Anatomy, Behavior, and Modern Human Origins

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The fossil record suggests that modern human morphology evolved in Africa between 150,000 and 50,000 years ago, when the sole inhabitants of Eurasia were the Neanderthals and other equally nonmodern people. However, the earliest modern or near-modern Africans were behaviorally (archaeologically) indistinguishable from their nonmodern, Eurasian contemporaries, and it was only around 50,000–40,000 years ago that a major behavioral difference developed. Archaeological indications of this difference include the oldest indisputable ornaments (or art broadly understood); the oldest evidence for routine use of bone, ivory, and shell to produce formal (standardized) artifacts; greatly accelerated variation in stone artifact assemblages through time and space; and hunting-gathering innovations that promoted significantly larger populations. As a complex, the novel traits imply fully modern cognitive and communicative abilities, or more succinctly, the fully modern capacity for Culture. The competitive advantage of this capacity is obvious, and preliminary dates suggest that it appeared in Africa about 50,000 years ago and then successively in western Asia, eastern Europe, and western Europe, in keeping with an African origin. Arguably, the development of modern behavior depended on a neural change broadly like those that accompanied yet earlier archaeologically detectable behavioral advances. This explanation is problematic, however, because the putative change was in brain organization, not size, and fossil skulls provide little or no secure evidence for brain structure. Other potential objections to a neural advance in Africa 50,000–40,000 years ago or to the wider "Out-of-Africa" hypothesis, include archaeological evidence (1) that some Neanderthals were actually capable of fully modern behavior

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and (2) that some Africans were behaviorally modern more than 90,000 years ago.

INTRODUCTION

My purpose is to place the origin of modern humans in the broad sweep of human evolution and to show that an understanding of modern human origins depends as much on archaeology as on the fossil record. My basic argument flows from the familiar, but controversial observation that a bundle of interrelated behavioral novelties appeared abruptly between 50,000 and 40,000 years ago (Table I). Preliminary indications are that key elements of this bundle originated in Africa, in keeping with fossil evidence that the first physically modern or near-modern humans evolved there between 150,000 and 50,000 years ago. During this same interval the sole inhabitants of Eurasia were the Neanderthals and other, equally non-modern ("archaic") people. In my view, the novel behavioral complex signals the emergence of fully modern cognitive and communicative abilities, or more succinctly, the emergence of the modern capacity for Culture. The development of this capacity in turn explains how modern humans were

Table I. Some Attributes of Fully Modern Human Behavior Detectable in the
Archaeological Record Beginning 50,000–40,000 Years Ago[a]

- Substantial growth in the diversity and standardization of artifact types.
- Rapid increase in the rate of artifactual change through time and in the degree of artifact diversity through space.
- First shaping of bone, ivory, shell, and related materials into formal artifacts ("points," "awls," "needles," "pins," etc.)
- Earliest appearance of incontrovertible art.
- Oldest undeniable evidence for spatial organization of camp floors, including elaborate hearths and the oldest indisputable structural "ruins."
- Oldest evidence for the transport of large quantities of highly desirable stone raw material over scores or even hundreds of kilometers.
- Earliest secure evidence for ceremony or ritual, expressed both in art and in relatively elaborate graves.
- First evidence for human ability to live in the coldest, most continental parts of Eurasia (northeastern Europe and northern Asia).
- First evidence for human population densities approaching those of historic hunter-gatherers in similar environments.
- First evidence for fishing and for other significant advances in human ability to acquire energy from nature.

[a]For elaboration, see Klein (1989), Mellars (1989), and Stringer and Gamble (1993).

able to expand from Africa about 50,000 years ago to supplant the Neanderthals and other archaic Eurasians whose cultural potential was more limited.

The most economic explanation for the relatively abrupt appearance of fully modern behavior is that it mirrors the relatively sudden development of the fully modern brain. This hypothesis follows largely from the observation that brain change was a conspicuous feature of human evolution from roughly 2.5 million years ago (mya) and that some early behavioral advances, as described below, coincided broadly with significant increases in average brain size. There is the problem, however, that the brain reached roughly its present size more than 150,000 years ago in both Africa and Eurasia, and any subsequent neurological differences or changes must have been limited to internal restructuring. Skulls that postdate 150,000 years ago often differed dramatically in shape, as, for example, between the Neanderthals and their modern or near-modern African contemporaries, but the neurological correlates of shape differences, if any, are unknown and perhaps unknowable. The problem is that brain organization, unlike brain size, is very weakly reflected in fossil skulls.

The literature on human evolution is huge and burgeoning. For economy's sake, I have therefore stressed sources published since 1989. These contain bibliographies with important older references.

THE AUSTRALOPITHECINES, *HOMO HABILIS*, AND THE OLDEST STONE TOOLS

Based on the estimated rate at which genetic differences accumulate, the last common ancestor of chimpanzees and people probably lived 5–6 million years ago (mya). The oldest known human (hominid) fossils come from deposits dated to about 4.4 mya and have been assigned to the species *Australopithecus ramidus* (T. D. White *et al.*, 1994). The initial sample of *A. ramidus* included arm bones, cranial fragments, and teeth that exhibit a remarkable mix of chimpanzee-like and human-like characters. It was the relatively reduced size of the adult canine and the forward placement of the foramen magnum/occipital condyles on the basicranium that indicated a link to later humans. There were no lower limb bones to show whether the species was habitually bipedal, and their absence was crucial, since habitual bipedalism, or more precisely, the lower limb anatomy that promotes it, is the key anatomical distinction of humanity. Lower limb bones have now been found (Gee, 1995), and when they are described, they should remove any lingering doubts about the human status of *A. ramidus*.

Around 3.8 mya, *A. ramidus* apparently evolved into the much better-known species, *A. afarensis*, which had more human-like teeth, though it still retained many ape-like features in its skull, dentition, and arms (Kimbel *et al.*, 1994; T. D. White *et al.* 1993). Its leg and foot bones and some spectacular fossil footprints demonstrate beyond all doubt that it moved from place to place using a typically human, striding bipedal gait. *A. afarensis* is usually considered ancestral to all later human species, but its precise relationship to later forms is disputed. Probably the most popular view is that it split into two separate human lineages between 3 and 2.5 mya (Fig. 1). The first comprised the "robust" australopithecines, which combined small, ape-size brains with characteristically human teeth and bodies. The "robust" australopithecines tended to be somewhat larger than *A. afarensis* but broadly similar in size to their contemporaries in the second human lineage (McHenry, 1992, 1994a), and the term "robust" applies mainly to the dentition and associated cranial structures. Relative to apes, all human species tend to have small front teeth (incisors and canines) and large cheek teeth (premolars and molars), but the later "robust" australopithecines carried this difference to its greatest known extreme. Many authorities divide the later "robust" australopithecines between two species, *Paranthropus robustus* (South Africa) and *P. boisei* (east Africa), which were derived from a more poorly known ancestor, *P. aethiopicus* (Fig. 1). Alternatively, *P. robustus* and *P. boisei* may have been only geographic variants of a single species. Both possessed truly enormous cheek teeth, set in skulls plainly shaped to permit powerful grinding between the upper and the lower cheek rows. Their composite dental and cranial morphology suggests that both specialized heavily on hard or grit-encrusted (?mainly vegetal) foods (Grine, 1988).

The second, widely accepted lineage comprised the "gracile" or "slender" australopithecine, *A. africanus*, and its postulated descendant, *H. habilis*, the earliest species of the genus *Homo*. Limb bones imply that *A. africanus* and the "robust" australopithecines were similar in size (McHenry, 1992, 1994a), and *A. africanus* is distinguished primarily by its less massive cheek teeth and skull. It is mainly in these features that it anticipates *H. habilis*. However, it is also true that *A. africanus*, *P. robustus/P. boisei*, and *H. habilis* share many features that are unknown in *A. afarensis*. A plausible inference is that *A. africanus* was ancestral not only to *H. habilis*, but also to *P. robustus/P. boisei* (McHenry, 1994a). In this instance, *P. aethiopicus* would represent the only known member of yet another extinct human lineage. The only viable alternative (implied in Fig. 1) is that *H. habilis* and *P. robustus/P. boisei* evolved a remarkable number of similarities in parallel.
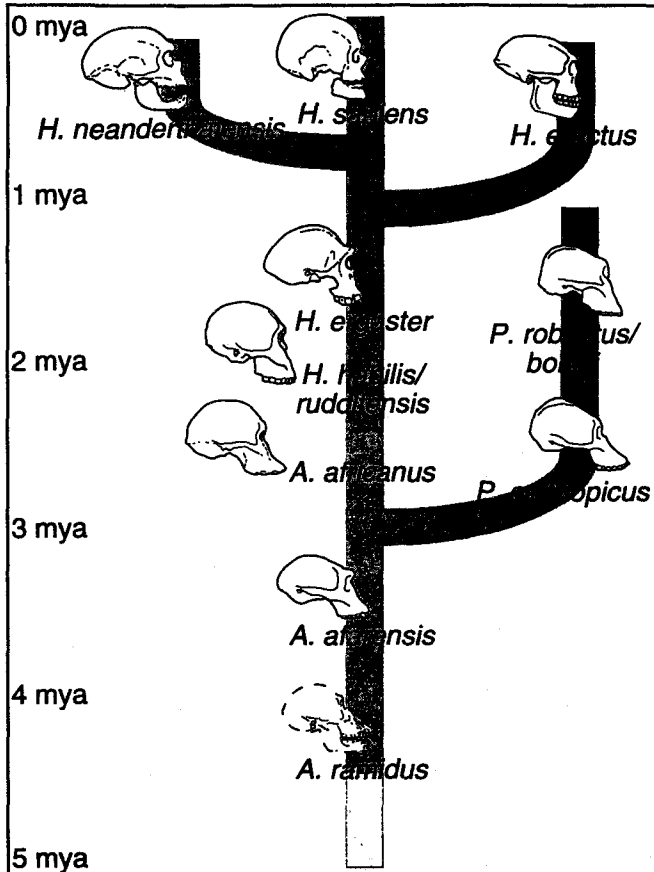
Fig. 1. A speculative phylogeny linking the human species discussed in the text. (*A., Australopithecus; P., Paranthropus; H., Homo*). The postulated branching events within *Homo* after 2-1.5 million years ago are particularly controversial.

It is now widely agreed that *Homo* had appeared by 2.4–2.3 mya, and most specialists recognize only a single stem species, *H. habilis* (Tobias, 1991). This differed most conspicuously from the australopithecines in its larger brain, which evolved in the absence of any significant increase in body size. On average, relative to the australopithecines, *H. habilis* also had smaller cheek teeth. However, there is the complication that both endocranial volume and cheek tooth size varied greatly within *H. habilis*.

Some individuals had large skulls and large, australopithecine-size teeth, while others had much smaller, australopithecine-size skulls and relatively small cheek teeth, similar in size to those of the succeeding species, *Homo erectus*. Conceivably, this variability implies extraordinary differences between the sexes (sexual dimorphism), but it might also mean that *H. habilis* was actually two species: *H. habilis* (in the narrow sense) for the individuals with smaller brains and teeth and *H. rudolfensis* for those with larger brains and teeth (Wood, 1991, 1992, 1993). Arguably, neither *H. habilis* nor *H. rudolfensis* constitutes a likely ancestor for later *Homo*, in which case, there must have been yet a third contemporaneous species of very early *Homo*. The most likely candidate for this third species would be "African *Homo erectus*," which is well documented in the fossil record only after 1.8 mya.

Whether or not *H. habilis* comprises more than one species, at least one of its variants apparently experienced a significant increase in mean brain size after 2.4–2.3 mya, and it is probably not coincidental that the most ancient archaeological sites also date from this time. These sites comprise clusters of stone artifacts and fragmentary animal bones that provide the oldest nonanatomical evidence for human behavior. The sites are usually grouped in the Oldowan Industrial Complex, named for Olduvai Gorge, where Oldowan artifact assemblages are particularly well known. In general, Oldowan tools include a range of sharp flakes and the cores or core (="pebble") tools from which they were struck (Fig. 2) (Schick and Toth, 1993). Oldowan stone working technology was primitive by later standards, and individual pieces are notoriously difficult to assign to discrete types. Still, the Oldowan Complex reflects an ability to flake stone that living chimpanzees can probably not acquire (Toth *et al.*, 1993), and the artifacts and associated fragmentary animal bones demonstrate a commitment to artifact manufacture and to carnivory beyond anything known in apes. They show further that at least one human species had developed the uniquely human habit of accumulating garbage at favored spots on the landscape.

The appearance and continuing development of stone artifacts is almost certainly linked to progressive brain expansion in *Homo*, while more sophisticated artifacts for processing food could explain a concomitant decline in average cheek tooth size (Fig. 3). This inference assumes that early *Homo* produced most, if not all the earliest stone tools, and it would be weakened if it could be shown that the "robust" australopithecines manufactured a significant number. This possibility cannot be evaluated directly, but it is perhaps suggested by the remarkable similarity between the thumbs of *Paranthropus robustus* and those of *Homo*, including *H. habilis* (Susman, 1994). Thumb form in *Homo* facilitates the precision grasp, in contrast to thumb form in chimpanzees which promotes the power grasp. Thumb bones
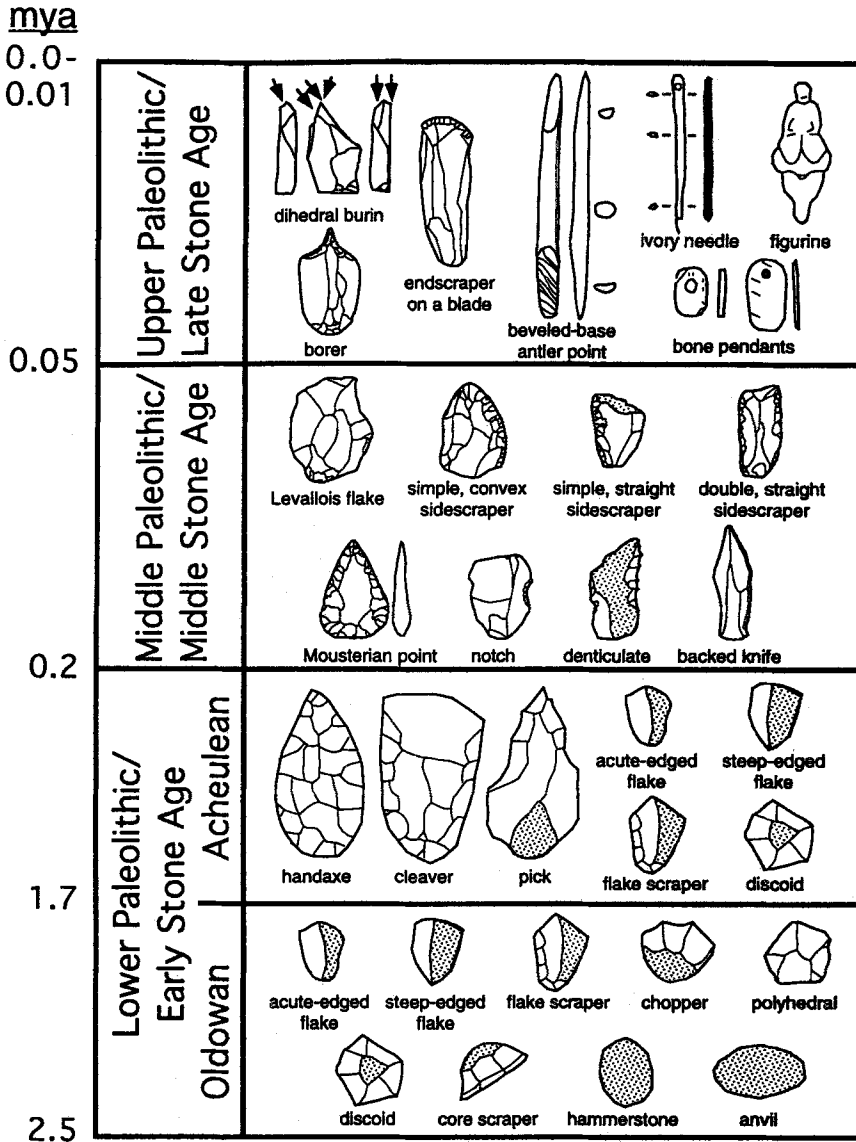
mya

Fig. 2. Some common artifact types in the main culture-stratigraphic units discussed in the text. The individual drawings are not to scale.

of *A. afarensis* indicate that the earliest humans had a chimpanzee-like power grasp.
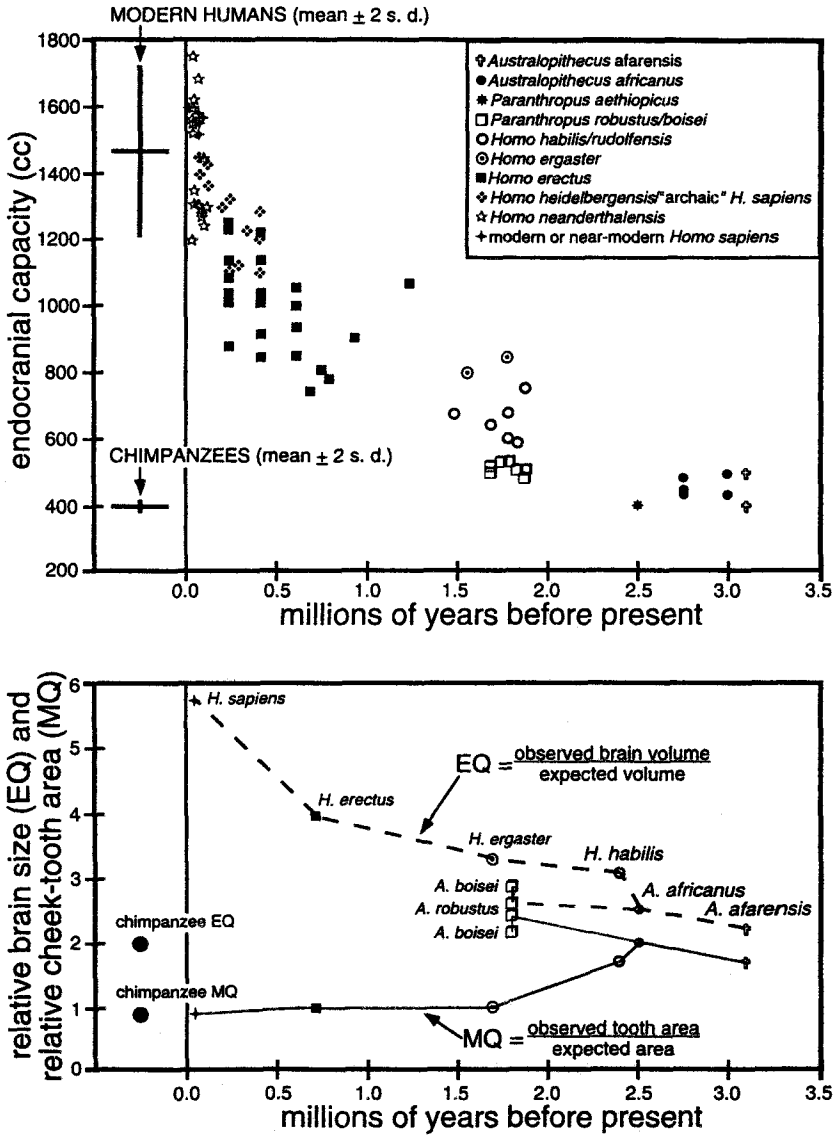
Fig. 3. Top: Endocranial volume versus time, illustrating the remarkable increase in volume that characterized the evolution of *Homo* (data from Aiello and Dunbar, 1993: pp. 188-189). Bottom: Relative brain size (endocranial volume) (EQ) and relative cheek tooth size (MQ) versus time, showing (1) that long-term increase in endocranial volume in *Homo* was not due simply to increased body size and (2) that it was accompanied by a less dramatic, but still conspicuous decrease in the relative size of the cheek teeth (premolars and molars). The data are from McHenry (1994a), who explains how relative endocranial volume and relative cheek tooth size were calculated.

If natural selection for dexterity in stone knapping drove the development of the human thumb, then it is reasonable to argue that *P. robustus* made at least some early stone tools. However, *P. robustus/P. boisei* and early *Homo* coexisted for perhaps a million years, from 2 mya or before until 1.2 mya or later (Fig. 1). During this long interval, stone artifacts changed significantly, but there is evidence for only one, not two evolving traditions. Additionally, there is no obvious rupture in the archaeological record at the time that *P. robustus/P. boisei* became extinct, sometime between 1.2 and 0.7 mya (Klein, 1988). The same kinds of artifacts were made before and after, when only *Homo* survived, and the most reasonable conclusion is that *Homo* produced most, if not all the earliest stone tools. Conceivably, *P. robustus* applied its precision grasp to food-processing or to some other activity besides stone-knapping. Alternatively, the thumb bone suggesting a precision grasp may actually have come from early *Homo*, which is represented in the same deposit (at the Swartkrans Cave, South Africa), but by many fewer diagnostic craniodental fragments (Susman, 1993).

HOMO ERECTUS, HANDAXES, AND THE INITIAL COLONIZATION OF EURASIA

In most current textbooks, *Homo habilis* (or one of its variants) is said to have evolved into *Homo erectus* approximately 1.8–1.7 mya. The oldest specimens of *H. erectus* include a nearly complete skull, a second partial skull, several lower jaws, and some postcranial bones from the east shore of Lake Turkana in northern Kenya (Rightmire, 1990, 1992; Walker, 1993; Walker and Leakey, 1993; Wood, 1991, 1992). The skulls differ from those of *H. habilis* in various features, including especially the presence of a conspicuous supraorbital torus (brow ridge) across the top of the orbits, thicker skull walls, and a yet larger brain (greater endocranial volume). Much of the increase in brain size, however, may relate to a dramatic, concomitant increase in body size, especially in females (McHenry, 1992, 1994a).

Homo erectus was perhaps the first human species to rely almost exclusively on bipedalism, in contrast to earlier species, which may have depended more on a mix of bipedalism and tree climbing (Spoor *et al.*, 1994). It was also the first human species in which body weight and stature increased to approximately their modern values, and it appears to have been the first in which males and females differed in size no more than in living people (McHenry, 1994b). Earlier humans were much more dimorphic, resembling chimpanzees in this regard. In extant higher primates, strong sexual dimorphism tends to reflect polygynous mating systems in which males

compete vigorously for females, while reduced sexual dimorphism is associated with monogamous mating systems in which males and females pair for long periods. Decreased dimorphism in *H. erectus* may thus indicate the beginnings of a distinctively human pattern of sharing and cooperation between the sexes, prefiguring the social organization of historic human hunter-gatherers.

The type specimens of *H. erectus* come from China and Java, and these arguably differ from early African *H. erectus* in having (1) somewhat larger, lower, flatter more angular braincases, (2) yet thicker skull walls, (3) thicker brow ridges from top to bottom, and (4) ear and nasal specializations that, together, may justify placement of the African fossils in a separate, more primitive species, for which the name *Homo ergaster* is available (Groves, 1989, 1992; Wood, 1991). If the validity of *H. ergaster* is accepted, it could be ancestral both to *H. erectus* narrowly understood (in the Far East) and to other forms of archaic *Homo* in Africa and Europe (Fig. 1). *H. ergaster* (or "African *Homo erectus*") was almost certainly responsible for the more sophisticated stone artifacts that appeared in Africa at about the same time (Asfaw *et al.*, 1992; Roche, 1994). These include the oldest known handaxes and other bifacial tools that are the hallmark of the Acheulean Industrial Complex (Fig. 2), named after St. Acheul, France, where abundant bifaces were found in the nineteenth century. Together with fully developed bipedalism and the changes in social organization, Acheulean tools and affiliated cognitive advances help explain how *H. ergaster* was able to colonize some new environments in Africa and also how it became the first human species to expand to Eurasia.

The oldest secure evidence for human presence outside Africa comes from the Acheulean ("handaxe") site of 'Ubeidiya in the Jordan Valley of Israel, dated to roughly 1.4–1.3 mya (Bar-Yosef, 1994a; Bar-Yosef and Goren-Inbar, 1993; Tchernov, 1987, 1992, 1994). However, an earlier emergence is possible, based especially (1) on the discovery of artifacts and a human mandible at Dmanisi in Georgia, where paleomagnetism and the dating of an underlying volcanic tuff suggest an age of roughly 1.8 mya (Bar-Yosef, 1994a; Dzaparidze *et al.*, 1992; Gabunia and Vekua, 1995), and (2) on recently obtained dates of 1.8–1.6 mya for *H. erectus* sites in Java (Swisher *et al.*, 1994). Since handaxes were invented in Africa only after 1.8 mya, the spread of early *Homo* to Java by this time might explain why typical Acheulean handaxes never appeared in the Far East and, more generally, why the artifact assemblages of Far Eastern *H. erectus* always retained an Oldowan cast (Schick and Dong, 1993). However, the Javan dates are based on fragments of volcanic pumice that could be significantly older than the fossil-bearing alluvial deposits in which they occur (de Vos *et al.*, 1994), and further investigation of the Dmanisi locality may suggest a much

younger date, perhaps near 0.9 mya. A date of this order would be consistent with (1) the relatively evolved morphology of the Dmanisi mandible (Dean and Delson, 1995) and (2) an estimated age of about 1 million years for the oldest archaeologically well-documented occupation of east Asia. This date is founded on a paleomagnetic assessment of sediments that have provided large, well-excavated artifact assemblages in the Nihewan Basin, 150 km west of Beijing, China (Schick and Dong, 1993).

It is commonly assumed that Europe and Asia were first occupied about the same time, but many putative European sites older than 500,000 years are problematic, either because the dates are insecure or because human presence depends on flaked stones that may be natural in origin. Until recently, the oldest known European human fossils were believed to date to about 500,000 years ago, and some specialists have argued that Europe was first colonized only about this time (Roebroeks, 1994). In this case, the oldest known European fossils, including, for example, a mandible from Mauer (Germany), a skull from Petralona (Greece), a partial skull from Arago (France), and a tibial shaft from Boxgrove (England), would in fact represent the first Europeans, and the oldest artifacts would be well-made Acheulean handaxes and associated pieces from Boxgrove (M. B. Roberts et al., 1994) and from broadly contemporaneous, well-documented Acheulean sites such as Hoxne in England (Singer et al., 1993), Cagny-la-Garenne in France (Bourdier, 1976; Villa, 1991), Fontana Ranuccio in Italy (Segre and Ascenzi, 1984), and Torralba and Ambrona in Spain (Howell, 1966; Freeman, 1994).

An initial colonization of Europe only about 500,000 years ago could explain why the Petralona skull is so remarkably similar to its presumed African contemporaries, including above all the famous Kabwe (= Broken Hill = "Rhodesian Man") skull from Zambia. Unlike like-aged skulls of Far Eastern H. erectus which have relatively small, angular brain cases with barlike brow ridges that flare out laterally, the skulls from Petralona and Kabwe have somewhat more rounded and expanded braincases, with brow ridges that arch upward over each orbit and thin toward the sides (Groves, 1992). In most textbooks, Petralona, Kabwe, and other broadly contemporaneous African and European fossils are called "archaic Homo sapiens," though some authorities prefer the term Homo heidelbergensis (Stringer and Gamble, 1993), reflecting the relatively early discovery of the Mauer mandible and the proximity of Mauer to Heidelberg.

Conceivably, humans could not colonize Europe permanently until it provided ample carcasses to scavenge, and an inadequate supply may have appeared only about 500,000 years ago, when two species of large, scavenging hyenas became regionally extinct (Turner, 1992). However, it is at least equally plausible that the hyenas disappeared because of a human

influx, and it is difficult to imagine how carnivore turnover or other environmental factors could have excluded people from Europe for at least 500,000 years after they had reached north China. Recent discoveries of human fossils at Cueva Victoria (Palmqvist *et al.*, 1995) and, especially, in the Gran Dolina (Atapuerca), Spain (Arsuaga *et al.*, 1994; Carbonell *et al.*, 1995; Parés and Pérez-González, 1995), suggest in fact that humans arrived in Europe nearer to 1 million years ago. If this is true, the close resemblance between 500,000-year-old European and African fossils might mean that there was a second human dispersal from Africa to Europe about this time, bringing with it the Acheulean Industrial Tradition. All European artifact assemblages that supposedly antedate 500,000 years ago lack handaxes and other bifacial tools, while immediately younger assemblages mostly contain them. A dispersal from Africa about 500,000 years ago might be signaled at the Israeli site of Gesher Benot Ya'aqov, where an Acheulean assemblage with striking African affinities could be about this age (Bar-Yosef, 1994a; Goren-Inbar *et al.*, 1992).

Artifact assemblages remained similar between Africa and Europe after 500,000 years ago, while the Far East continued on its own distinctive course. About 200,000 years ago, Acheulean (Early Stone Age/Lower Paleolithic) assemblages were widely replaced in both Africa and Europe by (Middle Stone Age/Middle Paleolithic) assemblages emphasizing a refined flake technology, usually without handaxes (Fig. 2). However, after 200,000 years ago, the human form came to differ markedly between the two continents, and by 100,000 years ago, Europe was occupied exclusively by the highly distinctive Neanderthals, while Africa was inhabited by people whose appearance was far more modern. Much older European fossils from sites such as Swanscombe (England), Atapuerca (Spain), Biache-Saint-Vaast (France), and Ehringsdorf (Germany), all probably between 300,000 and 150,000 years old, already anticipate the Neanderthals and imply that they were an indigenous European development (Stringer and Gamble, 1993; Arsuaga *et al.*, 1993, 1994).

The more modern African contemporaries of the Neanderthals are represented at Klasies River Mouth, Border Cave, and Die Kelders Cave in South Africa, Mumba Shelter in Tanzania, Omo Kibish in Ethiopia, and Dar es Soltan in Morocco (Bräuer, 1992; Rightmire, 1989). The famous modern or near-modern human remains from es Skhul and Jebel Qafzeh caves in Israel probably also belong on this list, since associated "Ethiopian" mammalian species imply that they date to a time when Israel lay within a slightly expanded Africa (Tchernov, 1992, 1994). Thermoluminescence dates on associated flints and electron spin resonance dates on animal teeth fix this time between roughly 110,000 and 80,000 years ago (Mercier and Valladas, 1994; Schwarcz, 1994). As a group, the key African

fossils reveal people with relatively short, high braincases overhanging the face in front, in stark contrast to the long, low braincases and forwardly mounted faces of the Neanderthals. It is this fossil difference that most strongly supports the now-famous "Out-of-Africa" theory, according to which modern humans spread from Africa to replace the Neanderthals and other equally archaic humans in Eurasia.

THE "OUT-OF-AFRICA" HYPOTHESIS AND ITS MULTIREGIONAL ALTERNATIVE

The "Out-of-Africa" hypothesis for modern human origins might be better called "Out-of-Africa 2" (Stringer and Gamble, 1993), since it really concerns the pattern of human evolution after "Out-of-Africa 1," the widely accepted original human dispersal from Africa at or before one million years ago. In effect, Out-of-Africa 2 posits that Out-of-Africa 1 was followed by a tendency for human populations to follow different evolutionary trajectories on different continents, culminating by 100,000 years ago in the emergence of at least three continentally distinct human populations (Fig. 1). In the Far East, there were the still poorly documented nonmodern people, who in some respects recall much older European and African fossils assigned to "archaic *H. sapiens*" (or *H. heidelbergensis*) (Aiello, 1993; Howell, 1994), but who might represent an evolved end product of the *H. erectus* lineage; in Europe, there were the equally nonmodern Neanderthals; and in Africa, there were modern or near-modern humans. In its most extreme form, Out-of-Africa 2 posits that modern people expanded from Africa, beginning 60,000–50,000 years ago, and replaced the Neanderthals and equally archaic East Asians without gene exchange (or interbreeding). In its less extreme form, Out-of-Africa 2 allows for some gene flow between expanding moderns and resident archaic populations (Bräuer, 1992; Smith, 1994).

The primary alternative to Out-of-Africa 2 is the Theory of Multiregional Evolution, which postulates that modern humans originated essentially everywhere—in Africa, but also in Europe and Asia—where nonmodern humans had lived previously. Proponents of the multiregional model agree that widely dispersed human populations tended to diverge morphologically immediately following Out-of-Africa 1, but they argue that continuous gene flow ensured the rapid spread of highly adaptive novelties (like larger brains) and thereby kept all human populations on the same fundamental evolutionary track toward modern people (Frayer et al., 1993, 1994; Wolpoff 1995; Wolpoff et al., 1994).

There is no independent evidence for the gene flow that multiregion-
alism requires, and small, widely scattered hunter-gatherer populations are
perhaps unlikely to have exchanged sufficient genes on an intercontinental
scale. In this light, the multiregional model is not so much a theory as it
is an after-the-fact explanation for apparent morphological resemblances
between nonmodern and modern populations in Asia and Europe. Mul-
tiregionalists argue, for example, that the skulls of the living Chinese share
relatively nonprotruding (nonprognathous) jaws, upper facial flatness, a
tendency for the development of a (sagittal) keel or torus along the top
of the skull, extrasutural ("Inca") bones between the main bones of the
skull, shovel-shaped upper incisors, and other features with fossils that have
been traditionally assigned to Chinese *Homo erectus*; that historic Austra-
lian aborigines share large, sometimes shelflike brow ridges, long, flat, re-
ceding frontal bones ("foreheads"), a ridge of bone (an occipital or nuchal
torus) around the back of the skull for attachment of the neck muscles,
forwardly protruding (prognathous) jaws, large teeth, and other characters
with fossils assigned to Indonesian *Homo erectus*; and that early modern
Europeans share large, prominent noses, a tendency for backward projec-
tion ("bunning") of the occiput (rear or the skull), and a propensity for a
"horizontal-oval" mandibular foramen (a natural perforation on the inner
surface of the mandible) with the Neanderthals. Ironically, multiregionalists
do not cite comparable indications of continuity between archaic and mod-
ern Africans, perhaps because the most conspicuous similarities are ones
that modern Africans share more broadly with other modern people. These
include "a high, convex frontal positioned directly above a vertical face, a
chin, a rounded occiput, and a short, flexed basicranium" (Lieberman, 1995:
177), whose early appearance in Africa in fact comprises vital support for
Out-of-Africa 2.

The multiregional theory has been criticized, because most key fea-
tures are not simply present or absent but vary in frequency among geo-
graphically far-flung human populations, both fossil and living. Many are
actually most common in recent populations where the multiregional theory
supposes them to be rare (Lahr, 1994). In addition, some features, such
as large brow ridges and occipital tori that do prevail where multiregion-
alists specify, are primitive characters that may simply have been conserved
more in some populations than in others, while other apparent regional
characters, such as large noses or especially flat faces, may be highly adap-
tive in certain environments and might therefore have evolved inde-
pendently in successive archaic and modern populations (Stringer and
Bräuer, 1994). Yet other critical traits, such as occipital bunning or sagittal
keeling, may not be developmentally homologous between archaic and
modern humans, or they may be mechanically forced by partially shared

cranial dimensions that themselves are not homologous (that is, that do not reflect shared descent) (Lieberman, 1995).

More generally, it can be argued that seeming evidence for multiregional continuity is inevitable so long as human fossils remain rare compared to the number of features among which multiregionalists can search for similarities (Harpending, 1994). Less arguably, the genetics of living human populations bolster Out-of-Africa 2 far more strongly than its multiregional alternative either (1) by suggesting a massive population expansion 50,000–40,000 years ago when Out-of-Africa 2 occurred (Sherry *et al.*, 1994) or (2) by indicating that all living humans share a relatively recent African ancestor (Bowcock *et al.*, 1994; Cann *et al.*, 1994; Cavalli-Sforza *et al.*, 1994; Mountain *et al.*, 1993; Stoneking, 1993). Based on genetic studies, multiregionalism may be valid only in a significantly modified or weaker form resembling the version of Out-of-Africa 2 that allows for gene flow between expanding modern and resident archaic populations. Conceivably, gene flow was particularly strong in the Far East, based (1) on the relatively numerous morphological resemblances that allegedly link Chinese and Indonesian *H. erectus* to the living Chinese and aboriginal Australians respectively and (2) on the absence, so far, of a conspicuous archaeological (behavioral) breach in southern China and adjacent southeast Asia around 50,000 years ago (Olsen and Miller-Antonio, 1992; Wolpoff *et al.*, 1994).

OUT-OF-AFRICA 2 AND THE EVOLUTION OF HUMAN BEHAVIOR

One potential objection to "Out-of-Africa 2" concerns the failure of modern or near-modern humans to expand from Africa immediately after they appeared there, at least 100,000 years ago. Instead, they seem to have been confined to Africa until roughly 60,000–50,000 years ago, and it is even possible that they were replaced by Neanderthals on the southwest Asian margin of Africa (in what is now Israel) roughly 80,000 years ago (Tchernov, 1992, 1994). Archaeology provides a partial answer to the apparent dilemma. The people who inhabited Africa between 100,000 and 60,000 years ago may have been physically modern or near-modern, but they were behaviorally very similar to the Neanderthals and other archaic humans (Bar-Yosef, 1994b; Jelinek, 1994; Klein, 1994). Admittedly, they had much more than an elementary grasp of stone flaking; they often collected naturally occurring iron and manganese compounds which they could have used as pigments; they apparently built fires at will; they buried their dead, at least on occasion; and they routinely acquired large mammals as

food. In all these respects and perhaps others, they may have been relatively advanced over earlier, archaic people. However, in common with earlier people and with their Neanderthal contemporaries, they manufactured a relatively small range of recognizable stone artifact types; their artifact assemblages varied remarkably little through time and space (in spite of notable environmental variation); they obtained stone raw materials overwhelmingly from local (vs. far distant) sources (suggesting relatively small home ranges or very simple social networks); they rarely if ever utilized bone, ivory, or shell to produce formal artifacts; they left little or no evidence for structures or for any other formal modification of their campsites; they were relatively ineffectual hunter-gatherers, who lacked, for example, the ability to fish; their populations were apparently very sparse, even by historic hunter-gatherer standards; and they left no indisputable evidence for art or decoration.

Based on what the earliest modern Africans did and did not do, it seems reasonable to conclude that they were cognitively human, but not cognitively modern in the sense that all living people are. It was only when they became cognitively modern, with the fully modern capacity for Culture, that they obtained an adaptive advantage over their archaic Eurasian contemporaries. If Out-of-Africa 2 is correct, we would expect the oldest secure evidence for art and for other indicators of modern mental abilities to appear first in Africa. In fact, the oldest secure dates for decorative items, in the form of ostrich eggshell beads, and for the accompanying increase in artifact standardization that is also a hallmark of fully modern behavior, come from the site of Enkapune ya Muto in the central Rift Valley of Kenya (Ambrose, 1994). These dates imply that beads and more formal ("Later Stone Age") stone artifacts, broadly similar to ones that were still being made in parts of Africa at time of European contact, appeared in east Africa by 46,000 years ago, several thousand years before analogous markers appeared in Europe. At least arguably, when modern human behavioral traits appear in Europe, they occur first in southeastern Europe (at roughly 43,000 years ago), 2000–3000 years before they appear in western Europe (Mellars, 1993). This is the expected pattern if the traits were introduced by immigrant African populations. An African origin is further implied by the appearance of broadly similar modern behavioral markers in southwestern Asia in the interval between their earliest appearances in Africa and Europe (Bar-Yosef *et al.*, 1995).

In sum, the relevant archaeological evidence both supports and supplements the fossil evidence for the African origin of modern humans.

SOME PROBLEMS WITH OUT-OF-AFRICA 2

I believe that Out-of-Africa 2 is the most plausible and parsimonious explanation of the available fossil and archaeological data, but some prominent authorities disagree. Clark (1992; Clark and Lindly, 1991), for example, has argued that the proponents of Out-of-Africa 2 have unwittingly imposed their intellectual preconceptions on contrary data, and this leads him to favor the multiregional model of modern human origins. However, carried to its logical extreme, his perspective precludes any resolution of the issue, barring the unlikely development of data collection procedures that do not require advance assumptions or expectations. I do not want to downplay the potential impact of new intellectual frameworks or paradigms, but my intent here is to outline some problems with Out-of-Africa 2 that are more evidentiary than epistemological.

(1) What explains the relatively abrupt appearance of modern human behavior (= the modern capacity for culture)? As I indicated in the introduction, I believe that the answer is the final development of the fully modern human brain. However, this argument relies primarily on two circumstantial observations: (1) that natural selection for more effective brains largely drove the earlier phases of human evolution and (2) that the relationship between morphological and behavioral change shifted abruptly about 50,000 years ago. Before this time, morphology and behavior appear to have evolved more or less in tandem, very slowly, but after this time, morphology remained relatively stable, while behavioral (cultural) change accelerated rapidly. What could explain this better than a neural change that promoted the extraordinary modern human ability to innovate? Given this ability, modern people have adapted rapidly to a remarkable range of natural and social circumstances with little or no physiological change. However, the neural hypothesis will be very difficult to test, since fossil skulls provide only speculative evidence for brain organization. Neanderthal skulls, for example, differ dramatically in shape from modern ones, but they were as large or larger, and on present evidence it is not clear that the difference in form implies a significant difference in function.

(2) Were Neanderthals fundamentally incapable of fully modern behavior? As I have outlined it, Out-of-Africa 2 postulates that the Neanderthals were replaced because they could not compete culturally with their modern human successors. The argument is bolstered over most of Europe by the relatively abrupt nature of the replacement. At many sites, Cro-Magnon/Upper Paleolithic occupations overlie Neanderthal/Middle Paleolithic layers with no evidence for a major break in time or for any transition between the two, suggesting the replacement took only decades, or at most, centuries. Demographic modeling shows that only a 1 or 2% rise in Ne-

anderthal mortality could have extinguished Neanderthal populations within 1000 years (Zubrow, 1989), and the Cro-Magnons might have induced such a rise simply by excluding the Neanderthals from essential resources. To accept this possibility, however, we must assume that there was little or no gene flow or culture trait diffusion between Neanderthal residents and Cro-Magnon invaders. Except to some multiregionalists, the fossil record provides no compelling evidence for gene flow, and even if this were possible, it might have been precluded by the biologically grounded behavioral gulf between Neanderthals and Cro-Magnons. In this sense, the Cro-Magnon invasion of Europe would have differed fundamentally from the historic, European invasion of the Americas or Australia, where the indigenes and invaders clearly had the same biological capacity for culture, and interbreeding was rampant.

However, there is a significant problem with the idea that the Neanderthals could not behave like moderns. This is the occasional discovery of artifact assemblages that comprise a blend of Neanderthal/Middle Paleolithic and Cro-Magnon/Upper Paleolithic artifact types. At some sites, such "mixed" assemblages may have been created when excavators inadvertently merged the contents of adjacent Neanderthal/Middle Paleolithic and Cro-Magnon/Upper Paleolithic layers, but this is surely not the case at several "Chatelperronian" sites in central and western France and adjacent, northern Spain. Chatelperronian stone artifact assemblages generally combine typical Middle Paleolithic "sidescrapers," "denticulates," and "backed knives" with numerous characteristic Upper Paleolithic "endscrapers" and "burins" (Harrold, 1989). At one site, the singular Grotte du Renne at Arcy-sur-Cure in the Paris Basin, typical Chatelperronian stone artifacts are accompanied by carefully shaped bone artifacts and by bone beads or pendants (Fig. 4) (Léroi-Gourhan, 1965; Baffier and Julien, 1990; Farizy, 1990, 1994; Taborin, 1990). The stone and bone artifacts were recovered from occupation floors with patterned arrangements of postholes, mammoth tusks, limestone plaques, and hearths that probably mark the positions of ancient huts (Fig. 5). By themselves, the stone artifacts might be ambiguous, but the bone artifacts, ornaments, and highly structured floors point unequivocally to the Upper Paleolithic. Remarkably, three associated human teeth exhibit enlargement of the pulp cavity and fusion of the roots ("taurodontism") that are generally considered Neanderthal (vs. Cro-Magnon) traits. Neanderthal authorship of the Chatelperronian is implied even more conspicuously at La Roche à Pierrot rockshelter, St. Césaire, west–central France, where a partial Neanderthal skeleton was directly associated with typical Chatelperronian stone tools (Lévêque et al., 1993).
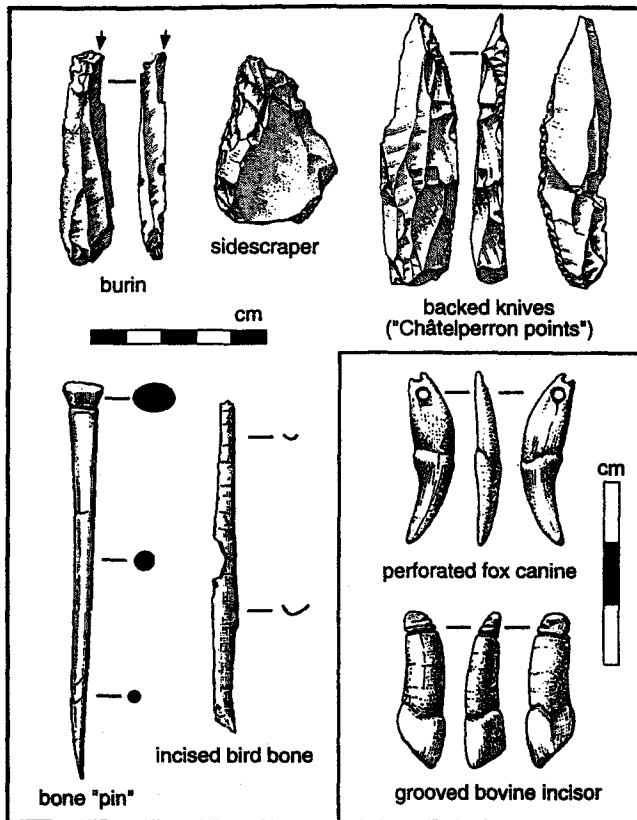
Fig. 4. Chatelperronian artifacts from the Grotte du Renne, Arcy-sur-Cure, France. The bone artifacts and perforated or incised teeth ("pendants") are particularly important in assigning the Chatelperronian to the Upper Paleolithic. The stone artifacts were redrawn after Farizy (1990, Fig. 4); the bone artifacts, after Baffier and Julien (1990, Fig. 1); and the modified teeth after Taborin (1990, Fig. 6).

Chatelperronian layers have been dated variously by radiocarbon, by thermoluminescence, and by correlation to regional or global climate stratigraphies. The results are somewhat inconsistent, but a reasonable inference now is that the Chatelperronian existed for a millennium or two sometime between 42,000 and 36,000 years ago. It was during this same interval that the earliest undeniable Upper Paleolithic culture or culture complex, known as the Aurignacian, appeared widely in southeastern, cen-
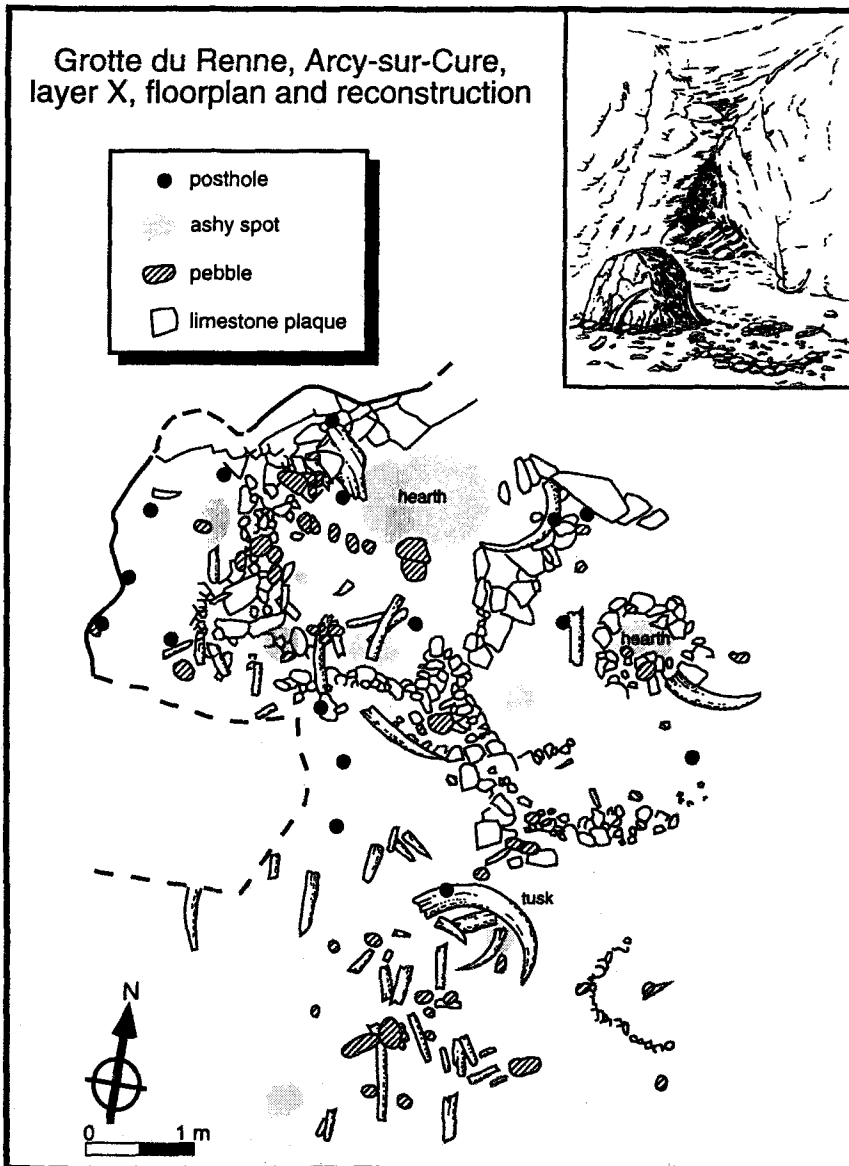
Fig. 5. The floorplan of a Chatelperronian layer (layer XI) in the Grotte du Renne at Arcy-sur-Cure, France, illustrating a degree of spatial organization that is typical only in the Upper Paleolithic. Redrawn after Farizy (1990, Fig. 5).

tral, and western Europe (Mellars, 1992; Straus, 1993/1994). The Aurignacian is marked by a multiplicity of highly formalized, distinctive Upper Paleolithic stone and bone artifact types and by a variety of art objects, including human and animal representations (Bahn, 1994; Mellars, 1993; R. White, 1989). At most sites where the Aurignacian and Middle Paleolithic occur together, the Aurignacian abruptly overlies the Middle Paleolithic, and in the version of Out-of-Africa 2 that I favor, the Aurignacian is a plausible artifactual manifestation of the Cro-Magnon invasion. So far, the makers of the earliest Aurignacian in France or Spain are unknown, but in Moravia (Czech Republic) they were unquestionably modern (rather than Neanderthal) (Frayer, 1986; Gambier, 1989; Hublin, 1990; Smith *et al.*, 1989).

How, then, to explain the Chatelperronian? Where Middle Paleolithic, Chatelperronian, and Aurignacian layers are superimposed, the Chatelperronian layers almost always lie in the middle. The exceptions are three sites where late Chatelperronian and early Aurignacian layers appear to interfinger, suggesting a brief period of culture contact. In this light, it is tempting to conclude that the Chatelperronian reflects cultural diffusion from Cro-Magnon Aurignacians to Middle Paleolithic Neanderthals, before the Neanderthals finally succumbed. However, even if this appears credible, it begs one fundamental question: If Upper Paleolithic culture was clearly superior and the Neanderthals could imitate it (that is, they were not biologically precluded from behaving in an Upper Paleolithic way), why did they not acculturate more widely, with the result that they or their genes would have persisted much more conspicuously into Upper Paleolithic times (after 40,000–35,000 years ago)? I have no compelling answer, and I regard the Chatelperronian as a major puzzle whose solution is important for closure on Out-of-Africa 2.

(3) Why were the earliest modern humans not as heavily built as the Neanderthals? Neanderthal limb bones are remarkably robust, with strong muscle markings, implying that Neanderthals of both sexes were exceptionally powerful people. In spite of this, they often broke their bones, they commonly developed arthritis or other senile pathologies in their 20s or 30s, and they seldom survived beyond age 40 (Berger and Trinkaus, 1995; Brennan, 1991; Trinkaus, 1995; Trinkaus and Shipman, 1993). The sum suggests that they led extraordinarily stressful lives. In contrast, their fully modern, Cro-Magnon successors were much less heavily built, they broke their bones much less often, and their maximum life expectancy was significantly greater. Since Neanderthals were culturally (artifactually) much less sophisticated, a reasonable explanation for the difference is that Neanderthals often accomplished physically what later people accomplished culturally (technologically).

The downside of Neanderthal robusticity was that it required a great deal of energy to sustain, and it is presumably this that favored reduced robusticity in modern humans—the same number of calories could now support larger populations, and larger populations are a measure of evolutionary success. However, the most completely known early modern contemporaries of the Neanderthals, from Qafzeh Cave in Israel, were much less heavily built than the Neanderthals, despite the fact that they made similar, relatively unsophisticated artifacts (Bar-Yosef and Vandermeersch, 1993; Trinkaus, 1992, 1993). To the extent that this casts doubt on the adaptive superiority of fully modern technology, it presents a problem for the version of Out-of-Africa 2 that I favor.

(4) What kind of people first occupied the Americas and Australia? A probable corollary of Out-of-Africa 2 is that they were fully modern. With regard to the Americas, this follows from (a) the likelihood that first entry was across a land bridge that linked northeast Asia to Alaska during glacial intervals (= periods of lowered sea level) and (b) archaeological evidence that northeast Asia was itself first colonized only after 35,000 years ago (Kuzmin, 1994; Goebel, 1995), when fully modern humans developed the housing, clothing, and other cultural wherewithal to adapt to very harsh, continental climates. The colonization of the Americas by fully modern humans is fully consistent with the archaeology of North and South America, neither of which was indisputably occupied before the closing phases of the Last Glaciation, after 14,000 years ago (Haynes, 1992; Hoffecker *et al.*, 1993; Meltzer, 1993). At least south of Alaska, human occupation prior to this time was probably precluded by an ice sheet that extended more or less continuously across Canada. In short, the American record presents no problem for Out-of-Africa 2.

The same may not be true for Australia, where the argument for an initial colonization by fully modern humans follows from the need to cross 80–100 km of open water, the minimum distance separating Australia from southeast Asia, even during periods of lowered sea level. It would be hard to deny an essentially modern capacity for Culture to people who could produce sufficiently sea-worthy water-craft. Until recently, it appeared that the first Australians were in fact fully modern people who arrived between 40,000 and 30,000 years ago, bringing with them complex burial practices, fishing technology, art, and probably other modern behavioral markers (Jones, 1990). An entry at about 40,000 years ago could itself be regarded as an indicator of the modern human ability to innovate, this time with respect to water transport.

It now appears possible, however, that Australia was occupied much earlier, by 60,000 years or before. The relevant dates were obtained by the thermoluminescence and optically stimulated luminescence methods on un-

burnt quartz sands enclosing and overlying artifacts at the Malakunanja II and Nauwalabila I sites in northern Australia (R. G. Roberts *et al.*, 1994). Both methods are experimental, but the results are particularly compelling at Nauwalabila I, where optical and calibrated C-14 dates on the upper layers agree closely. At Nauwalabila I, a layer dated by the optical method to approximately 53,000 years contains ground hematite fragments that the excavators believe were used for painting. If so, this could mean that the first Australians were behaviorally advanced over their European and African contemporaries. However, the hematite might have been used for hide processing or some equally mundane purpose, and similar hematite fragments are common in Middle Paleolithic/Neanderthal sites, with no other evidence for art (Bordes, 1952; Combier, 1988). They also occur without apparent art at many (Middle Stone Age) sites antedating 50,000 years in southern Africa (Thackeray, 1992). Modified hematite fragments are actually more common in such sites than they are in much younger (Later Stone Age) ones, including some whose occupants surely painted on nearby rock faces.

For proponents of Out-of-Africa 2 the problem, then, is not that 60,000-year-old Australian dates imply an especially early, non-African emergence of art, but that they raise two other fundamental questions: (a) Is it possible that modern humans left Africa as much as 60,000 years ago? and (b) Assuming that they did, how is it that they reached the Far East (Australasia) 20,000 years before they reached the Far West (France and Spain)? In this context, it is important to note that the Middle Paleolithic/Upper Paleolithic interface in France and Spain cannot be much older than 40,000 years. This estimate is based not on radiocarbon dates, which provide only minimal ages in the 40,000 year range, but on thermoluminescence dates from Le Moustier (France) (Valladas *et al.*, 1986) and uranium-series dates from Abric Romani (Spain) (Bischoff *et al.*, 1988, 1994) which show that the Middle Paleolithic survived in western Europe until roughly 40,000 years ago.

(5) Is it really true that modern behavioral markers appear widely only about 50,000–40,000 years ago? With regard to art, for example, virtually all specialists agree that it becomes commonplace only after this time and that earlier examples are both rare and crude. However, authorities disagree sharply on what this combination of rarity and simplicity implies. To some, like Bednarik (1992), Hayden (1993), or Marshack (1991), it means that modern cognitive abilities were present but were weakly expressed before 50,000 years ago, while to others, such as Chase and Dibble (1987, 1992), Davidson and Noble (1989), and myself, it suggests that the fully modern capacity for Culture may have appeared only about this time.

In my view, some of the very rare art objects that antedate 50,000 years ago are probably younger intrusions that even the most careful ex- cavations cannot detect, while others are probably the result of human or natural actions that will inevitably, on rare occasions, mimic crude human attempts at art. In this regard, I believe that the only credible claims for art or other modern human behavioral markers before 50,000 years ago involve relatively large numbers of highly patterned objects from well-docu- mented contexts. Using this criterion, perhaps the most serious obstacle to the Out-of-Africa scenario I favor is the discovery of carefully shaped barbed points and accompanying evidence for fishing at the Katanda sites in the Semliki Valley of Zaire (Brooks *et al.*, 1995; Yellen *et al.*, 1995). Electron spin resonance dates on associated hippopotamus teeth and ther- moluminescence dates on covering sands suggest an age between 155,000 and 90,000 years ago. If this estimate is valid, it implies that modern be- havioral traits and modern morphology may have appeared together, at or before 100,000 years ago, and we will be forced to find a nonbehavioral explanation for why modern or near-modern humans were confined to Af- rica until roughly 50,000 years ago. We will also have the difficult task of explaining why even larger, well-excavated artifact and bone assemblages from apparently contemporaneous African sites completely lack evidence for either formal bone work or for fishing.

CONCLUSION

In summary, I have argued that an abrupt change in the archae- ological record about 50,000–40,000 years ago registers the onset of fully modern human behavior. Prior to this time, human morphology and be- havior evolved slowly, hand-in-hand. Afterward, fundamental morpho- logical evolution all but ceased, while behavioral (cultural) evolution accelerated rapidly. Preliminary evidence suggests that key archaeologi- cal markers of fully modern behavior appeared first in Africa, in keeping with fossil evidence that anatomically modern humans also appeared there earliest, between 150,000 and 50,000 years ago. During this same interval, the sole inhabitants of Eurasia were the Neanderthals and other comparably archaic humans. The novel archaeological traits effectively signal the development of the fully modern capacity for Culture, and it was almost certainly this capacity, or more broadly, the cognitive and communicative abilities behind it, that explains why anatomically mod- ern Africans largely or wholly replaced archaic Eurasians, beginning 50,000 years ago.

Among objections to a causal link between an African origin for modern human behavior and the replacement of archaic humans, perhaps the most serious concerns the basis for the development of modern behavior. The archaeological record suggests that from the very beginning, fully modern humans were distinguished by a remarkable ability to innovate (a central element of the modern capacity for Culture), and I believe that this ability was rooted in the final development of the modern human brain. This is not to say that the Neanderthals and other late archaic humans had ape-like brains or that they were as biologically and behaviorally primitive as yet earlier humans. It is only to suggest that an acknowledged genetic link between morphology and behavior in yet earlier people persisted until the emergence of fully modern ones.

The natural selective advantage of an enhanced ability to innovate (or of the fully modern capacity for Culture) is obvious, but the idea that it was made possible by neural change is very difficult to test, because fossil skulls, even ones that differ markedly in shape, provide so little evidence for differences in brain function. In this context, it might seem equally reasonable to argue that fully modern behavior originated among people who had long possessed the capacity for it, but expressed their modern potential only following some biologically irrelevant technological or social change (Hayden, 1993; Soffer, 1990). However, this kind of explanation is more circular than its neural (biological) alternative, since it does not explain why social organization or technology changed so suddenly and fundamentally. Surely, it is more economic to invoke a selectively advantageous neural change like those that were probably linked to earlier behavioral advances in human evolution. Arguably, the key neural change promoted the modern capacity for rapidly spoken phonemic speech, that is, for "a fully vocal language, phonemicized, syntactical, and infinitely open and productive" (Milo and Quiatt, 1994, p. 321). This suggestion follows logically from the obvious dependence of modern culture on modern language, but hard evidence for it is admittedly circumstantial and fragmentary.

New discoveries may strengthen or weaken the neural hypothesis or other ingredients of the wider Out-of-Africa scenario, but full closure is probably impossible one way or the other. The fossil and archaeological records are inherently incomplete and noisy, and evidence for modern human origins may always be partly circumstantial, ambiguous, or even contradictory. Similar uncertainty is common in the legal system, where juries are enjoined to reach a verdict based on the weight of the evidence. The most fundamental conclusion of this paper is that a combination of fossil and archeological evidence favors the Out-of-Africa hypothesis much more strongly than its multiregional alternative.

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