Human Evolution in the Middle Pleistocene: The Role of *Homo heidelbergensis*

G. PHILIP RIGHTMIRE

For paleoanthropologists working in the Middle Pleistocene, these are interesting times. New discoveries of artifacts and human fossils have been reported from western Europe, so that it now looks as though this continent was populated 800,000 years ago, if not earlier. One of the fossils, from Ceprano in Italy, is described as *Homo erectus.* Whether this ancient species ever reached Europe has been repeatedly questioned, but the Ceprano cranium is complete enough to provide some hard evidence.

Other finds from Spain are even more spectacular. The Sima de los Huesos ("Pit of Bones") in the Sierra de Atapuerca has yielded a wealth of skeletons that are best interpreted as early Neanderthals, perhaps close to 300,000 years in age. Older but unfortunately more fragmentary remains, also from Atapuerca, display no Neanderthal features and are claimed as representatives of a new species. *Homo antecessor* will require close study.

These European discoveries focus fresh attention on the evidence accumulating from Africa and Asia. Human bones are known from the earlier Middle Pleistocene of Africa at localities such as Bodo in Ethiopia and Broken Hill in Zambia. The crania

G. Philip Rightmire is Professor of Anthropology at the State University of New York at Binghamton. In his research, which focuses on the evolution of the genus *Homo,* he has studied fossils from many of the important prehistoric localities in Europe, Africa, and the Far East. He is particularly interested in questions about *Homo erectus,* Middle Pleistocene hominids, and the origins of more modern humans.

Key words: species; phylogeny; *Homo erectus; Homo heidelbergensis;* Neanderthals

show anatomical features that distinguish them from *Homo erectus.* In the Far East, the people at Dali and other sites are also more advanced than *Homo erectus,* but their affinities to groups in the West are uncertain.

This Middle Pleistocene record, still sparse but increasingly well dated, raises important questions. One concerns the fate of *Homo erectus* in different regions of the Old World. Another is how many distinct species should be recognized among the descendants of this ancient lineage. It is apparent that the traditional approach of lumping diverse humans together as "archaic" *Homo sapiens* will no longer work. The picture is highly complex, and several taxa probably are needed to accommodate the fossils. Evolutionary relationships among these populations must be clarified, but pose some major problems. I will address only a subset of these topics pertaining mainly to earlier Middle Pleistocene hominids.

HOMO ERECTUS IN PERSPECTIVE

This extinct species has been at the center of much controversy. At present, there is no firm consensus as to whether it should be defined as a long lasting, polytypic lineage or as a group of relatively specialized populations geographically confined to the Far East. In my view, *Homo erectus* originated in Africa and then spread to Eurasia. The hypodigm is made up of specimens from Java, Zhoukoudian, and other sites in China, Ternifine (now Tighenif) in Northwest Africa, Olduvai Gorge, the Turkana Basin, and Swartkrans in South Africa (Fig. 1). Several fossils recently discovered in western Asia and in Europe probably should be counted as well. This

species spans an interval of at least 1.5 million years. Indeed, some East Asian populations may have survived into later Pleistocene times.

As documented by Weidenreich, von Koenigswald, Le Gros Clark, and others, members of this taxon share a suite of characters by which they can be distinguished from recent humans. Some of the principal differences relate to cranial capacity, keeling on the midline of the vault, parietal length, occipital proportions, the anatomy of the cranial base, facial projection, the form of the mandibular symphysis, tooth size, the relative narrowness of the pelvis, and the length of the femoral neck. A large number of traits generally describe *Homo erectus* and diagnose this species relative to living people.

These assumptions have been challenged by several workers, on highly diverse grounds. One point of contention concerns the material from the Turkana Basin. It has been claimed that the early Kenyan crania lack special features developed by the Asian populations. A midline keel on the vault, an angular torus at the postero-inferior corner of the parietal bone, certain characters of the base, and overall thickening of the braincase are said to be absent from the specimens at Koobi Fora but well expressed in the remains from Trinil, Sangiran, and Zhoukoudian. These differences have prompted investigators, including Andrews,[1] Groves,[2] and Larick and Ciochon,[3] to recognize two species and to suggest that *Homo erectus* must be geographically restricted to the Far East. Wood[4,5] agrees, on the basis of facial measurements, perhaps some aspects of temporal bone morphology, and dental differences, that the early African hominids should be set apart
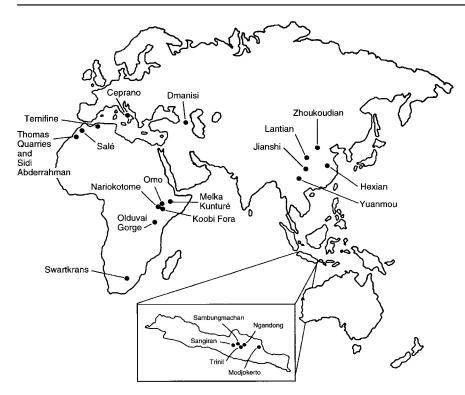
Figure 1. A map showing the principal localities that have yielded fossil remains of *Homo erectus.* Ceprano in Italy is the first site to demonstrate that the species reached Europe, probably before the onset of the Middle Pleistocene.

from later *Homo erectus.* Wood now refers the Turkana Basin specimens to *Homo ergaster,* which, in his opinion, is more likely than *Homo erectus* to have played a role in the evolution of later people.

A quite different interpretation has been offered by Wolpoff and coworkers,[6] who now claim that the nomen *Homo erectus* is unnecessary and should be discarded altogether. Here the question is really whether there is continuity from earliest Pleistocene times right to the present; that is, whether just one long lineage, with no branches or extinctions, can be recognized. Such a lineage would include the ancient Turkana populations as well as those later resident in Africa and Eurasia. If it could be demonstrated that no splitting had occurred, one might argue that any division between taxa would have to be arbitrary. Wolpoff et al.[6] and Wolpoff[7] (see also Tobias[8]) go a step further and say that there simply is no basis for keeping more than one species, which must then be *Homo sapiens.*

It does not seem to me that either of these scenarios can be supported fully. Certainly there is geographic variation among the several assemblages of *Homo erectus,* but the fossils from the Turkana Basin, Olduvai Gorge, and other sites in Northwest Africa exhibit essentially the same set of traits as do those from the Far East.[9] Discrete characters said to be unique to the Asian populations are variable in their expression and, in fact, most can be identified in the earlier East African material.[10] Cranial dimensions show much overlap.[11,12] Vault thickness, as measured near the junction of the frontal and parietal bones, is about the same in the African and Asian samples.[13] The faces of KNM-ER 3733 from Koobi Fora and KNM-WT 15000 from Nariokotome conform in nearly all respects to the anatomy of *Homo erectus* as reconstructed from the Sangiran and Zhoukoudian specimens.[14] Also, the teeth from the Turkana Basin are close in size and shape to those from Zhoukoudian.[15] Apparently there are not many traits that can be used to diagnose *Homo ergaster,* and probably just one polytypic species should be recognized. Nevertheless, *Homo erectus,* as broadly defined, does possess many anatomical distinctions, extending not only to the skull and teeth but

to the postcranial skeleton as well. All of the better-preserved individuals, including even the late surviving ones from some of the Far Eastern sites, can be set apart from *Homo sapiens.* The boundary between these taxa is not arbitrarily defined.

NEW EVIDENCE FROM EURASIA

Although there is disagreement about taxonomy, most workers would concede that populations resembling *Homo erectus* dispersed from Africa into Eurasia well before 1.0 million years ago. These movements occurred probably over a long period. The hominids may have made repeated

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sorties, introducing crude chopping tools and stone flakes or Acheulean handaxes into different regions.[16]

Evidence documenting the spread of humans into western Asia comes from several sites, including Dmanisi in Georgia and 'Ubeidiya in Israel. At Dmanisi, a lithic industry and a well-preserved mandible with teeth have been recovered.[17] The jaw resembles those of *Homo erectus.*[18] The bone-bearing levels overlie a lava flow dated at 1.8 million years, but the age of the tools and fossils remains problematical.[16] At 'Ubeidiya, an extensive mammalian fauna excavated from lake sediments suggests a relatively cool climate at a date of perhaps 1.4 to 1.0 million

years. In addition to the fauna, there are stone choppers, spheroids, picks, and bifaces, which Tchernov[19] compared to the lithic material from upper Bed II at Olduvai Gorge. How the differences between the non-Acheulean and Acheulean assemblages at this Jordan Valley site should be interpreted is unclear, but the tools most probably were used by groups of *Homo erectus.*

Ancient traces of hominid activity are found also in Europe, at French localities such as Le Vallonet, Isernia in Italy, and in the Neuwied Basin in Germany. This scattered archeological evidence, consisting mainly of corechoppers and flakes, sometimes found with broken animal bones taken to be food waste, may demonstrate a human presence in the Early Pleistocene[20] (but also see Roebroeks[21]). Unfortunately, the oldest European sites have not produced more than a few bits of human skeleton. A notable exception is Ceprano in central Italy. Here a fragmentary but fairly complete braincase was discovered in 1994.

The fossil was picked up in clay deposits, which contain no volcanic material that is directly datable. Potassium-argon dates have been obtained from volcanic sands higher in the stratigraphic sequence; these are said by Ascenzi and coworkers[22] to indicate an age greater than 700,000 years. Insofar as can be determined from the description provided by its discoverers, this hominid displays the heavy continuous brow, low vault, angled occiput, and thick cranial bones that are characteristic of *Homo erectus.* This is important information. Although the Ceprano specimen is damaged in some key respects, it seems to confirm the identity of one group of people who entered Europe in the Early Pleistocene.

Representatives of *Homo erectus* also reached the East Asian tropics before moving into more temperate regions. It has been assumed that movement into the Far East began 1.0 million years ago or slightly earlier, but radiometric dates from mineral samples collected at Modjokerto and Sangiran now suggest that the oldest Indonesian localities may be 1.8 to 1.6 million years old.[23] If this result can be verified, then it will look as though *Homo erectus* spread quite rapidly across the

Old World. These hominids flourished for a long time. At sites including Zhoukoudian and Longtandong (Hexian) in China, the species is known from deposits of the later Middle Pleistocene, while at Ngandong in Java, at least one group of archaic people may have survived into the Late Pleistocene.[24] Populations such as that at Ngandong may document the last appearance of the lineage.

SPECIATION IN AFRICA?

The picture emerging is one of *Homo erectus* as a widespread, polytypic species, with groups persisting longer in some regions than in others. The pattern documented in China and especially in Java contrasts with that in the

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West, where *Homo erectus* seems to disappear from the record at a relatively early date.[25,26] Also, it is interesting that the Asian populations apparently are more specialized in the sense of exhibiting a higher incidence of some morphological characters associated with cranial robusticity. These traits are subject to geographic variation and do not mark a species boundary, but they may nevertheless delimit groups that had different evolutionary fates.

There is no reason to suppose that all demes of *Homo erectus* evolved further. The evidence is consistent with eventual extinction of some or all populations in the Far East. A less specialized branch of the species may well have given rise to later humans.[9,27]

This budding of a daughter lineage from *Homo erectus* must have occurred very early in the Middle Pleistocene, if not before. African and western Asia are likely areas in which the first more advanced humans originated (Fig. 2). An Africa locus is consistent with findings from archeology, environmental reconstruction, and patterns of animal dispersal.[28]

Fossils that shed light on this speciation event have turned up at several localities in Africa. One is Bodo in the Middle Awash region of Ethiopia. The Bodo cranium and, later, a broken parietal from a second individual, were found in conglomerates and sands containing mammalian bones and Acheulean artifacts.[29,30] Fauna from the site has been compared to that from Bed IV at Olduvai Gorge and Olorgesailie in Kenya, and an early Middle Pleistocene age is indicated. New argonargon dates reported by Clark and colleagues[31] support this biochronology. The evidence from fauna, archeology, and laser-fusion determinations points to an age of about 600,000 years for the Bodo hominids.

The face and anterior portion of the braincase are reasonably complete; it can be established that Bodo is like *Homo erectus* in some features. The massive facial bones, projecting brow, low and constricted frontal with midline keeling, parietal angular torus, and thick vault give the specimen an archaic appearance. In other respects, the cranium is more advanced in its morphology. Brain size is close to 1,300 cc, which is substantially greater than is expected for *Homo erectus.* The frontal bone proportions, arched shape of the squamous temporal, and some traits of the cranial base are like those of more modern humans. Although the face is very broad and heavily constructed, the supraorbital tori are divided into medial and lateral segments, the margin of the nose is vertical rather than forward sloping, and the incisive canal opening into the front of the hard palate shows a derived condition present in recent *Homo.*[32]

This mix of characters suggests that the Middle Awash individuals are "intermediate" in their morphology. However, several of the resemblances to *Homo erectus* are plesiomorphies that cannot be considered diagnostic.
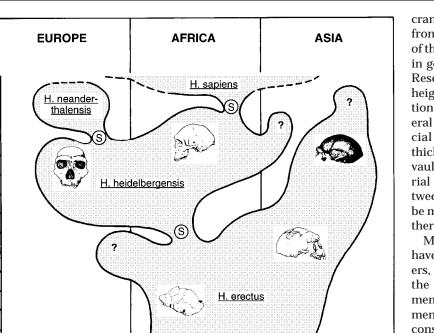
Figure 2. A tree illustrating the evolution and geographic distribution of *Homo* in the Pleistocene. *Homo erectus* is assumed to have originated in Africa and then spread quickly to Asia and probably to Europe. *Homo heidelbergensis* is distributed from Africa into Eurasia during the Middle Pleistocene. Whether this species reached the Far East is still a question. European *Homo heidelbergensis* gave rise to the Neanderthals, while an African branch of *Homo heidelbergensis* is ancestral to modern humans. Four speciation events (S) are depicted.

crania differ only slightly in orbit size, frontal proportions, and prominence of the torus crossing the occipital bone; in general, they are remarkably alike. Resemblances are apparent in the height, breadth, and massive construction of the upper face and cheek, several measures of projection in the facial midline, configuration of the thickened brows, and many aspects of vault shape.[9] Because the Bodo material is less complete, comparisons between it and the Greek cranium must be more limited in scope, but here also there are similarities.[32]

Multivariate studies of skull form have been carried out by several workers, who noted resemblances between the African and European specimens.[37–39] Van Vark[40] has used 17 dimensions of the face and braincase to construct a measure of generalized distance (D^2), which shows that the Broken Hill and Petralona specimens differ from one another less than is the case for Upper Paleolithic and recent humans. When a reconstruction of the partial cranium from Arago Cave in France is included in this analysis, it also falls close to that from Broken Hill. There seem to be good phenetic grounds for lumping these hominids together.

Other ancient European finds are more fragmentary. Human bones and teeth have been recovered from the quarry at Bilzingsleben in Germany and from several earlier Middle Pleistocene sites in Italy, while an occipital bone is on record from Vertesszöllös in Hungary. There is also the rear portion of a braincase from Swanscombe in England. The mandible from Mauer in Germany and a tibia associated with Acheulean bifaces at Boxgrove in England are arguably among the oldest hominids from Europe. Both are on the order of 500,000 years in age.[41] Of course there are questions about the affinities of this material, as few anatomical clues are preserved. But if the Mauer mandible is grouped with the other specimens from Europe and Africa, then the entire assemblage can be referred to *Homo heidelbergensis*.[9,42,43]

This species was named by Schoetensack in 1908 to accommodate the jaw found a year earlier in the basal sand and gravel complex of the Grafenrain pit near Heidelberg.

Moreover, it is clear that the cranium shares other apomorphic features with more modern populations. It seems reasonable to group Bodo with the famous fossil from Broken Hill (Kabwe) in Zambia (Fig. 3), along with specimens from Elandsfontein in South Africa, Lake Ndutu in Tanzania, and probably Eyasi, also in Tanzania. These localities are Middle Pleistocene in age. In addition to the human skullcap, deflation surfaces ("bays") at Elandsfontein have yielded a large fauna, together with Acheulean handaxes. Dating of this assemblage is complicated by the fact that several of the extinct mammal species are unknown elsewhere, but comparisons with other African sites imply that the bones were accumulated between 700,000 and 400,000 years ago.[33] Ani-

mal remains possibly associated with the Broken Hill cranium suggest an age within this same broad interval.[34]

As has been recognized for some time, the African hominids are similar to other, roughly contemporary people known from Europe. Like that from Broken Hill, the cranium from Petralona in Greece is particularly well preserved (Fig. 4). Although there is doubt about both its original provenience within layers of stalagmite deposited on the cave floor and its association with animal bones, this individual is of Middle Pleistocene antiquity. Some of the flowstone may be about 200,000 years old,[35] but other fossils from the site imply a greater age for the cave contents (see Cook and coworkers[36] for a review). In any case, the Petralona and Broken Hill

Figure 3. Facial and lateral views of the Broken Hill cranium. Broken Hill is one of the most complete Middle Pleistocene specimens, here attributed to *Homo heidelbergensis.* Along with increased brain volume, the cranium exhibits features of the nasal region, palate, occiput and base that distinguish it from *Homo erectus.*

Schoetensack was impressed with the primitive character of his fossil but recognized that it must be human, as the canines are reduced in size and the tooth crowns generally display the proportions expected for modern populations.
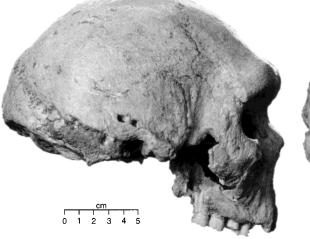
Later authors continued to emphasize the primitive appearance of the mandible. Howell[44] pointed to its massive construction, multiple mental foramina, and very thick symphysis, which lacks any indication of a chin, as characters shared by other early representatives of *Homo.* However, Howell was careful to note that other features of the specimen, including its ramus breadth, relatively great anterior depth of the corpus, and moderate size of the dentition, distinguish it from both Far Eastern *Homo erectus* and the Ternifine people. He argued that the Mauer hominid must be spe-

cifically distinct from archaic lineages in Asia or Northwest Africa. Howell left open the relationship of this isolated fossil to other European groups, including the Neanderthals. While there are still obvious difficulties with linking the mandible to individuals such as that from Petralona, for which no lower jaw has been recovered, the fossil can be lumped with earlier Middle Pleistocene humans in the way I have outlined. As defined on this basis, *Homo heidelbergensis* retains a number of archaic characters and may be the stem from which both Neanderthals and modern people are derived.

ALTERNATIVE VIEWS OF *HOMO HEIDELBERGENSIS*

Just as there is controversy about whether *Homo erectus* should be partitioned into two taxa, so there are

questions about the make-up of *Homo heidelbergensis.* Some authorities hold that the European and African specimens should be set apart as representatives of distinct lineages. Proponents of this view agree that the French, German, and Greek fossils share a series of features with the hominids from Bodo and Broken Hill. But they claim that even the earliest Middle Pleistocene Europeans exhibit apomorphic traits that align them only with Neanderthals.[45–49]

In this reading of the evidence, the fossils from Mauer and probably Boxgrove, Arago Cave, Petralona, Bilzingsleben, Vertesszöllös, and Swanscombe document a single line evolving toward the populations at Steinheim in Germany and Atapuerca in Spain. These assemblages can be referred to *Homo heidelbergensis.* However, it is recognized that there is no clear sepa-

Figure 4. Lateral and facial views of the Petralona cranium. This individual from Greece resembles that from Broken Hill in many metric features relating to facial proportions and vault shape. Whether the Petralona face also displays characters unique to the Neanderthal lineage is currently debated.

ration of the latter from early Neanderthals such as those from Biache in France, Ehringsdorf in Germany, or Saccopastore in Italy. Eventually this same lineage produced the "classic" Neanderthals of the Late Pleistocene. So an alternative classification is possible in which not only the "classic" populations, but also all the older fossils, are placed in one species termed *Homo neanderthalensis*[50] (see also Carbonell and coworkers[51] and Arsuaga and coworkers[52]).

According to this "accretion" hypothesis, distinctive Neanderthal characters appear first in the facial skeleton. Advocates of the model argue that such traces can be identified in the Mauer and Arago remains. At later evolutionary stages, apomorphies accumulate in the occiput and finally in the temporal region. It is suggested that the ancestors of Neanderthals became increasingly isolated through time as a consequence of colder climate conditions. In the second half of the Middle Pleistocene, barriers formed by glaciers and associated tundra to the north, ice sheets in the mountains to the east, and the Mediterranean to the south reduced contact and gene exchange with people outside Europe.[49] Isolation in this relatively harsh environment led to the full expression of the morphology that distinguishes Neanderthal skulls and postcranial bones from those of other populations.

Much of this scenario seems sound. Certainly it is easy enough to track the Neanderthals back in time to Steinheim or even to Swanscombe. The occipital bones of both specimens display signs of a suprainiac fossa (a centrally placed elliptical depression with a pitted floor). Moreover, Swanscombe possesses a transverse torus that is weak near the midline but bilaterally projecting. These traits are diagnostic for the lineage. The Sima de los Huesos at Atapuerca confirms that Neanderthal features are present in an assemblage that may be close to 300,000 years in age.[53]

As described by Arsuaga and his colleagues,[47,52] the Sima skulls present a combination of plesiomorphic and derived characters. The well-preserved face of cranium 5 is quite large in relation to the braincase. This, by itself, is not a Neanderthal apomorphy,

but the topography of the midface seems to anticipate that of later populations. The infraorbital surface and the side wall of the nose meet at a shallow angle, producing a slight concavity. The cheek region is thus not "inflated" in the extreme manner of Neanderthals, but can be interpreted as intermediate in form. Also in the Sima sample, brows are very thick. Continuity of the supraorbital tori at glabella is said to be reminiscent of Neanderthals. At the rear of the cranium, the suprainiac area is large but not very depressed. This trait and the shape of the occipital torus seem to foreshadow the Neanderthal condition.

Earlier in the Middle Pleistocene,

More crucial to the accretion hypothesis, or at least the version of it that encompasses the earliest fossils, are the crania from Arago and Petralona. Here the question is whether there are signs of ''incipient'' Neanderthal morphology, especially in the facial region.

Neanderthal roots are more difficult to find. Some authors have pointed to Vertesszöllös or even Bilzingsleben as documenting evolutionary continuity, but most of this material is too fragmentary to provide convincing information. The jaw from Mauer is complete but, in fact, shows few if any traits that can be taken as specific links to later European populations. More crucial to the accretion hypothesis, or at least the version of it that encompasses the earliest fossils, are the crania from Arago and Petralona. Here the question is whether there are signs of "incipient" Neanderthal morphology, especially in the facial region.

The face of the partial cranium from Arago is largely complete but unfor-

tunately damaged as a result of its long interment in compacted cave sediments. The frontal bone, interorbital pillar, nose, and cheeks show numerous cracks; localized areas of crushing are also present. The discoverers have been able to correct some of this damage in a reconstruction,[54,55] but significant distortion remains. In spite of these problems, some workers can discern definite resemblances to Neanderthals. Hublin[49] notes that the infraorbital surface of the maxilla is flattened and the cheek bones are obliquely oriented. Arsuaga and colleagues[52] suggest that the Arago midface is actually more Neanderthal-like than that of Sima cranium 5 in the extent to which the infraorbital plate and the side wall of the nose are continuous, and this surface is inflated or convex. Also, there is much forward protrusion of the face at subspinale (in the midline, just below the nasal opening). The nose itself is limited inferiorly by a sharp rim, as in Neanderthals.

These observations must be tempered by the fact that cracking and plastic deformation make it difficult to assess some key aspects of morphology. The wall of the Arago maxilla is generally flattened or even inflated in the manner characteristic of Neanderthals, but there is slight hollowing laterally, below the orbit. This cannot be discounted as due entirely to damage. Also, it is not clear that the zygomatic bone is swept back (obliquely oriented) as noticeably as it is in later populations. In facial forwardness at subspinale, as measured by the zygomaxillary angle of Howells,[56] the Arago cranium, at 113°, is in the Neanderthal range, and the Petralona specimen, at 118°, shows almost as much protrusion. But the value for Broken Hill is only 116°. Consequently, a low zygomaxillary angle does not necessarily align Arago and Petralona with Neandertals rather than with other Middle Pleistocene specimens. The sharp inferior margin of the Arago nose is indeed reminiscent of that in Neanderthals. However, there is variation in this feature. Petralona is rather less like the Neanderthals, while some later Europeans, including the Sima people, have a pattern of cresting on the nasal floor resembling that in the Broken Hill or Bodo fossils. Finally, it is worth

noting that neither the Arago nor the Petralona cranium exhibits the apomorphic traits identified recently by Schwartz and Tattersall.[57] A medial projection from the inner margin of the nose and a swelling of the posterior nasal wall itself are present in Neanderthals but seem to be lacking in earlier Middle Pleistocene hominids.

Given this level of doubt concerning specific Neanderthal affinities of the Arago and Petralona crania or the Mauer jaw, perhaps it is premature to disassociate these specimens from contemporary Africans. In my view, all of the earlier Middle Pleistocene hominids share both *erectus*-like features and a suite of derived traits common to later humans. It is hard to find any morphological basis for restricting *Homo heidelbergensis* to Europe. This taxon may well have evolved elsewhere. However, these people did reach Europe at an early date. Sometime later, as climatic conditions changed and populations became isolated by ice barriers, speciation produced the first Neanderthals (Fig. 2). Just when this event occurred is uncertain, but the ca. 300,000-year-old Sima fossils, as well as those from Steinheim and Swanscombe, foreshadow the Neanderthal condition. There are good reasons to postulate deep roots for the Neanderthal lineage, and here the accretion model must be broadly accurate.

MORE FOSSILS FROM SPAIN

New evidence challenging both the phylogenetic role of *Homo heidelbergensis* and the accretion model has been reported recently from Spain. The Sierra de Atapuerca contains many sites in addition to the Sima de los Huesos. One is a limestone cave deposit exposed by workers cutting a railway trench at the turn of the century. The collapsed cave of Gran Dolina is filled with a substantial thickness of sediments. The most ancient levels must be of Early Pleistocene age. Paleomagnetic sampling indicates that the TD6 layers may lie just below the Brunhes-Matuyama magnetic reversal, dated at 780,000 years.[58] Excavations in one of the TD6 strata have produced a collection of stone tools consisting of core-choppers and flakes, but no handaxes or cleavers.

Along with the artifacts, there are human bones representing at least six different individuals. Given the uncertainties surrounding the age of the find at Ceprano in Italy, these Spanish discoveries may be the oldest anywhere in Europe.

Although many of the fossils are fragmentary, they provide information about the teeth, skull, and postcranial skeleton. Preliminary descriptions have been provided by Carbonell and colleagues[51] and Bermudez de Castro and colleagues.[59] One important specimen is part of a lower jaw with the molars still in place. More teeth belonging to this hominid have been recovered and it is possible that a piece of frontal bone should also be assigned to the same individual, an adolescent about 14 years old. Differ-

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Confirmation that the Gran Dolina people are more advanced than *Homo erectus* comes from a partial face discovered in 1995. The morphology of this specimen, representing another young individual, is said to be remarkably modern.

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ences from *Homo erectus* are apparent in the expansion of the lower incisor crowns, the size relationships of the premolar teeth, and the relative gracility of the mandibular body. Frontal breadth, which can be estimated as a minimum behind the brows, exceeds that for all but the largest of the *Homo erectus* crania from Asia.

Confirmation that the Gran Dolina people are more advanced than *Homo erectus* comes from a partial face discovered in 1995. The morphology of this specimen, representing another young individual, is said to be remarkably modern. Below the orbit, hollowing of the bone surface is accentuated by forward bending of the side wall of the nose. Such a degree of "flexion" of

the maxilla is not seen in archaic hominids. That hollow, the canine fossa, is not well developed in specimens such as those from Bodo, Arago, or Petralona. As noted earlier, Neanderthal faces have quite a different appearance, with the cheek region inflated and swept to the rear. If the identification of the Ceprano braincase is corroborated, the Gran Dolina people may have coexisted with *Homo erectus* in the Mediterranean region. However, these people seem to be set apart, not only from *Homo erectus,* but also from *Homo heidelbergensis* and later Europeans.

The evidence from midfacial topography, along with other cranial, mandibular, and dental characters, has persuaded the Atapuerca researchers to name a new species, *Homo antecessor.*[59] As described so far, the fossils do not exhibit any of the derived features of Neanderthals and so do not fit neatly into the accretion model, which holds all early Europeans to be Neanderthal ancestors. Members of the new taxon can be interpreted as close relatives to Middle Pleistocene hominids such as Mauer and Arago. Moreover, some features of its mandibular body are very similar to those of the Sima population. This suggests evolutionary continuity with *Homo heidelbergensis,* taken to be a strictly European lineage. At the same time, *Homo antecessor* may be generalized enough in its morphology to be ancestral to more modern humans. The species from Spain thus seems to be a candidate for the stem from which both Neanderthals and *Homo sapiens* are descended. Here the role played by Middle Pleistocene populations in Africa is left unexplained, but Bodo and Broken Hill apparently are neither *antecessor* nor *heidelbergensis* and must represent still another (unnamed) taxon.

Undoubtedly, the exciting new material from Atapuerca will be subjected to further comparative study. In the meantime, there are questions. Attention has been focused particularly on the facial skeleton. The morphology of the ATD6-69 midface does seem to be distinctive with respect to other Middle Pleistocene hominids, and a well developed canine fossa is characteristic of more modern humans. A complication is that this Gran Dolina individual is juvenile, maybe only 10 or 11 years

old. It is always tricky to compare children to adults, for little is known of the growth patterns in archaic people. Almost certainly, the shape of the maxilla changes as the sinuses expand and the teeth are fully erupted. In another (adult) specimen from the site, less hollowing of the cheek is present. So one must ask whether this feature is an appropriate component of the diagnosis of a new species. It seems to me that one can make a good case for attributing the Spanish fossils to *Homo heidelbergensis,* where the hypodigm for this taxon is defined broadly to include European and African remains. In this view, *Homo heidelbergensis,* like *Homo erectus,* was a wide-ranging species rather than just a short segment of a lineage sandwiched in between the Gran Dolina hominids and later Neanderthals.

CONTINUING QUESTIONS

Several questions about the evolutionary role of *Homo heidelbergensis* have still to be touched on. In my reading of the record, this species is ancestral *not* only to *Homo neanderthalensis* but also to modern humans. Figure 2 suggests speciation to *Homo sapiens* in Africa or western Asia sometime in the later Middle Pleistocene. However, there are more fossils from the Far East that complicate this picture. Particularly in China, many localities document the presence of humans more advanced than *Homo erectus,* certainly after 300,000 years ago and perhaps much earlier. Whether the skeletons should be lumped with *Homo heidelbergensis* is one issue; how they are related to recent Asian populations is another. Both are fraught with controversy.

Two important crania have been discovered in terrace deposits of the Han River at Yunxian in western Hubei.[60] The finds were made in a clay layer and both hominids were encased in hard calcareous matrix. The same level has produced mammalian fossils and some stone cores and flakes. The fauna suggests a Middle Pleistocene age. Paleomagnetic work coupled with other approaches now indicates that the Yunxian assemblage may be as much as 600,000 or even 800,000 years old.[61,62]

Unfortunately, the crania themselves are heavily damaged. One has been crushed nearly flat. In the other the face is reasonably well preserved, although the vault has been deformed and the base is filled with small cracks. There are some resemblances to *Homo erectus.* The brow is thickened and the vault is long and low, with an angled occiput. The cranial base is generally similar to that in the Zhoukoudian specimens and does not seem to exhibit the flexion apparent in later populations. At the same time, the Yunxian crania share many features with more advanced humans. The braincase is large and not very constricted behind the orbits, and the squamous temporal is arched. Some traits of the nose and palate may also be derived relative

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to *Homo erectus.* The midface of the second individual is described as especially "*sapiens*-like" in that a canine fossa is present and the infraorbital region is set at an angle to the flaring cheek. Given this mix of characters, Li and Etler[60] and Etler[61] choose to place the skulls with *Homo erectus,* but Zhang[63] identifies them with later humans.

Other fossils are known from later Middle Pleistocene localities in China. The Dali and Jinniushan specimens are often described as archaic or premodern *Homo sapiens.*[64] The Dali cranium is quite complete. Its massive brow, keeled frontal, and low vault are reminiscent of *Homo erectus.* In many other respects, the Dali braincase is more like that of later humans. Even when crushing of the maxilla is accounted for, the face must be relatively short. Also, the margin of the nose is vertically oriented and the incisive canal is placed anteriorly on the hard palate, as in Middle Pleistocene Africans and Europeans. As with one of the Yunxian faces, the wall of the cheek is hollowed to produce a canine fossa.

If it is accepted that these Chinese individuals (including Yunxian?) are not *Homo erectus,* then sorting them to *Homo heidelbergensis* is one alternative that must be explored. This is suggested in Fig. 2. Depending on the age of the Yunxian material, the entrance of *Homo heidelbergensis* into eastern Asia might have occurred earlier than depicted. The taxon would then have persisted alongside *Homo erectus* for a substantial time. A question arises as to the fate of these Chinese populations. The scenario of Fig. 2 shows eventual extinction, but a case for continuity with recent humans must be considered. In fact, this point is still difficult to resolve from the paleontological record. Comparative molecular studies keep open the possibility that there was some contribution from archaic Asians to the modern gene pool.[65]

Some workers elect instead to separate the Chinese hominids from Middle Pleistocene populations in the West. This preference is based largely on observations of the midface, which is said to show modern features at a relatively early date. These workers emphasize the development of a canine fossa, along with lateral prominence of the cheek. If these differences are taken to preclude an identification as *Homo heidelbergensis,* then the fossils may have to be allocated to a new taxon. However, as noted earlier, hollowing of the infraorbital surface can be documented for faces outside of China. Furthermore, the new finds from Gran Dolina suggest that this feature may appear in Europe at the beginning of the Middle Pleistocene. Such evidence will make it harder to argue for isolation of the major Old World geographic provinces. The spread of some populations of *Homo heidelbergensis* into the Far East cannot be ruled out.

CONCLUSIONS

In their well-known 1975 volume *After the Australopithecines,*[66] Karl Butzer and Glynn Isaac noted many uncertainties surrounding human evolution in the Middle Pleistocene. Almost a quarter of a century later, the "muddle in the middle" is still evident, especially in respect to systematics and classification of the hominids. Perhaps the most vexing questions concern fossils of earlier Middle Pleistocene antiquity. Specimens from Africa and Eurasia have most frequently been described as "archaic" representatives of our own species, but this situation is unsatisfactory for several reasons. Fossils such as those found at Bodo, Broken Hill, Arago, Petralona, and Dali retain many primitive *erectus*-like characters, and this anatomy sets them apart from recent humans. Simply lumping diverse ancient groups with living populations obscures these differences.

There is increasing acceptance of the suggestion that distinct lineages may have evolved during this period. One possibility is that fossils from Africa and Europe can be sorted together to a single taxon, appropriately called *Homo heidelbergensis.* This species may have originated in Africa. If the Gran Dolina fossils are also *Homo heidelbergensis,* then these people apparently reached Europe at an early date. In this region, populations isolated by glacial conditions perhaps were eventually ancestral to the Neanderthals. In other parts of the species range, including Africa, there are indications that later Middle Pleistocene groups were evolving in the direction of *Homo sapiens. Homo heidelbergensis* is thus the stem from which both Neanderthals and modern humans are derived.

A problem is whether the same taxon can be identified in the East. Fossils such as those found at Dali and Jinniushan in China are more advanced than *Homo erectus* and exhibit some of the same derived characters as do the specimens from Africa and Europe. But it can be argued that the Chinese hominids are distinctive in aspects of their facial morphology. Some workers will prefer either to place them in a new species or lump them as early *Homo sapiens.* This question remains to be resolved.

ACKNOWLEDGMENTS

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