Sambungmachan (Jacob 1976) and the later Ngawi and Ngandong people (Weidenreich 1951) are otherwise remarkably similar to the earlier individuals. In particular, the large cranial series from Ngandong, which recent evidence suggests may be only about 100,000 years old (Bartstra, Soegondho, and van der Wijk 1988), is a striking demonstration of this.

The earliest Australians arrived by sea before 60,000 years ago (Jones 1989). The first inhabitants are clearly modern, as judged by their behavior and anatomy. Yet, their skeletons show the continuing presence of the Javan complex of features, along with further braincase expansions and other modernizations (Wolpoff, Wu, and Thorne 1984). Several dozen well-preserved Late Pleistocene/Early Holocene fossils demonstrate three things: (1) the continued regionality of the combination of Australasian skeletal features described above, (2) the Javan source area for the majority of Australia's first colonists, and (3) the fact that the combination of features that distinguishes modern Australoids from other living human populations is precisely that which distinguished their regional predecessors from their contemporaries in East Asia, Africa, and Europe (Thorne 1980; Wu 1987). These linking features are not limited to the vault and facial features we listed above. For instance, Kramer (1991) has isolated seven features in the fragmentary Middle Pleistocene Indonesian mandibles that uniquely resemble modern Australians and differ from the African descendants of Eve.

The situation in Java itself is less clear. The populations of today are heavily influenced by relatively recent invasions from the Asian mainland, to which Java was connected during the lowered sea levels of the glacial maxima. Exactly when and how this happened is uncertain, as the Indonesian fossil record is lacking between the time of the Ngandong folk and the Mesolithic remains from Wadjak.

In spite of this wealth of detail, several authors have questioned the evidence for continuity in Australasia, beginning with the "Eve" theorists Stringer and Andrews, who attributed the Australian evidence to pathology (1988a:1266, 1267) or cultural practices (1988a:1267; see also Tattersall and Delson 1984). Also, Rightmire (1988) has challenged the morphological intermediacy of the Ngandong hominids. Most recently, Stringer (1992) proposes an "outgroup comparison" to analyze the regional features shown in the Willandra Lakes cranium WLH 50, and, like Groves before him (1989), does it incorrectly. While Groves chose a different outgroup to ascertain the character states for each comparison in his analysis, Stringer (1992:table 1) confuses the sample being compared to WLH 50 with the outgroup that is supposed to be used in judging the character states for the comparison. Thus, he never provides an actual outgroup for his "outgroup comparisons," and there is no way of accounting for the basis of his determination that some of the character states are "primitive." Formal outgroup analysis, the weakness in each of these studies, is problematic within species under the best of circumstances, since it involves determining the character states of features that vary within the species being analyzed.

However, comparisons are critical and we have compared WLH 50 with the Ngandong sample and with an early African Eve (Table 1), to ascertain how this particular trichotomy would be resolved by a series of features with unknown character polarities. The Eve theory requires that WLH 50 must be in a sister group to the African Eves, while the multiregional prediction is that the earlier and later Australasians will be more closely linked. We chose Ngaloba (LH 18) to represent the Eve population because it is the most complete of the *earliest* African Eve crania (the other specimens are from the Late Pleistocene) accepted by the two Eve theorists (Bräuer 1992; Stringer 1992). In our analysis (Table 1) we were able to find 12 features that linked WLH 50 with the Ngandong sample to the exclusion of Ngaloba, *but not one feature* that linked WLH 50 and Ngaloba to the exclusion of the Ngandong sample, as the Eve theory would require. All of these links cannot be simply discarded as "primitive retentions"—an argument that the Eve theorists apply to all evidence of continuity, even when different character states of the same feature are involved. Moreover, if comparisons to the African crania from the earlier Lower Pleistocene (such as ER 3733 and ER 3833) are valid, a number of these features must be regarded as synapomorphies. Wilson criticized multiregional evolution on the grounds that it is not based on statistical analysis (see Vigilant et al. 1991). We do not think there is sufficient information to accurately calculate the probability that 12 features link WLH 50 and Ngandong, while none exclusively link WLH 50 and Ngaloba.

Table 1
Features linking the Ngandong crania with the Australian Willandra Lakes hominid 50 (WLH 50) that are *not* found in the African Ngaloba specimen (LH 18).

	Shared condition in the Australasian specimens Ngandong and WLH 50	Condition in Ngaloba (LH 18)
Greatest cranial breadth	At the cranial base, across the supramastoid crests	Medium to high across the parietals
Parietal boss	Absent	Distinct
Angular torus	Pronounced	Absent
Form of the external mastoid process triangle	Height much greater than basal width	Approximately equilateral
Sagittal keel	Marked on anterior half of the parietals	Absent
Sagittal region at bregma	Smooth	Slight bulge at bregma with a postbregmatic depression
Sagittal length of the frontal	Relatively long compared to vault length	Relatively short compared to vault length
Sagittal curvature of the frontal just above the supraorbital region	Relatively flat and uncurved	More curved
Ridge for the temporal line	Extends across the entire frontal	Only encompasses the temporal notch
Nuchal torus and supratoral notch	Both present; torus projects markedly	Both absent
Inion	Strong, inferiorly pointing triangle extending onto the nuchal plane, beginning above it	No special inion prominence
Occiput along the lambdoidal suture at or near the midline	Distinctly bulging parallel to the suture	Flat along the suture

Yet, we suspect that if such a probability could be calculated, it would reach impressive statistical significance.

In sum, the assertions that the fossil evidence for links between the Sangiran people and many of today's Australians are poor, or that they are based only on "primitive" characters, are demonstrably incorrect. In the face of these data, the only way that the Eve theory could be correct is if these resemblances, spanning 750,000 years, were accidental. If the earliest Australians were uniquely descended from Africans, as the Eve theory predicts, this would mean that the continuity we observed was merely apparent. It would imply that all the cranial, facial, and mandibular features evolved a second time, while the African features disappeared without trace. Evolution of an individual feature a second time would be rare, but the repetitive evolution of a complex of features is improbable to the extreme. Homoplasy at this level of detail is unheard of in the history of evolutionary biology.

North Asia

In northern Asia there is considerable evidence of anatomical links across time and of transitional specimens that connect the area's ancient to its modern inhabitants. What makes this evidence a convincing rebuttal of the Eve theory is the fact that the links in-

volve different features than those in the south, discussed above and in Wolpoff, Wu, and Thorne (1984) and Wu (1987). Patterns based on a separate set of features of the face and forehead show that the different southern and northern Asian links are unlikely to be fortuitous. In China, there is a continuous sequence of human fossil remains, both earlier and later than the "Sinanthropus" site of Zhoukoudian Locality 1. The very earliest Chinese fossil crania, perhaps slightly older than one million years (Pope 1988, 1991), differ from their Javan counterparts in many ways that parallel the differences between North Asians and Australians today. The Chinese fossils are less robust and have smaller faces and teeth, flatter, flaring cheeks in a very anterior position, and rounder foreheads separated from their arched browridges. Their noses are much less prominent and flattened at the top.

This combination continues at Zhoukoudian, where a full third of all known Middle Pleistocene human remains have been found, including six partial crania (Weidenreich 1943; Chiu et al. 1973). Here, there are specimens with larger brains and other features that show the evolution of ancient Chinese in a modern direction. As Wu demonstrated in a review of the site (Wu and Lin 1983), evolutionary changes in the modern direction can be established within the 150,000 or more years spanned by the Zhoukoudian occupation. Also, Zhang (1991) was able to show a parallel modernizing trend in the Zhoukoudian dentitions. Moreover, even the latest-dated of these Middle Pleistocene humans, such as the Hexian partial cranium, shows both obvious morphological tendencies in the direction of modern humans and specific anatomical affinities to the Zhoukoudian sample (Pope 1991).

The origin of the complex of multiple characteristics that distinguishes the modern Asian face is to be found in the Chinese fossil record of the last million years. In addition to the features described above, which characterize the earliest fragmentary specimens, the most distinctive midfacial features include relatively horizontal and anteriorly facing cheekbones, anteriorly facing frontal process of the maxilla with distinct paranasal inflation, and the frequent presence of a distinct notch along the lower border of the cheek. Perhaps the most inarguable indication of morphological continuity is the high frequency in living Asians of the strong manifestations of maxillary incisor shoveling (Cadien 1972), which also characterizes virtually every fossil Asian hominid preserving the anterior teeth. Moreover, the morphology of Asian shoveling is different from that of populations further west (Crummett 1991) and incisor shoveling is rare in fossil and recent Africans (see below).

After the Zhoukoudian material, crania from Dali (Wu 1981) and Jinniushan (Lü 1991) in northern China and Yunxian (Li and Etler 1992) to the south—dated to the late Middle Pleistocene—illustrate the continuing modernization of the Chinese cranium. These specimens also provide the strongest evidence of a unique regional craniofacial complex that links the earliest remains to modern Chinese populations (Pope 1991; Wolpoff 1985). There is no evidence of African anatomical features, even though such evidence is required by the Eve theory for specimens from this time span. With respect to the later Middle Pleistocene in northern China, Bräuer (1992) has argued that morphologically and chronologically transitional samples exist only in Africa. But our examination of Jinniushan suggests just the opposite, especially since the facial features of Jinniushan so closely resemble the Zhoukoudian female remains, while the cranial vault is quite modernized in its thin bones, smooth occiput, and enlarged cranial capacity. For Dali, Wu (1988, 1989, 1990, 1991) has demonstrated that a number of its features may be considered transitional. Moreover, in the similarly dated Xujiayao sample (Jia, Gai, and You 1972; Jia, Wei, and Li 1979) at least 11 individuals are represented and these include a mosaic of archaic and modern features (Pope 1992b). Other specimens, such as Hexian and Yunxian, have been a continuing source of taxonomic controversy because of their morphologically intermediate anatomy (Li and Etler 1992; Pope 1992b; Rightmire 1990). Statements contending that transitional fossils are *only* found in Africa are certainly not supported by the skeletal record in North Asia.

The later remains from China, right down to the Zhoukoudian Upper Cave specimens to the north and the Liujiang skeleton to the south, reflect the consequences of a smooth transition into the living peoples of North Asia (Turner 1987; Stringer 1989). While we believe there was gene flow in and out of the region throughout the Pleistocene, this evidence unequivocally demonstrates the absence of a complete invasion and total replacement by modern (or other) Africans.

In spite of the overwhelming evidence in the Chinese fossil record, some of the Eve proponents continue to declare that all early *Homo sapiens* specimens display essentially the same morphology, regardless of their geographic location (Bräuer 1990; Stringer 1992). For instance, the recent assertion that “rather generalized ‘archaic *sapiens*’ populations [are present] in both Africa and East Asia in the middle-early Late Pleistocene” (Stringer 1992:21) runs completely counter to the morphological distinctiveness of specimens such as Dali, Jinniushan, and Yunxian (Li and Etlar 1992; Pope 1991, 1992b) from other roughly contemporary specimens from Africa (e.g., Bodo and Kabwe) and Europe (e.g., Petralona and Arago). Even a cursory comparison of published line drawings of these specimens (compare facial and lateral views of Dali with Bodo, Kabwe, Petralona, and Arago in Larsen, Matter, and Gebo 1991) shows that Dali is fundamentally different in browridge morphology, forehead pattern, maxillary notch, and facial size and morphology. Holding sex constant, these same features are not characteristic of the vast majority of middle-early Late Pleistocene *Homo* from outside the region. While some of these features occur in much later African specimens (such as Djebel Irhoud), they have a much greater antiquity in the East. Their appearance in Late Pleistocene North Africans is perhaps the result of gene flow from east to west, rather than from the opposite direction. They may also represent parallelisms across the areas.

Further confusing this issue, Stringer (1992) has suggested that ostensibly North Asian features of anatomically modern humans occur in high frequencies in subfossil North Africans. There are problems with this assertion since, in the first place, it contradicts Stringer’s 1989 analysis, which clusters the Zhoukoudian Upper Cave material with Asians and Amerinds, and not Africans. Second, he uses features that purportedly mark regional morphological variation (Stringer 1992:18) to argue that North Asian regional features are in fact not localized, but widespread across the Old World. However, most of the traits he uses are not included in any recent evaluation of regional morphological variability nor in recent definitions of the North Asian clade (Pope 1991; Wolpoff, Wu, and Thorne 1984). Some are not even traits under genetic control. For example, relying upon Weidenreich’s 1939 list, Stringer includes “ear exostoses” as an Asian marker. Yet, it has been known for some time that this trait has no genetic basis. Rather, auditory exostoses originate from the exposure of the ear channel to cold water (Kennedy 1986) and are completely mediated by the environment. Thus, the distribution of auditory exostoses across the populations of the world tells us nothing about phylogenetic relationships.

This is not the only weakness in his “test.” We have great difficulty in verifying Stringer’s (1992) finding that “Mongoloid” features are also well represented in recent North African materials. One example will suffice. Upper incisor shoveling is listed as a trait that occurs at a frequency of “>70%” at Jebel Sahaba and Wadi Halfa in the Sudan of North Africa (Stringer 1992:18). Data to support this unusually high frequency are taken from Anderson (1968), Greene and Armelagos (1972), and Greene, Ewing, and Armelagos (1967). However, observations published by these authors are not directly comparable. Anderson (1968) used a three-category scoring technique for shoveling (none, +, ++), while Greene, Ewing, and Armelagos (1967) scored incisor shoveling with a four-category scale (none, trace, semi, shoveled). The degree of incisor shoveling varies continuously and, consequently, the degree of expression is subjectively determined. Many dental anthropologists use Hrdlička’s (1920) four state designations and combine the “semi and shoveled” categories as shoveled (Dahlberg 1949). However, it is inappropriate to combine all categories other than “none” to define incisor shoveling in the North

African samples. This is because “trace” is not equivalent to the higher categories. Thus, it is methodologically invalid for Stringer to collapse the data reported for Jebel Sahaba and Wadi Halfa. Using only the Wadi Halfa material, we report frequencies of maxillary incisor shoveling for European, African-American, and Asian populations from Hrdlička’s (1920) seminal study in Table 2. It is obvious that incisor shoveling at Wadi Halfa is *not* similar to the Asian pattern. The Chinese in this sample, and East Asians more generally (Cadien 1972), are unique in their very high frequency of the most marked expression for shoveling. The only way to arrive at shoveling frequencies of “>70%” reported by Stringer (1992:18) is to combine “trace,” “semi,” and “shoveled” into a single category. But combining shoveling categories in this manner is biologically meaningless and misleading, and the statistic cannot be validly compared with the very high frequencies for the “marked” shoveling category reported for East Asians. We agree with Stringer (1992:16) about the “great need for comprehensive critical reviews of [regional] characters, their precise definitions, variation and regional significance,” but his analytic procedures have serious shortcomings that do not comply with these recommendations. From our analyses of the East Asian materials, we find undeniable evidence for the development of distinctive morphologies that are not only specific to the region, but that also persist over the long sequence of fossil to many recent and living Asians.

Europe

The case for continuity in Europe has the most contentious history, primarily because of the deep-seated opinion in Europe and the United States that Neanderthals could have had nothing to do with subsequent European human evolution (Spencer 1984). Statements abound in the literature that Neanderthals possess a series of unique features not found in later Europeans (Santa Luca 1978; Stringer, Hublin, and Vandermeersch 1984; Stringer and Andrews 1988a) and that Upper Paleolithic groups are “instantly recognizable” as being modern humans (Howells 1981). In this tradition, Stringer attempts to use the question of regional continuity in Europe to refute multiregional evolution:

If it can be shown that the construction of detailed gradualistic evolutionary trends from Neanderthals to moderns is misleading [in Europe] where the fossil record is most complete, it should give a clear signal about the reliability of similar constructions based on less complete material from south west Asia and the Far East. [Stringer 1992:14]

Such a Eurocentric interpretation ignores the rich fossil record for East Asia we have reviewed above, the marked variability of European Neanderthals (Brose and Wolpoff 1971; Wolpoff 1980), and the demonstrable trends over time in a number of metric and

Table 2
Incidence of shoveling in European, African-American, and Chinese samples compared to the Wadi Halfa Mesolithic sample.

	No shovel	Trace	Semi-shovel	Shovel-shaped	Sample size
Europeans ^a	62.5	28.5	7.4	1.6	1,000
African Americans ^a	51.0	35.0	9.9	4.1	807
Chinese ^a	8.3	1.4	23.2	67.2	651
Wadi Halfa ^b	22.2	55.6	11.1	11.1	9

^aFrom Hrdlička (1920:453); represents an average for males and females and for central and lateral incisors.

^bFrom Greene and Armelagos (1972:31). These authors report shoveling for central and lateral maxillary incisors grouped together. They divide shoveling into “child” (deciduous) and “adult” (permanent) categories. Since shoveling in deciduous teeth shows a different expression than permanent incisors, there is no justification for combining them with the permanent ones (Greene, personal communication, 1992). Only permanent upper incisors are reported here.

morphological features toward the more modern condition (Frayer 1978, 1992a; Smith 1978, 1991, 1992a; Smith and Ranyard 1980; Wolpoff 1975, 1989b). Besides these problems, others have implied that once the Upper Paleolithic is reached, all the features that characterize living Europeans are established (Andrews and Stringer 1989; Campbell 1992; Howell 1984; Klein 1989) or that the Upper Paleolithic Europeans are just "robust" without any archaic retentions (Gambier 1989; Howells 1973). Some assume that no transitional fossils exist and that none of the Neanderthal features continue into the Upper Paleolithic, as the Eve theory requires (Stringer and Andrews 1988a). Still others, in the absence of any documentation, suggest that "the ancestors of the inhabitants of Europe . . . consisted of modern Africans with some admixture of Neanderthals" (Bräuer 1989:138).

However, the rich skeletal record from the Middle and Upper Paleolithic of Europe rejects each of these contentions. Evidence represented in the fossil record of late Pleistocene Europe demonstrates a persistence of so-called unique Neanderthal features over time, bridging the populations of the Mousterian and Upper Paleolithic. Contrary to Bräuer's recent pronouncement that there is a "large and generally recognized morphological gap between the Neandertals and the early moderns" (1992:93), the actual evidence provided by the extensive fossil record of late Pleistocene Europe shows considerable continuity between Neanderthals and subsequent Europeans.

For example, browridge size and form show clear trends in reduction from the Mousterian to the early Upper Paleolithic for sites in Central Europe (Smith 1982, 1984, 1985, 1992a; Smith and Ranyard 1980; Wolpoff et al. 1981). As shown in Figure 3, browridge size reduces from the early Mousterian (Krapina) to the late Mousterian (Vindija) to the early Upper Paleolithic (Velika Pećina) condition. Accompanying this reduction in supraorbital dimensions is a continuity in morphological patterning over time, showing that the evolution of this feature in Europe is not simply one of gracilization, with reduction only a consequence of metric changes in robustness. Beginning with the continuous supraorbital torus in the Krapina Neanderthals, in the Vindija brows the overall dimensions are reduced and the supraorbital torus is broken by a thinning (or pinching) in the midorbital region. Simultaneously, the medial portion of the torus becomes vertically taller over the nose (Wolpoff 1989a). In the subsequent early Upper Paleolithic brow-

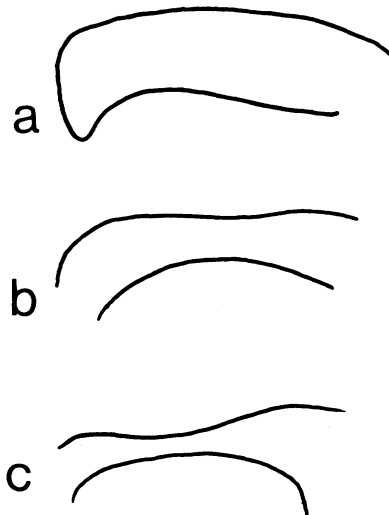


Figure 3

Browridge changes in Central Europe: (a) Krapina 28, (b) Vindija 202, (c) Velika Pećina 1.

ridges these trends continue, with the midorbital region becoming further reduced, but maintaining the midorbital pinching. In addition, the medial region attains an even greater vertical height. Metrically and morphologically, then, the Central European sequence shows continuity across time, a pattern inconsistent with the predictions of the Eve model. Despite attempts to discount the importance of this continuous evolutionary sequence (Bräuer 1992), as Smith and Raynard wrote more than a decade ago, the brow-ridge morphology shown by the Neanderthals at Vindija “is precisely the pattern of reduction one would expect in a morphologically intermediate form between the Krapina Neandertals and early modern *Homo sapiens*” (1980:605).

Moreover, there is other evidence of a transitional nature in these late-dated Vindija Neanderthals. Additional intermediate features or those specifically resembling the subsequent European populations include nasal narrowing, anterior tooth size reduction, shortened retromolar space in the mandibles (Figure 4), and a more anterior position of the mental foramen (Wolpoff et al. 1981). We find it difficult to understand how Bräuer (1992) can dismiss the relevance of this sample—accepted by virtually all other workers, including Stringer (1992)—but at the same time regard the much smaller and more fragmentary Klasies specimens (see below) as the centerpiece of the theory that modern humans originated in Africa.

Evidence of a transition is not limited to Central Europe. The late French Neanderthal from Saint-Césaire (Vandermeersch 1984, 1985) shows a number of features approaching the “modern” condition. Many of these parallel the transitional features noted for Vindija. These characteristics include markedly reduced lateral supraorbitals, a narrow nasal breadth, squared orbits, an incipient chin (certainly much more developed than three of the Klasies mandibles [KRM 13400, 21766, and 14695] which are considered “modern”), and anterior tooth size reduction. While other features align Saint-Césaire with earlier Neanderthals (such as the degree of total facial prognathism), and we regard it, like the Vindija specimens, as an example of the Neanderthal population, the specimen clearly shows transitional features in the direction of the Upper Paleolithic.

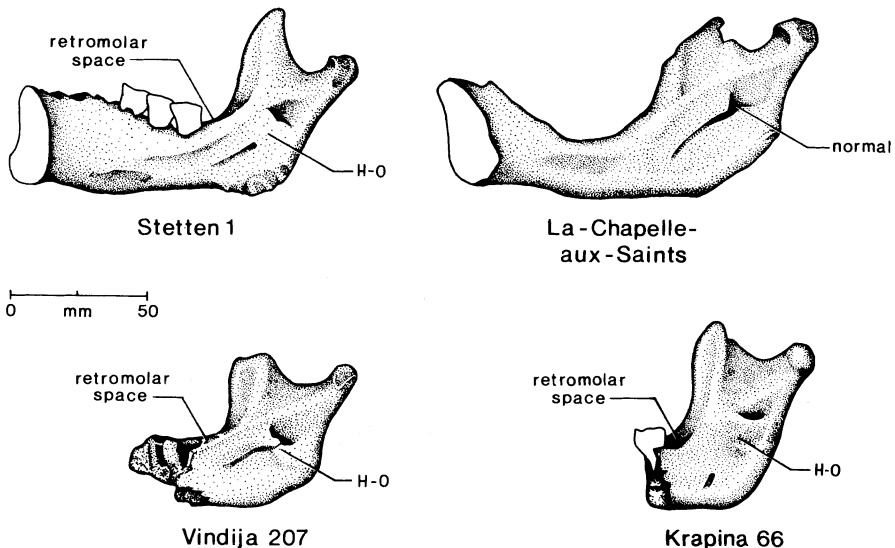


Figure 4

Normal and horizontal-oval (H-O) mandibular foramen in European Neanderthal (La Chapelle-aux-Saints and Krapina 66) and early Upper Paleolithic (Stetten 1 and Vindija 207) specimens.

Some do not consider Saint-Césaire a transitional specimen because it possesses some “typical” Neanderthal features (Stringer and Grün 1991). Yet, the mosaic nature of the specimen is exactly what one would expect if Neanderthal populations were evolving into later *Homo sapiens* (Wolpoff 1989b; Wolpoff and Frayer 1992). Others who do not consider it transitional (cf. Bräuer 1992) provide no observations or metrical data to support their assertions. Transitional specimens by their very chronological placement contain features of the past and harbingers of the future, and while Saint-Césaire is clearly different in some respects from the Upper Paleolithic people who succeed it, the specimen also exhibits substantial and important differences from Neanderthals that predate it. Finally, some have denied that Saint-Césaire can be transitional because it is contemporary with modern populations (e.g., Stringer 1988; Stringer and Grün 1991). Yet, it is important to note that there is currently no fossil evidence that demonstrates the coexistence of Neanderthals and more modern people in Europe (Wolpoff and Frayer 1992). Stringer’s (1992) assertion that Saint-Césaire cannot be considered transitional because it is contemporaneous with the modern hominids of the European early Aurignacian is invalid because no modern hominids have been clearly associated with the European early Aurignacian. Unless an unwarranted correlation between human types and stone tool industries is accepted, the European fossil record shows that these two groups were *not* contemporary.

In addition to specimens that bridge the gap between Neanderthal and Upper Paleolithic morphology, it is possible to assess the persistence of morphological features considered typical of Neanderthals into later populations. The persistence of a large number of features is improbable if Neanderthals were completely replaced or “swamped out” by an invasion of people from Africa (or anywhere else). All the features we discuss here were originally compiled to demonstrate the uniqueness of European Neanderthals (Stringer, Hublin, and Vandermeersch 1984:55) and are regionally autapomorphic in European Mousterian groups, not plesiomorphic retentions. Following the predictions of the Eve theory, if European Neanderthals were completely replaced by invading Africans, common and unique features of Neanderthals would not be expected in the people who followed them in Europe, unless these identical features evolved a second time in the descendants of the purported African invaders. On the other hand, the multiregional evolution model would be supported if marker or regional features of the Neanderthals persist into the Upper Paleolithic. As with the Asian sequence for morphological continuity, rather than an acceptance of the convoluted reasoning that the exact same features evolved twice in succession for a particular region, which would be required with the Eve model, the persistence of “unique” Neanderthal morphologies into the Upper Paleolithic would be powerful evidence contradicting the Eve hypothesis.

With regard to the European sequence, Stringer and Andrews assert that

there is little or no continuity in 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. [1988a:1266]

This statement is not accompanied by a list of features to support such a contention, and, to the contrary, with few exceptions it is common to find Neanderthal features that Stringer himself has regarded as “genuine” in the succeeding Upper Paleolithic hominids. One example is the horizontal-oval (H-O) mandibular foramen. Located on the internal surface of the lower jaw, this morphological feature consists of a broad bar of bone spanning the most superior portion of the mandibular foramen. Because of the bony bar, this foramen takes on an oval shape (Figure 4). This condition contrasts with the configuration in living *Homo sapiens*, in which the bridge is generally absent and a groove separates the anterior and posterior regions below the mandibular foramen, making the rim of the mandibular foramen discontinuous.

First described by Gorjanović-Kramberger (1906) for the Krapina mandibles, presence of the H-O mandibular foramen is considered a common characteristic of Neander-

thals by Stringer, Hublin, and Vandermeersch (1984:55). In 1978, Smith reviewed the variation on the H-O and normal patterns in Neanderthals and subsequent humans, arguing that the feature is a nonfunctional, discrete trait and serves as a marker for Neanderthals. Indeed, the H-O mandibular foramen is found very rarely outside Europe and Western Asia. While present in some Levantine Neanderthals, it is not found on the mandibles from Skhūl or Qafzeh. Except for an archaic *Homo* mandible (OH-22), it is totally absent in all known Pleistocene mandibles from Africa, including the single mandible from Klasies River Mouth which preserves this anatomical region (KRM 16424). However, the identical H-O feature commonly occurs in the earliest Upper Paleolithic sample (Fraye 1992a). In European Neanderthals the H-O form is found in about 53% of known individuals, while in the early Upper Paleolithic sample its incidence is 25% (Table 3). In the late Upper Paleolithic the frequency of the H-O pattern drops below 7% and reaches frequencies less than 2% in the Mesolithic and Medieval Hungarian samples. Thus, compared to European Neanderthals, the frequency of the H-O mandibular foramen is lower in the early Upper Paleolithic, but it is obviously neither "rare" nor "absent." Coupled with the fact that the H-O pattern is not found in the fossil Eves from Western Asia or Africa, the persistence of this "typical" Neanderthal trait into the Upper Paleolithic contradicts any hypothesis that demands total populational replacement.

In addition to this trait, there are other Neanderthal autapomorphies (mastoid tubercle, retromolar space, lambdoidal flattening, suprainiac fossa, dorsal scapula border, proximo-lateral femoral flange) that are anything but rare in the Upper Paleolithic (Fraye 1992a, 1993; Smith 1982, 1992a, 1992b; Trinkaus 1987; Wolpoff 1980, 1989b). Another feature considered unique (or as an evolutionary reversal) is the flattening of the cranial base, which has led to speculations of linguistic deficiencies in Neanderthals (Lieberman and Crelin 1971; Laitman, Heimbuch, and Crelin 1979). However, with the new reconstruction of La Chapelle-aux-Saints (Heim 1989) and expansion of the comparative sample to the Upper Paleolithic and Mesolithic (Fraye 1992b), cranial base flattening can no longer be demonstrated to be significantly different between Neanderthals and later *Homo sapiens*. In short, while no one would argue that European Neanderthals are identical to the succeeding Upper Paleolithic people, the two groups share a number of cranial and postcranial nonmetric features signaling regional continuity. As with other geographic areas, the more modern inhabitants bear the morphological marks of their more archaic forerunners.

Finally, it has recently been suggested that body proportions and stature of the earliest Upper Paleolithic specimens support an African ancestry: "early modern humans look like they walked straight out of Africa" (Ross 1991). From this statement, one might presume that there is reliable postcranial evidence for the African Eve fossils. Yet, to the

Table 3
Mandibular foramen types in European Neanderthal, African Eves, Skhūl/Qafzeh, early Upper Paleolithic, late Upper Paleolithic, Mesolithic, and Medieval samples.

	Horizontal-oval		Normal	
	%	(n)	%	(n)
European Neanderthals	52.6	(10)	47.4	(9)
African Eves	0.0		100.0	(1)
Skhūl/Qafzeh	0.0		100.0	(2)
Early Upper Paleolithic ^a	25.0	(4)	75.0	(12)
Late Upper Paleolithic ^a	6.7	(2)	93.3	(28)
Mesolithic	1.9	(3)	98.1	(158)
Medieval Hungarians	1.4	(3)	98.6	(205)

^aThese frequencies differ from Fraye (1992a:table 2) as a result of expanding the time range of the early Upper Paleolithic sample.

contrary, there is no consistent picture of body size in this sample, and nothing is known of proportions. A newly excavated humerus shaft from Border Cave is quite large, while in contrast the Klasies mandible and postcanine dentitions KRM 16424 and KRM 14695 are so small that any recognition of tooth-body size scaling in humans (Wolpoff 1985) would suggest exceedingly small individuals.

Moreover, climate-body size correlations are confusing at best for supposed warm- and cold-adapted samples from Europe and Western Asia. It is broadly assumed that the European Neanderthals have a cold-adapted body shape, fitting both the Bergmann and Allen "rules" in their large bulk and relatively short distal limbs (Coon 1962; Stringer 1984; Trinkaus 1981; Wolpoff 1980). The problem comes with the succeeding Upper Paleolithic Europeans. Their longer limbs, whether expressed as limb-trunk ratios or as relative distal limb lengths, are taken by some (Stringer 1984; Trinkaus 1981) to indicate a southern (heat-adapted) ancestry. Wolpoff (1989b) has questioned this interpretation because Upper Paleolithic populations exhibit no evidence of postcranial adaptations to the cold climate of late Würm Europe.

[If] post-Neanderthal populations of Europe show longer distal limb segments because they were descended from warm-adapted populations, . . . why, then, didn't the succeeding European populations also eventually develop short distal limb segments? [Wolpoff 1989b:122]

The answer often given is that culture is presumed to be a better climatic buffer in the Upper Paleolithic. But the early Upper Paleolithic Europeans have high brachial and crural indices, considerably higher than Lapps and Eskimos, who have lived in frigid climates for a much shorter period of time, presumably with even better cultural buffers but nevertheless adjusted to cold with distal limb shortening, if cold is indeed the catalyst. Equally important is the fact that limb-segment indices show no trend over time in Europe, but remain high throughout the Upper Paleolithic and into the Mesolithic (Frayser 1993). This is not what one would expect if the Upper Paleolithic Europeans were heat-adapted (African) populations, adjusting biologically to the cold of the most extreme Würm maxima.

In contrast to the completely stable limb indices, stature shows marked fluctuations from the beginning to the end of the Upper Paleolithic. As shown in Figure 5, the earliest Upper Paleolithic specimens have low statures within the European Neanderthal range and at the lower limits of the Skhül-Qafzeh range. Then, just before 20,000 years ago, body size increased dramatically, so that the highest statures in post-Neanderthal Europe occur in the period of the greatest cold. This is followed by a substantial decline in stature after 20,000 years ago. Upper Paleolithic Europeans have been likened to Africans in their combination of long distal limbs and great stature (Trinkaus 1981). However, if tallness is an indication of African ancestry, it is the Upper Paleolithic people from just before 20,000 years ago who look like Africans, and not their earlier Upper Paleolithic ancestors. In fact, samples from the earliest part of the Upper Paleolithic resemble European Neanderthals in stature as much as they do their undisputed descendants from the later Upper Paleolithic.

In summary, despite the long-standing notion that there is a great anatomical gap between the European Neanderthals and the populations that followed them in Europe, a number of features of the cranium and postcranial skeleton provide evidence for continuity between the two groups. This does not mean that European Neanderthals were exactly like the Upper Paleolithic people, but rather that Middle and Upper Paleolithic Europeans share morphological links over time. It is impossible to regard these persistent morphological traits as "questionable frequencies of features whose relevancies are themselves frequently questionable" (Bräuer 1992:95). Such a perspective ignores the extensive data for the Late Pleistocene Europeans, misconstrues the reasons for focusing on Neanderthal autapomorphies, and is especially peculiar given the fragmentary nature of the African Eve skeletal record, discussed below. Thus, despite the assertions of a "generally recognized gap" that invalidates any connection between Mousterian and Upper

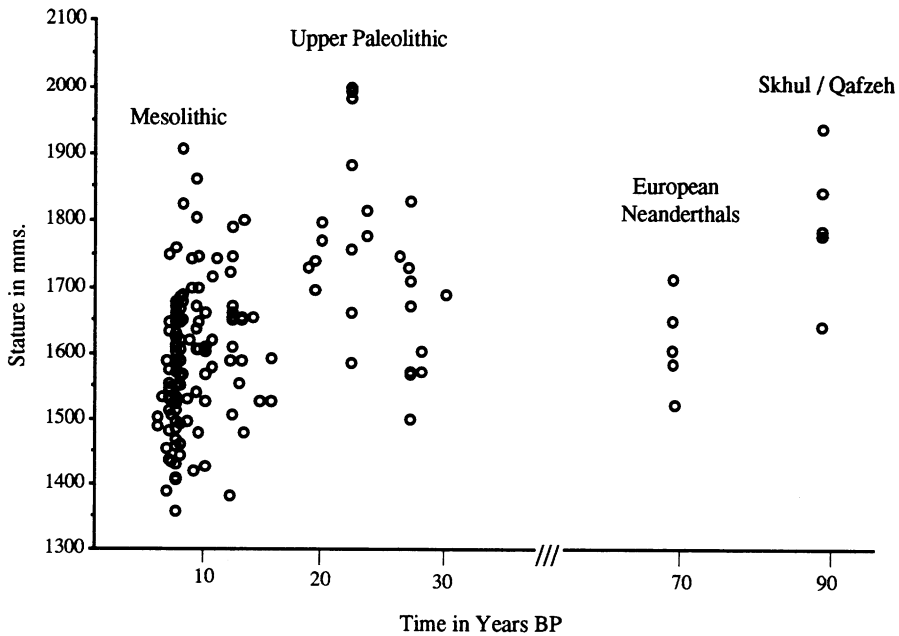


Figure 5
Stature trends in the European Late Pleistocene.

Paleolithic populations in Europe, actual analysis of specific morphological traits reveals considerable evidence to support a measure of continuity. Such evidence is incompatible with the predictions of the Eve total replacement theory.

Africa

The ultimate prediction of the Eve theory is that Africa is the unique source for all living people, the equivalent of the Garden of Eden and the embarkation point for Noah's Ark rolled into one. Yet, as we write this paper, the data once said to prove that Africa was the unique source is now questioned by some of the very people who proposed and defended it so vigorously in the first place (Hedges et al. 1992). According to the Eve perspective, Africa must yield both the *only* evidence of a morphological transition from archaic to modern humans and the earliest fossil remains of modern-looking people. Several workers have contended that the earliest modern human skeletal remains are unquestionably from Africa (Bräuer 1984, 1989; Protsch 1975; Stringer 1990; Stringer and Andrews 1988a) and some have taken issue with evidence for a transition outside Africa (Bräuer 1992; Stringer 1990, 1992). Our research shows that the African fossil record does provide evidence of a transition from archaic humans to more modern-looking ones. Late Middle Pleistocene African *Homo sapiens* remains, such as Bodo from Ethiopia or the well-known Kabwe (Broken Hill) skull from Zambia, are rare in the prehistory of Africa. However, when they are found, they are relatively primitive, measured by very large faces, massive supraorbital tori, angled occiputs, and low, receding frontal bones (Rightmire 1989; Smith 1985; Wolpoff 1980).

Although unquestionably ancient, Kabwe epitomizes the problems that beset much of the crucial African evidence. The skull, other human remains, stone tools, and animal bones were discovered accidentally in 1921. Because these specimens were not excavated systematically, questions will always remain regarding their context and contemporaneity. If the recovered Final Acheulean tools are associated with the Kabwe skull, and if the

Final Acheulean always predates the Middle Stone Age (MSA), the Kabwe skull may be presumed to be minimally 180,000 years old. Rarely discussed with the skull is a second, much smaller, partial maxilla, some isolated cranial fragments, and an extensive post-cranial sample. The difficulties of date determination, the questions of provenience, and the neglect of all but one specimen from the site are common problems for most of the sites discussed below.

Fossils from the sites of Djebel Irhoud (Morocco), Ngaloba (Tanzania), and Florisbad (South Africa) demonstrate that humans were evolving in the direction of the modern morphological patterns by the early Upper Pleistocene. These specimens, regarded as "anatomically modern humans" by some workers (Stringer 1988; Delson 1988; and, for the first two, Bräuer 1992) and later archaics by others (Smith, Falsetti, and Donnelly 1989; Wolpoff 1980), are most like modern humans in their faces. For example, upper facial height reduces an average of 16% compared to Kabwe. Moreover, the lower margin of the cheek forms almost a right angle with the side of the upper jaw and a distinct canine fossa is present—features absent in Kabwe. However, the mosaic nature of their morphology is demonstrated by the fact that the form of their frontal bones and other aspects of cranial vault morphology retain an archaic nature, as evidenced by their low foreheads coupled with moderately large browridges.

The evidence generally cited in support of a great antiquity for completely modern-looking people in Africa comes from three sites—Omo (Kibish Formation site KHS) in Ethiopia, and Border Cave and Klasies River Mouth caves, both in South Africa. Fragmentary crania and mandibles from the first two sites exhibit some morphological details that could be commensurate with early representatives of modern people (Day 1972; Rightmire 1979, 1986; Smith Falsetti, and Donnelly 1989). We concur with the contention that Omo 1 has some modern features, although we do not accept the validity of the multivariate analysis linking the specimen with ancient Norwegians (Day and Stringer 1982), as it is based on the all-plaster reconstruction of the missing face. At the same time, the Omo 1 calvarium retains certain archaic features (Smith 1985; Smith, Falsetti, and Donnelly 1989). The mixture of archaic and modern features, however, is less of a problem for their interpretation than the cultural context or the dating for these two sites. The Omo 1 (KHS) partial skeleton was found partly in situ in Member I of the Omo Kibish Formation. A uranium/thorium date on *Etheria* shell of 130,000 B.P. was obtained from just above the specimen and a standard radiocarbon date of >37,000 B.P. (also from shell) was derived from the overlying Member III. However, both techniques give generally unreliable results when used on shell and have yet to be confirmed by additional dating. The faunal remains associated with Omo 1 are, according to Howell, "unconvincing of any remote antiquity" (1978:216).

The Border Cave partial cranium and mandible are claimed to derive from a stratum dated from 70,000 to 80,000 B.P. by electron spin resonance (ESR) on presumably associated nonhuman remains (Grün, Beaumont, and Stringer 1990). Yet, the context of the human material relative to the dated nonhuman remains is anything but certain. For example, Border Cave 1 was recovered by workers digging for guano in the cave. The stratigraphic context of this fragmentary human material will always be uncertain, so that directly dating the human bones is the only way to establish their chronological age, and this has so far failed (Morris 1992). A second adult mandible (Border Cave 5) with a well-developed chin is also of questionable antiquity. While supposedly excavated in situ from a 50,000- to 65,000-year-old level, it may actually be from an intrusive burial. This is suggested by the fact that the human and animal bones from this level exhibit a marked contrast in the state of preservation (Klein 1983). The animal bones experienced considerable postdepositional leaching and are heavily fragmented as a result of profile compaction. However, the human mandible exhibits little effect of leaching, is more complete, and is generally much better preserved compared to the nonhuman faunal collection. Using even loose criteria, it is difficult to accept any confirmation of antiquity of the human material from either Border Cave or Omo 1.

The most reliably excavated remains come from the Klasies River Mouth caves (SAS member) and are reasonably securely dated to between 80,000 and 100,000 years ago, the latter estimate based on uranium disequilibrium dating (Deacon and Geleijnse 1988; Deacon and Schuurman 1992; Thackeray 1989). The Klasies human remains are quite fragmentary. Despite their incompleteness, they have been described as fully anatomically modern (Bräuer 1984, 1989, 1992; Rightmire and Deacon 1991; Stringer and Andrews 1988a). Yet, the claim that the Klasies humans are unequivocally fully modern is dubious (Caspari and Wolpoff 1990; Smith, Falsetti, and Donnelly 1989; Wolpoff and Caspari 1990a) and highly influenced by the morphology of the Omo 1 and Border Cave specimens, which are almost certainly of considerably less antiquity than the Klasies people. Despite the statements about the modernity of the material from Klasies, three of the four mandibles preserving the symphyseal region lack well-developed chins (Figure 6), and the development of the mental trigone on the two symphyses totally lacking chins is absent or very weak. Specimen KRM 41815, which does have some development of the mental eminence, is not the earliest specimen to show this morphology, if the most recent ESR dates for the Tabūn B mandible are correct (Grün, Stringer, and Schwarcz 1991). Moreover, we are uncertain as to how much of the projection of the mental eminence is a consequence of resorption at the anterior alveolar margin. This artifact of premortem incisor loss makes the chin appear much more distinct than before the resorption took place.

Facial morphology is represented by just four fragmentary specimens, two deriving from the older LBS level and two from the recent SAS member. The material from LBS consists of two separate maxillary fragments. The larger of these is quite heavily constructed, while the smaller one "seems gracile even in comparison to recent human specimens" (Rightmire and Deacon 1991:145). Differences between the two specimens suggest marked sexual dimorphism in LBS times, but this is hardly evidence for the appearance of a modern morphology. From the higher SAS member, an isolated left zygomatic (KRM 16651) is far larger and more robust than a series of Holocene people from the same area and a sample of recent humans (Wolpoff and Caspari 1990a). Among African fossils of any age, its size can only be matched with the much older Bodo face. Furthermore, in this specimen the lateral orbital pillar (the bony area forming the outer orbital rim) is columnar-like, a condition common to other archaic humans but quite rare in modern humans from anywhere in the world. The final facial piece is a portion of a right frontal with attached superior nasal bones (KRM 16425). While the specimen exhibits modernlike supraciliary arches, the innerorbital area is markedly broad and distinctively

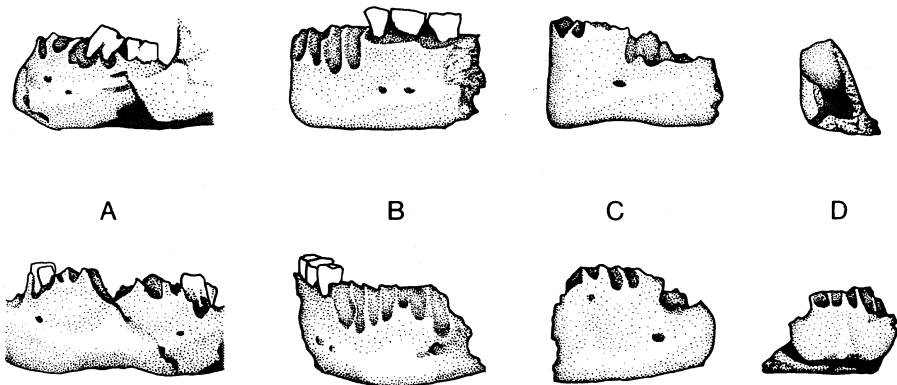


Figure 6

Lateral and anterior profiles of the four Klasies River Mouth mandibles with preserved symphyseal regions: (A) 41815, (B) 13400 (reversed), (C) 21776, (D) 14695 (from casts).

nonmodern. This dimension is totally outside the range of recent Africans from the region and can only be matched by the broadest Pleistocene African faces. Beyond this, the KRM 16425 specimen may be a juvenile, which undermines the potential taxonomic significance of the modernlike brows. Thus, the reduced brows in this specimen may be more a function of age than an indication of taxonomic modernity.

But even if the KRM 16425 frontal and KRM 41815 mandible each have a modern feature, the question of how to define modernity in a sample must be addressed. Does the earliest appearance of modernity in one or two features of an otherwise archaic sample mean that the sample is modern? If so, there are earlier cases for the initial appearance of modern features. Modern midfacial traits first appear in the Middle Pleistocene of China (Pope 1991), and Jinniushan is the earliest specimen to combine a very large cranial vault with thin vault bone (Pope 1988). Vertésszöllös is the first specimen to show a distinct supreme nuchal line. Tabūn B may be the first to show a prominent chin. The point is that these specimens are not regarded as modern because of a few modern features, and we wonder why the same rationale should not be applied to the superciliary arches of the KRM 16425 frontal fragment.

Thus, in spite of the fragmentary nature of the Klasies sample, several archaic, taxonomically important features characterize this collection of cranial and mandibular pieces. For the skull fragments, a number of important features are no more modern than those found in Florisbad or Kabwe. Moreover, since none of the African transitional specimens preserve mandibles, it is impossible to judge if even the most "modern" of the five incomplete Klasies mandibles shows "advanced features." Despite previous claims, it is not clear that the Klasies fragmentary material represents "modern" humans.

Additionally, it should be noted that the studies by Rightmire (1986) and Habgood (1989b) have failed to identify any uniquely African features in either the African transitional sample or the supposedly early moderns from Omo, Border Cave, or Klasies. Consequently, this anchors the case for Eve solely on the date for the earliest "modern" populations. Yet, it is the *early* appearance of regional features in Africa (whether they specifically resemble modern African features or not) that is a prediction of the Eve hypothesis (Stringer and Andrews 1988a:1263), while a late appearance of regional features in Africa, the center of the range for *Homo sapiens*, is predicted by the multiregional evolution model (Thorne 1981). Finally, the form of the frontal bone and occipital in Djebel Irhoud suggests considerable genetic exchange between human populations around the circum-Mediterranean prior to 100,000 years ago (Simmons and Smith 1991). The shared morphological features of Djebel Irhoud with specimens outside Africa suggest a web of interconnected lineages extending back into the Middle and early Upper Pleistocene, one of the basic predictions of multiregional evolution. It indicates that isolation of an African lineage, a critical factor in the speciation scenario of the Eve theory, did not occur during this period of time.

In summary, the African fossil record offers little in support of the Eve hypothesis. Certainly, dogmatic assertions about the earliest appearance of modern morphology in Africa do not bear up under close scrutiny of the generally poorly dated, fragmentary material identified as the fossil candidates for the Eve hypothesis. It is also noteworthy that features typical of later samples outside Africa are seldom found in the jumble of material from Omo, Border Cave, or Klasies. While the relatively poor fossil record from these three sites may be responsible for this, there is clearly nothing in this material that would signal any kind of a close relationship with more modern humans in Europe and Asia. Given doubts about an exclusive African ancestry for subsequent humans and the lack of unequivocal evidence showing that modern people first appeared there, nothing in the African fossil record supports this continent as a unique motherland.

Western Asia

With the failure of the African evidence to convincingly demonstrate that "Eve" lived there, for some investigators, attention turned to the Levant, ironically the home of the

biblical Eve. There, the new dating of such sites as Skhūl and Qafzeh by the electron spin resonance (ESR) and thermoluminescence (TL) techniques suggested the possibility of an early (100,000 years or older) date for people (Schwarcz et al. 1988; Stringer et al. 1989) regarded as “anatomically modern humans” by some of Eve’s supporters (Stringer 1988; Delson 1988). “Eve” found near Africa seemed to mean the same as an African Eve, although this Western Asian sample shows no unique African features (Sohn and Wolpoff 1990) and none of the biochemical interpretations ever suggested a Levantine ancestry for modern humanity.

When the human remains from Skhūl were described and systematically compared to other human fossils, they were not considered “modern humans” or even in “modern human ancestry,” but rather “Neanderthaloid collaterals or cousins” to the ancestors of modern humans (McCown and Keith 1939:17). Because of the many cranial, dental, and postcranial similarities various specimens had in common with the Tabūn remains, the combined sample was regarded as a single population by its describers, who commented: “We encountered so many characters which linked the Skhul to the Tabun type that we were ultimately obliged to presume that we had before us the remains of a single people” (McCown and Keith 1939:12). It is significant that the sample was subsequently divided among three institutions, because this prevented the range of morphological variation from ever being observed again in the original specimens. Later, without any additional comparative analysis, the Skhūl remains alone and burials from nearby Qafzeh were described as “Proto-CroMagnoids” (Howell 1959). Subsequent excavations led to the recovery of more Qafzeh individuals (Vandermeersch 1981), and an adolescent (Qafzeh 9) came to serve as the “type” specimen for those (e.g., Klein 1989) who see evidence of Eve at these sites.

But the case that the human remains from Skhūl and Qafzeh are “anatomically modern,” or even uniquely ancestral to the Upper Paleolithic Europeans has never been established on anatomical grounds. Phenetic analysis of the male crania using measures of size and shape fails to show any unique links of the Skhūl and Qafzeh populations to the early Upper Paleolithic populations of Europe (Wolpoff 1989b)—the European Neanderthals are actually closer in both the magnitude and the pattern of variation of their metrical features. A similar comparison for females is not possible because of much smaller sample sizes. Prior analyses that found more distinction between these samples, such as that done by Howells (1975), used mixed sex samples, and the varying sex ratios in the Neanderthal, earlier European Upper Paleolithic, and Skhūl and Qafzeh samples provide the main reason why this relation has not been observed before. Comparisons of the dental metrics reveals a virtual identity of the Skhūl and Qafzeh samples to the European Neanderthals, and numerous differences from the European Upper Paleolithic (Frayer 1978; 1993). There is not and was never any justification for the “Proto-CroMagnoid” appellation, a conclusion also reached by Stringer (1989, 1992).

Continued studies have supported the original interpretations of McCown and Keith; mainly, the Levant sample as a whole cannot be clearly separated into “Neanderthaloid” and “modern” sets on either anatomical or behavioral (archeological) grounds (Arensburg 1989, 1991; Wolpoff and Caspari 1990b). The total variation is less, often considerably less, than normally found in a modern city (Wolpoff 1992). Cluster analyses, whether based on phenetic or cladistic techniques, never divide the total Levantine sample into clearly separated groups (Simmons and Smith 1991; Crummett, Kramer, and Wolpoff 1992), although the Eve theory insists that these two sets of individuals must represent different species and that one is so superior to the other that a complete replacement occurred.

It is reasonable to wonder why evidence for anatomical difference is not reflected in the skeletal anatomy. For example, two recent, independent multivariate analyses of the Skhūl and Qafzeh samples support this point. Corruccini (1992) has demonstrated, based on size and shape analyses, that Skhūl 9 and Qafzeh 6 depart significantly from the morphological patterns of Skhūl 5 and Qafzeh 9, respectively. These specimens show

convergences away from Skhül 5 (or Qafzeh 9) toward a pattern more typical of Neanderthals. As Corruccini argues, his results “raise perplexing questions about the interpretation of two supposedly long-separated species. The variation within Skhul alone spans much of the phenetic spectrum between archaic/Neanderthal and modern cranial form” (1992:441). In a second study, Kidder, Jantz, and Smith (1992) compared a number of Upper Pleistocene specimens to recent *Homo sapiens*. In eight different multivariate shape analyses, Skhül 5 falls outside the modern human range, and in all five that can include measurements for Skhül 4, this specimen is also outside the modern range. For Qafzeh, the subadult specimen (9) lies within the human range for the only two analyses that can include the specimen. In the single analysis that includes Qafzeh 6, the size/shape D² is outside and the shape D² falls within the modern range. Clearly, the continued, but unsubstantiated notions that the Skhül and Qafzeh material is “modern *Homo sapiens*” or even “Proto-CroMagnoid” is an attribution that has been and remains without support. In most cases, the specimens portray a morphology unlike modern patterning.

This conclusion also extends to certain aspects of the postcranial skeleton, and it would be a mistake to believe that the relations exhibited by the crania and teeth were negated by the postcranial remains. It is true that the postcranial remains, as a whole, show less overlap with the Neanderthals than do the crania, and that the Tabün pubis particularly resembles the unique Neanderthal pubic conformation known from Europe, but even in this feature the Skhül remains show overlap. The Skhül IX pubic length is extremely long for a male. This could be used to support a female sex allocation for the specimen, but most other sexing criteria on the pelvis and cranium more closely resemble the typical male condition. The expanded Skhül IX pubic length, then, would be a Neanderthal resemblance. In another example, relative distal limb length has been the focus of authors who would derive the early Upper Paleolithic Europeans from tropical habitats because they are supposed to be heat adapted (Trinkaus 1981; Stringer 1984). The tibial-femoral ratio (crural index) for Tabün is similar to the European Neanderthals, and the ratios for Skhül 4 and 6 are much higher, which could be interpreted to fit that model. However, the Skhül 5 crural index is like the Neanderthals. If this reflects climatic adaptation, then Tabün and Skhül 5 must be considered as cold adapted and the sample would have to be regarded as a mixture of cold-adapted and heat-adapted people. If, on the other hand, the ratio does not reflect climatic adaptation, then we can conclude that Skhül 5 is Neanderthal-like and supports the mixed morphology interpretation.

McCown and Keith reported other postcranial elements that did not divide neatly into two groups. To cite just a few of their conclusions:

The Skhül vertebrae show certain primitive features in the length and horizontal direction of the spinous processes of the cervical and lumbar segments of the vertebral column. They resemble the Neanderthals of Europe in this. [1939:109]

Our men, so far as their ribs are concerned, form a series passing from a Neanderthaloid condition in Skhül V to an almost modern condition in Skhül IV. [1939:124]

we have amongst the Palestinians a range of [clavicle] forms which serves to link the highly characteristic clavicle of the Neanderthal skeleton to the type which prevails in modern races. [1939:144]

The discussion of Neanderthal and Neanderthal-like features in the Skhül sample is not meant to disguise the fact that there are many non-Neanderthal features in the Levant sample, and (if the TL and ESR dates are correct) some of them have an early appearance relative to many other sites. We can ask two questions regarding these features: are they modern, and do they reflect a unique African ancestry? We believe the links of the presumed “modern” features of the Levant sample to Africa are very poorly established. Neither morphological analysis nor archeological comparisons show *any* evidence of an ancestry for the Levant folk in sub-Saharan Africa, let alone a *unique* ancestry, as the Eve theory demands. Instead, detailed analyses of the so-called modern Levantine features that show geographic differences link most of them to the earlier populations of East Asia,

and specifically *not* to early Upper Paleolithic Europeans, nor to Africans of any Pleistocene age (Pope 1991; Sohn and Wolpoff 1990). East Asian features can be found throughout the Levant specimens, in some individuals more than in others. In most cases these are the features characterized as “modern” in publications claiming that ancient modern people lived in Western Asia. But if we consider them modern features, the point is that their earlier Asian origin would show the Zhoukoudian people to be the first moderns, using the same criteria for modernity (the earliest appearance of modern features) that are being applied in the Levant. Alternatively, we suggest that, as in the discussion of the Klasies specimens, the origins of a few modern features are not the origins of a modern population. For instance, since our study shows that the source of these features is geographic, and Asian rather than African, this work means that no known African population can be the unique ancestor to all modern populations. In our opinion, a more parsimonious explanation is that while the Middle Paleolithic populations of the Levant have a number of features that differ from the Neanderthals, *non-Neanderthal does not mean modern*, as McCown and Keith realized. This is not meant to argue for an “out-of-Asia” theory (cf. Turner 1991), but it does clearly reject an “Eve” explanation in the region closest to Africa, where the sample size is large and we might expect evidence supporting the Eve theory to be best.

Interpreting the mtDNA Data

With the disproof of the unique African ancestry theory for the living people of all areas outside Africa and the lack of fossil evidence showing that modern people first appeared in Africa, we conclude that the five predictions of the Eve theory are each falsified. Since virtually all of this evidence was in existence long before the appearance of the Eve hypothesis, we wonder why an analysis of mtDNA could suggest a theory so contrary to the known facts. From the Templeton article included in this issue, it is now apparent that the mtDNA has been misinterpreted from the beginning.

While certainly not the only interpretation of the mtDNA results, beginning with the work of Cann, Stoneking, and Wilson (1987), the African Eve perspective has been the dominant theme—forming the genesis of Eve theory as it is understood today (Cann 1987, 1988; Stoneking and Cann 1989; Wilson and Cann 1992). Despite the full acceptance of this view of modern human origins by some geneticists and paleoanthropologists, others have questioned and in many cases rejected every assumption required by the Eve theory. From the geneticists, the fatal blow comes from Templeton (in this issue), who dismisses all claims of an African Eve deriving from either the mtDNA or nuclear DNA data. We review two of the faulty linchpins for the theory below.

The most critical, rejected assumption is the demonstration that all human mtDNA cannot be traced to an African source through the construction of phylogenetic trees. The phylogenetic trees that allegedly demonstrated the rooting in Africa have now been uprooted (Barinaga 1992; Maddison 1991; Templeton 1992), a point accepted by some of the Eve supporters (Hedges et al. 1992). Because there are many equally parsimonious solutions to the mtDNA variation and because some of these coalesce to non-African ancestries, it is no longer statistically valid to define Africa as the ancestral place from the mtDNA data. There is no statistically reliable mtDNA evidence for an African, or any other single, geographically centered origin for Eve (Excoffier and Langaney 1989; Maddison, Ruvolo, and Swofford 1992).

A second critical and rejected assumption concerns the ticking of the molecular clock. This clock was recognized as extraordinarily inaccurate, even by its supporters; Stoneking and Cann (1989), for instance, estimated an order-of-magnitude error range. Three factors undermine the clock’s validity and reliability in producing accurate readings for the evolution of a species.

1. All molecular clocks require evolutionary neutrality, essential for constancy in the rate of change. But continuing work on mtDNA has documented the increasing evidence

for selective importance in mtDNA. For example, studies by Fos et al. (1990), MacRae and Anderson (1988), Palca (1990), Wallace (1992), and others have conclusively demonstrated that mtDNA is not neutral, but under strong selection. Since selection acting on part of the molecule must affect the survivorship of the whole because the entire molecule is effectively a single genetic locus (Spuhler 1988), mtDNA is a poor gear to drive a molecular clock.

2. As demonstrated by Avise, Neigel, and Arnold (1984) and Avise, Ball, and Arnold (1988), small sample effects make stochastic loss a major evolutionary force in subdivided populations. Since random mtDNA losses result in pruning off the evidence of many past divergences, the trees constructed to link present populations are altered by unknown and unpredictable factors. Each of these unseen divergences is a genetic change that was not counted when the number of mutations was used to determine how long ago Eve lived. Since these changes are influenced by fluctuations in population size and the exact number of uncounted mutations depends on the particular details of the pruning process, unless the complete populational history is known, there is no way to calibrate (and continually recalibrate) the ticking of the clock. Given the fact that each population has a separate demographic history (with respect to random loss events), this factor alone invalidates the use of mtDNA variation to "clock" past events (Thorne and Wolpoff 1992).

3. Finally, even if the above restrictions for predicting the ticks of the clock are somehow met, there are problems with the mathematical underpinnings of the mtDNA clock. Lovejoy and his colleagues (Lovejoy et al. 1993) propose that in the most recent calculation of Eve's age (Vigilant et al. 1991) the wrong transition-transversion ratio was used. The correct ratio places Eve's age at at least 1.3 million years ago, well beyond the chronological placement of any of the fossil material used to argue for the single appearance of modern humans.

In sum, we contend with others (Lewin 1990; Templeton, this issue; Wayne et al. 1990) that the calibration of any mitochondrial clock has major accuracy problems, which probably can never be resolved. Despite all that has been assumed about the accuracy of the molecular clock, it is not a reliable timepiece.

Finally, in addition to Templeton's conclusions (this issue), recent developments in nuclear DNA analysis provide support for the multiregional evolution model. Xiong et al. (1991) report on two rare nucleotide polymorphisms, which, the authors argue, would have disappeared had there been significant bottlenecks during human evolution (a necessary consequence of the single-origin Eve theory). The rare mutant allele sequences differ from the common form in a number of bases and appear to have a common origin due to a single phase-shift mutation between a half-million and two million years ago. These allele sequences were found, respectively, in a Japanese and a Venezuelan individual, each natives of their own country. Because of the statistical improbability that the allele sequences are due to independent events, the occurrence in the two identical sequences in these individuals separated by the Pacific likely derive from their distant, common Asian ancestors, ruling out the contribution of some Caucasoid sailor. In either case, however, the identical sequences could not reflect a shared African ancestry. Therefore, this evidence both argues against the validity of a key element of the Eve theory and supports the interpretation of regional continuity, most probably in Asia.

In short, with the continuing analysis of mtDNA and reconsideration of nuclear DNA variation it is becoming increasingly clear that the original prediction of a recent African origin for all modern humans is without a genetic basis. If anything, both the mitochondrial and nuclear DNA variation better support the predictions of the multiregional evolution model as initially outlined in Thorne (1981) and Wolpoff, Wu, and Thorne (1984).

Conclusions

At the beginning of this article we outlined the conflicting predictions of the fossil record according to the Eve and the multiregional evolution hypotheses. We argued that the

differences between the two views over the nature of the fossil record for the origin of modern humans are so contradictory that both cannot be correct. Moreover, we argued that the specifics of both hypotheses can be subjected to falsification by the skeletal record representing the emergence of more modern *Homo sapiens*. We examined the fossil data in a number of different regions of the world for five predictions of the Eve theory that could potentially refute it. Since the Eve theory requires total replacement in all areas, the demonstration of continuity in just one area would be enough to show that it is false, because this alone would invalidate the interpretation of mtDNA data that requires a recent populational replacement everywhere. However, the Eve predictions are not just rejected for one region. Each geographic region we examined contains a wealth of information that shows the continuous evolution of *Homo* populations over time. We find neither specimens nor traits that could reflect an infusion of any African genes and their so-called more-modern morphology. There is an absence of features in the earliest moderns of any region outside Africa that can be uniquely traced back to Africa. Thus, there are not just a few problem spots for the theoretical expectations of the Eve model, but rather its predictions consistently lack support for all areas outside of Africa.

Turning to the African evidence, it is inaccurate to categorize the fossil candidates for African Eves as modern, although the appearance of moderns first in Africa is perhaps the most critical prediction of the theory. African Late Pleistocene prehistory seems plagued with well-dated but controversially interpreted sites holding fragmentary specimens such as Klasies, or sites with more complete materials that are unreliably dated (Omo) or unprovenienced (Border Cave). Moreover, if Stringer and Andrews (1988a) are wrong in their Eve theory interpretation that modern humans evolved first in Africa, then took on African features, and then spread around the world, only Bräuer's (1992) out-of-Africa interpretation would remain. Given the absence of any features defining the early modern humans, who form the centerpiece of this theory, this proposal cannot be tested on evidence from outside Africa. The only remaining way to test Bräuer's interpretation of the Eve theory would be to examine whether the unequivocally earliest moderns were found in Africa, as Protsch (1975) first proposed. However, even though they represent the most incomplete of all the regional fossil records, the few African remains that are convincingly provenienced and dated always exhibit a mosaic set of features—a few modern, but more archaic ones. We believe that a few modern features are insufficient to diagnose the first modern population, but if they were to be used this way, the fact is that there are much older candidates than the African Eves for the initial appearance of modern features. We conclude that the Eve theory is not only rejected by the existence of transitional specimens and by the persistence of morphological traits over time outside of Africa, but can similarly be rejected by the absence of any confirmatory evidence for the earliest appearance of modern *Homo sapiens* in Africa.

There appears to be recognition of this in the most recent papers by the Eve theorists. In 1988, Stringer and Andrews concluded that “an African origin for *Homo sapiens* is *highly probable*” (1988a:1267, emphasis added). Now, however, Stringer describes his earlier paper as “controversial” and states that it was not his intention “to imply that there was no evidence against the model or no problems with the supporting paleontological and genetic evidence cited” (1992:10). Bräuer goes further, describing the theory that he once embraced but that he now calls the “extreme Recent African Evolution model,” as a “test model” (Bräuer 1992:84). From the paleontological analyses presented here, it is apparent that this model does not hold up under scrutiny and must be rejected.

What does a disproof of the Eve theory imply? Various workers have suggested that the Eve and multiregional evolution views discussed here are merely the extremes of a range of possible genetic and morphological explanations for modern human origins, and that the “true” explanation must lie somewhere between. It is usually desirable to compromise positions when there are disputes, but is science by compromise a reasonable approach to the modern human origins problem? A compromise hypothesis, or really a range of hypotheses, would argue that while there has been widespread, long-term genic

exchange between human populations, modern humans originated from the expansion of a single, once-localized population within a species. Since this hypothesis allows for admixture, it is not a speciation event. Nevertheless, the ultimate origin of unique modern features is traced to a single (yet to be discovered) population. There is no theoretical reason why the notion of partial regional continuity with an influx of catalytic "modern" features could not have been the case, but we (except for Smith) believe that paleontological, archeological, and genetic evidence contradicts it.

One of the reviewers of this paper argued that disproof of the Eve theory is not the same as proof of multiregional evolution. We concur with this judgment. Hypotheses are rejected through disproof, and can never be proven. Our approach to science is Popperian and we examine hypotheses about human evolution by holding the current theory as the focus for refutations. Based on the substantial fossil record of various regions in the Old World, we find clear evidence for transitional samples and transitional characters within regions. From Australia to Europe, there is an undeniable degree of morphological connection between the archaic forms of *Homo sapiens* and the more modern inhabitants of the same region. These represent anything but the "few isolated traits" that some have supposed. The case for continuity is based on different combinations of features in each area, and it is clear that modern human origins cannot be described as a single genetic incident nor as an event appearing in the diverse areas of the world simultaneously. We take this to mean that multiregional evolution is the most explanatory hypothesis we have at the moment, and as such it should become the focus of attempted refutations, just as the Eve theory was.

Stoneking (cited in Edelson 1991:58) speculates that a date for Eve in excess of 800,000 years would remove all conflicts with the fossil record. We concur and suggest that such a date is where the preponderance of the genetic as well as fossil evidence points. With increasing convergence of ideas, we propose that this be taken as the null hypothesis and that future paleoanthropological research might productively focus on attempts to disprove it rather than on attempts to shoehorn fossils into a discredited genetic framework they do not (and never did) match.

The dramatic genetic similarities throughout living humans reflect the consequences of genetic linkages among people that extend to the time when our ancestors first populated the Old World, more than a million years ago. They are the results of an ancient history of population connections and mate exchanges that have characterized the human species from its inception. Human evolution happened everywhere, because every area was always part of the whole.

DAVID W. FRAYER is Professor and Chair, Department of Anthropology, University of Kansas, Lawrence, KS 66045. MILFORD H. WOLPOFF is Professor, Department of Anthropology, University of Michigan, Ann Arbor, MI 48109. ALAN G. THORNE is Professor, Department of Prehistory, Australian National University, Canberra, ACT 2601, Australia. FRED H. SMITH is Professor and Chair, Department of Anthropology, Northern Illinois University, DeKalb, IL 60115. GEOFFREY G. POPE is Assistant Professor, Anthropology Program, William Paterson College, Wayne, NJ 07470.

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