Patterns of hominid evolution and dispersal in the Middle Pleistocene

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Abstract

At the onset of the Quaternary, hominids identified as *Homo erectus* spread widely across the Old World. These populations persisted in the Far East until late in the Middle Pleistocene, while in the West, the species disappeared at a relatively early date. Humans that are different from *Homo erectus* evolved first in Africa or western Eurasia. One of the most important fossils now thought to document a distinct species was discovered at Broken Hill (Kabwe) in Zambia in 1921. This well-preserved cranium reveals many aspects of the morphology of the face, braincase, and skull base. Broken Hill is similar to other less complete fossils from Elandsfontein and Bodo in Africa and also to hominids including Arago and Petralona from Europe. These crania exhibit some archaic (*erectus*-like) characters, but there is an increase in brain size. Also, the morphology of the nose and palate, the temporal bone and the occipital region is advanced relative to the condition in *Homo erectus*. This evidence is in keeping with an episode of speciation occurring in the mid-Quaternary and giving rise to populations that are more modern anatomically. Although there is disagreement about taxonomy, it can be argued that the new species is appropriately called *Homo heidelbergensis*. Key questions awaiting resolution concern the geographic region where this taxon originated, its subsequent dispersal, and the role played by these populations in the spread of Acheulean stone technologies. Other issues are phylogenetic, and it is important to clarify the relationship of *Homo heidelbergensis* to Neanderthals and recent humans. © 2001 Elsevier Science Ltd and INQUA. All rights reserved.

1. Introduction

Stone artifacts and fossils attest to the movement of humans out of Africa, probably many times during the Quaternary. My contribution to this INQUA symposium deals with the hominid fossil remains, treated with reference to dispersals in the Early to mid-Pleistocene. This topic is controversial. Surely several of my colleagues will prefer interpretations that differ from the story outlined here. Nevertheless, a point on which we would likely agree is that the first people to spread from Africa to Eurasia were either *Homo erectus* or representatives of a closely related species. This exodus must have begun at least 1.5 Myr ago, if not before. I will comment only briefly on these early events, before turning to the Middle Pleistocene.

It should be emphasized that documenting the evolution of mid-Quaternary humans continues to be problematical. For many regions, archaeological records have been poor relative to those for other time periods, and dating is less precise than for the Late Pleistocene (but see

Turner, 1996). With a few exceptions, such as the magnificent assemblage from Sima de los Huesos in Spain, human skeletal remains are scarce, particularly in comparison to the large collections of Neanderthals from Europe. Partly, as a consequence of such gaps in the record, it has been possible to advocate several very different interpretations of the course of human history. These encompass a multiregional hypothesis, which posits gradual change within populations all representing a single biological species (Wolpoff, 1999). Other views call for (probably several) speciation events in restricted geographic areas, followed by dispersals and extinctions (Rightmire, 1995; Tattersall, 1997; Klein, 1999).

2. Early dispersals from Africa

Let me begin with *Homo erectus*. This species has deep roots in Africa, and the oldest fossils are from the Turkana Basin in Kenya. Several good crania, mandibles and a partial skeleton from Koobi Fora are dated minimally to 1.8 Ma (Feibel et al., 1989), and the famous boy (KNM-WT 15000) from Nariokotome is 1.5 Ma in age (Brown and McDougall, 1993). These hominids are

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referred by some workers to *Homo ergaster*, although it is acknowledged that there are clear similarities to *erectus* elsewhere. In any case, this ancient group (the Nariokotome paleo-deme recognized by Howell, 1999) likely constitutes the source from which populations expanded into other parts of Africa (Fig. 1). In South Africa, the species may be represented by an incomplete cranium, and by other specimens from Member 1 of the Swartkrans cave breccias, considered to be about 1.7 Ma in age (Brain, 1993). However, taxonomic attribution of the SK 847 cranium has proved to be contentious. A mandible with teeth from Member 2 can be identified more securely as *Homo erectus*, and this fossil is perhaps 1.5 Ma old. At Casablanca in Morocco, stone tools document the spread of the same species northward. Acheulean artifacts recovered at Thomas Quarry 1 are from late Early Pleistocene deposits dating to about 1.0 Ma (Raynal et al., 2001).

It is apparent that these people moved rather quickly into regions outside of Africa. Some of the best evidence for an ancient dispersal comes from 'Ubeidiya in the central Jordan Valley, where there are large collections of stone choppers, picks and bifaces. As determined from faunal comparisons, the lower levels in the site are about 1.4 Ma old (Tchernov, 1992). There are few human fossils from 'Ubeidiya, but the artifacts must document the activities of incoming bands of *Homo erectus* (Bar-Yosef, 1995). At Gesher Benot Ya'aqov, also located in the north of the Dead Sea Rift and dated to ca. 780 ka

(Verosub et al., 1999), there are signs of a rather different lithic tradition. Saragusti and Goren-Inbar (2001) suggest that the lack of direct links between the Acheulean of 'Ubeidiya and the later industry at Gesher Benot Ya'aqov may be explained as a result of multiple pulses of people or ideas out of Africa and into the Levant, during the latest Early Pleistocene (see also, Goren-Inbar and Saragusti, 1996).

Additional evidence for early occupation in western Asia occurs at Dmanisi in the Georgian Caucasus. Here excavations have uncovered fauna and a core-chopper industry stratified above a lava flow dated at 1.8 Ma (Gabunia and Vekua, 1995). Whether the bone-bearing layers are close in age to the basalt, or perhaps substantially younger, has been disputed, but new work may now provide an answer to this question (see below). Along with the animal fossils, there is a human mandible. Several workers have studied this specimen, and there is general agreement that it is *erectus*-like, with some derived (advanced) traits especially in the morphology of the symphysis and the size of the dentition (Bräuer and Schultz, 1996). Rosas and Bermúdez de Castro (1998a) acknowledge the similarities to Asian *erectus* but prefer to group the fossil with *Homo ergaster* instead. Quite recently, discoveries of additional remains from Dmanisi have been reported (Gabunia et al., 1999). There are two partial skulls, again linked to *Homo erectus*. These finds, which have still to be described in detail, promise to be of great interest.

For the Far East, there are now some radiometric ages that suggest the presence of *Homo erectus* at Sangiran in Java between 1.7 and 1.0 Ma ago. These results obtained by Swisher et al. (1998) are controversial, as there are questions about the provenience of the hominids. A number of the discoveries were made before World War II, and in some cases it has been difficult to relocate the sites from which the bones were originally collected. Nevertheless, the dated tuffs in the Pucangan and Kabuh formations must bracket many of the important fossils. It looks as though *Homo erectus* reached southeastern Asia first, before moving into more temperate latitudes.

After spreading widely across the Old World, this species apparently persisted longer in some geographic areas than others. The upper layers in the famous cave at Zhoukoudian in China are (only) about 300 ka in age (Grün et al., 1997). The hominids at Ngandong in Java are even younger, and by one recent estimate, Ngandong *Homo erectus* may have survived until less than 50,000 years ago (Swisher et al., 1996). The pattern documented for the Far East contrasts with that in the West, where *Homo erectus* seems to disappear at a relatively early date. Also, the Asian populations became more specialized. The skulls have thick walls and show a high incidence of mid-line keeling, parietal angular tori and other characters associated with robusticity. This may signal a different evolutionary fate. There is no reason to
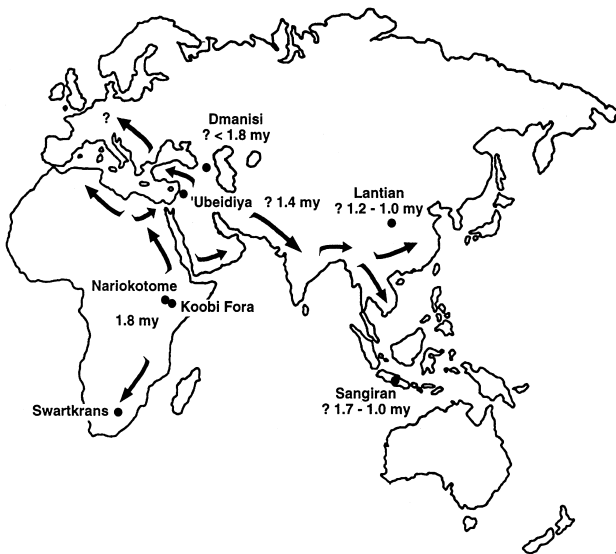

Fig. 1. Map showing likely routes of dispersal of *Homo erectus*. After originating in eastern Africa, populations of this species probably moved into the southern and northern parts of the continent, while dispersing into western Asia. Whether *Homo erectus* can be recognized at sites such as Ceprano in Europe is still a question. At a relatively early date, representatives of this taxon must have pushed across Asia to populate the southeastern tropics before moving into the more temperate latitudes of China.

suppose that all demes of *Homo erectus* evolved further, and the evidence is consistent with extinction of at least some populations, particularly in Java.

3. Significance of the Broken Hill discovery

All of this suggests that a western branch of *Homo erectus* must have given rise to later people. Indeed, it is in Europe and Africa that more advanced humans make their first appearance. Some of the best evidence in this regard comes from the mid-Quaternary of Africa. One famous fossil is the cranium from Broken Hill (now Kabwe) in Zambia. This specimen was found by miners, who were digging for lead ore, in 1921. Extensive quarrying had already removed most of a small kopje, when the miners broke into the lower part of a deep cavern. Records of the discovery are vague (in some cases contradictory) on this point, but apparently the cranium was uncovered by itself, not in close association with other bones or artifacts. Other sections of the cave were filled with ore containing animal bones, and some of this material had been removed on previous occasions. As a whole, the fauna is in keeping with a Middle Pleistocene date (Klein, 1994).

The specimen is remarkably well preserved. The face is massive, with some of the heaviest supraorbital tori recorded anywhere. The frontal is flattened, and in its overall morphology, Broken Hill resembles *Homo erectus*. It is not surprising that the skull has been attributed to this taxon on more than one occasion. At the same time, there are derived features found in later humans. This mix of characters is brought out in Fig. 2, where 12 measurements are treated in a ratio diagram. Here the most complete cranium from Java is taken as the standard, represented by the (vertical) zero line. Log deviations measure the extent to which other specimens differ in their proportions from this standard. Individuals from Zhoukoudian, within the shaded envelope, are generally a little smaller in their dimensions. There is variation, but the envelope does not suggest substantial differences relative to Java. Broken Hill is also similar to Sangiran 17 in most proportions of the vault. Only in the shape of the temporal squama (which is high and arched) and in the expanded upper scale of the occipital is there a clear departure from the primitive condition.

Other differences from *Homo erectus* can be identified, however. Along with increased cranial volume, several discrete characters of the temporomandibular joint region are specialized. These include the articular tubercle, which is prominent enough to stand out against the preglenoid surface, and the downward projecting sphenoid spine. More changes are evident in the face, where the nose is set vertically, and the palatal anatomy is like that of later people. In fact, Broken Hill shares a number of apomorphic traits with populations that are
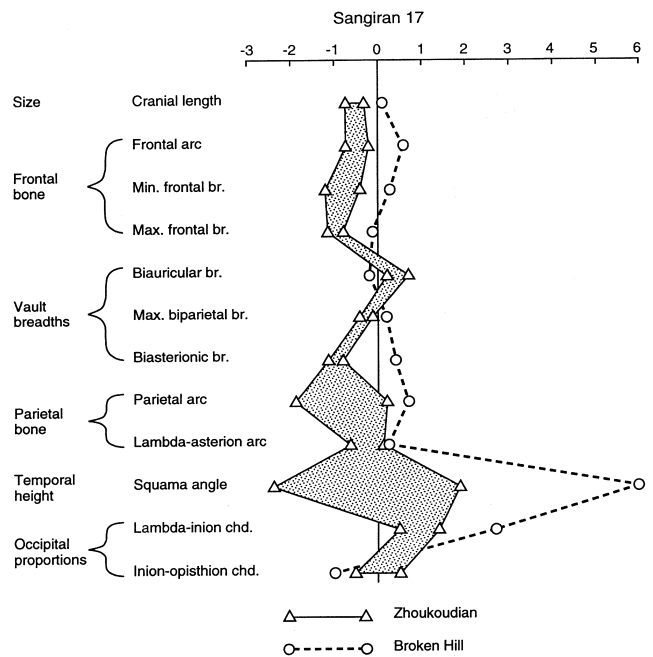

Fig. 2. Ratio diagram constructed for 12 measurements of the cranial vault. Skull number 17 from Sangiran is taken as the standard against which other specimens from Asia and Africa are compared. The track for Broken Hill suggests similarities to *Homo erectus* in a number of dimensions. However, there is a clear departure from the standard in both height of the squamous temporal and proportions of the occipital bone.

Table 1
Affinities of the Middle Pleistocene cranium from Broken Hill (Kabwe), Zambia

Characters shared with earlier Quaternary hominids (*Homo erectus*)
Supraorbital torus thickened and projecting
Frontal bone flattened, with slight midline keeling
Marked postorbital constriction
Parietal angular torus well developed
Face massive, especially the orbital region and the cheek
Characters that appear to be apomorphic for later humans
Cranial capacity increased (to ca. 1280 cm³)
Frontal and parietal arcs lengthened
Temporal squama high and arched
Occipital upper scale high, nuchal plane reduced
Basicranial line shows marked flexion
Articular tubercle of glenoid fossa is raised, bar-like
Sphenoid spine present
"Crista nasalis" oriented vertically
Anterior nasal sill crested
Incisive canal opens anteriorly on palate

more modern (Table 1). Since 1921, other hominids that display similar morphology have turned up at Elandsfontein (near Saldanha Bay in South Africa), Lake Ndutu in Tanzania, and Bodo in the Middle Awash of Ethiopia. These are again Middle Pleistocene localities. For Bodo, radiometric dates along with the evidence from animal

bones and archaeology point to an age of about 600 ka (Clark et al., 1994).

The face and front of the Bodo braincase are reasonably complete. As with Broken Hill, Bodo is *erectus*-like in some of its features. The face is heavily constructed, with a prominent brow. The frontal exhibits mid-line keeling, and there is a strong parietal angular torus. The individual vault bones are thickened, both in the original specimen and in the case of an isolated parietal picked up later. In other respects, the cranium is more advanced. Brain size (close to 1300 cm^3) is greater than the norm for *Homo erectus*. Frontal proportions, the parietal vault, squamous temporal, cranial base and the face show resemblances to recent *Homo* (Rightmire, 1996).

As has been recognized before, these African hominids are similar to other roughly contemporary people known from Europe. The cranium from Petralona in Greece is of uncertain provenience within a cave containing a large extinct fauna, but the mid-Quaternary antiquity of this material is not in doubt. Petralona and Broken Hill differ slightly in orbit size, frontal width and prominence of the torus crossing the occipital bone. In general, however, they are remarkably alike. Resemblances are apparent in the height, breadth and massive construction of the upper face and cheek, several measures of facial projection, configuration of the brows, and many aspects of vault shape (Rightmire, 1990). Much the same conclusion applies to the partial cranium from Arago Cave in France.

It seems to me that there are good phonetic grounds for lumping all of these fossils together (Rightmire, 1998).

4. Speciation and brain size

From the evidence outlined so far, one can argue that there was a splitting event, at or before the beginning of the Middle Pleistocene. *Homo erectus* speciated to produce a daughter lineage, and the new people then dispersed across Africa and into western Eurasia. A number of anatomical changes serve to distinguish these descendants from their ancestor. Some of these differences (breadth of the mid-vault with signs of parietal bossing, height of the temporal squama, other characters of the cranial base) are likely the result of an increase in brain size. As already noted, Broken Hill and Bodo have rather large endocranial capacities, in comparison to most *Homo erectus*.

This link between brain size and speciation can be explored in more detail. A plot of volume against geological time is provided in Fig. 3. Here all (28) of the measurable *erectus* specimens from Africa, Ceprano in Europe, and localities in the Far East are included. Mean capacity for the sample is 983 cm^3. The regression line shows that there is a trend, and brain size increases by about 163 cm^3/Myr. Although this change is minor, the slope is significantly different from zero, and the trend is
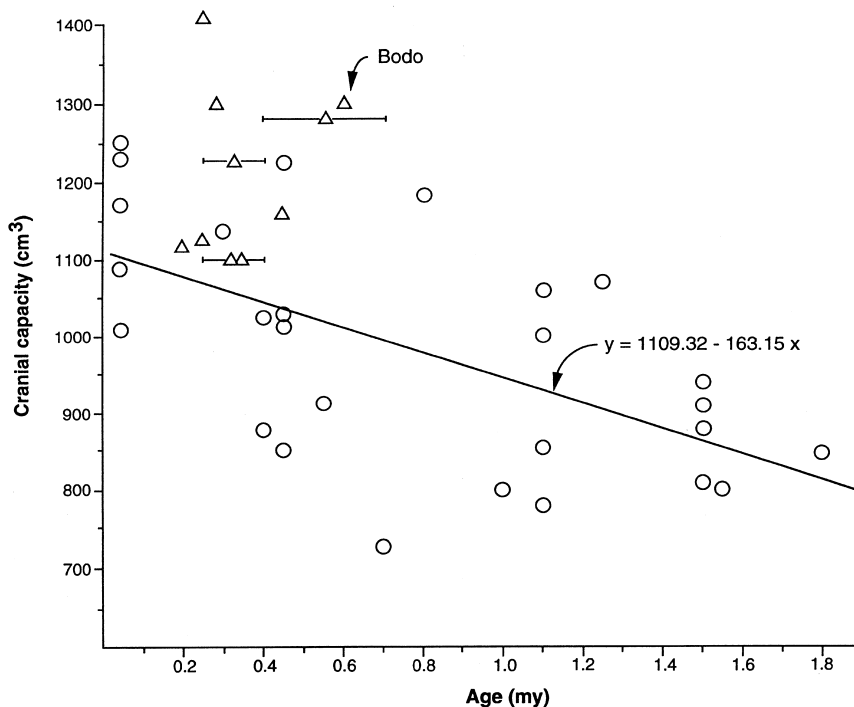

Fig. 3. Cranial capacity and geological age plotted for Quaternary hominids. Twenty-eight measurable specimens of *Homo erectus* are the basis for least-squares regression analysis. Within this species, there is a slight increase in brain size over time. Ten additional specimens from Bodo and other Middle Pleistocene localities (Broken Hill, Ndutu, Arago, Petralona, Steinheim, Sima de los Huesos, Dali and Jinniushan) are also plotted. These individuals have capacities that are larger than expected, even for late *Homo erectus*.

real. Bodo is also plotted in the figure, and this individual falls well above the regression line. For other mid-Pleistocene crania including Broken Hill, Ndutu, Arago, and Petralona (also Dali and Jinniushan from China), there is some uncertainty about dating. Nevertheless, it is clear that these hominids have larger capacities than would be expected, even for late *Homo erectus*.

Speciation seems to have triggered an increase in volume, not only in absolute terms but also relative to body size. Comparing brain size to body mass is important, in order to assess the evolutionary significance of any changes that are documented. Measures of encephalization (EQ) can be calculated in different ways. Ruff et al. (1997) use the method of Martin (1981) to find EQ values for a number of Quaternary-age hominid assemblages, and their results point to a period of stasis in relative brain size from 1.8 Ma to about 600 ka ago. Middle Pleistocene people then show a distinct increase in EQ, although these values are still low in comparison to those for "early anatomically modern" *Homo sapiens* or recent humans.

5. Taxonomic questions

So far, I have avoided saying much about taxonomy, but of course, there is the question of what the new people should be called. In the past, it has been common to describe the fossils as "archaic" representatives of our own species. This situation is unsatisfactory for several reasons. Specimens such as Broken Hill or Arago (and others from Asia) retain a number of primitive (*erectus*-like) characters, and this anatomy sets them apart from recent humans. Simply lumping diverse ancient groups with living populations obscures these differences. Some authors continue to argue for a system of intraspecific grades based on morphology and dating (Dean et al., 1998), but this sort of scheme has not solved the problem.

If it is agreed that the mid-Pleistocene hominids are to be separated from *Homo sapiens* at the species level, then another issue is the extent to which regional variation is important. In Europe, the Neanderthals constitute a distinctive group, now widely recognized as *Homo neanderthalensis*. Some of my colleagues feel that this lineage has deep roots, extending back to the Sima de los Huesos at Atapuerca in Spain, or even to earlier populations at Arago and Mauer (Arsuaga et al., 1993, 1997; Hublin, 1996). If this is correct, then the entire European Middle Pleistocene sequence might best be lumped with later Pleistocene "classic" Neanderthals and named accordingly.

However, this treatment of the fossils seems to overstep the evidence from anatomy. While it is clear that the later Neanderthals display a number of apomorphic characters of the face, braincase and mandible, it is less well established that either the Arago cranium or the Mauer jaw display any of the unique traits that would

link them with this group. Unfortunately, Arago 21 has sustained substantial damage, and both the maxillae and the frontal bone are cracked. Despite efforts to correct for the resulting deformation in a reconstruction, the facial parts remain skewed in relation to the anterior cranial fossa, and this makes it difficult to assess the original morphology. On the right side, the infraorbital surface can be described as generally flattened in a plane that is coincident with the wall of the nose. Nevertheless, the zygomatic process of the maxilla is hollowed slightly, and on the left this depression is more pronounced. These "fossae" are lateral to the vertical grooves associated with the infraorbital foramina. Although the extent to which the hollowing on the left may be accentuated by cracking is uncertain, it is evident that the Arago midface differs from that of Neanderthals. The sharply defined (lower) margin of the nasal aperture is more Neanderthal-like, but some later Europeans including the Sima fossils have a different pattern of cresting in this region.

The Mauer jaw has most often been regarded as "primitive" in its anatomy, sharing its massive build, thickened but chinless symphysis, transverse tori and multiple mental foramina with earlier *Homo*. Recently, however, the specimen has been described as showing "unequivocal" Neanderthal apomorphies (Rosas and Bermúdez de Castro, 1998b). One such trait is the retromolar space. As understood by most workers, this is a gap between the third molar and the anterior margin of the ascending ramus, visible from the side. A retromolar space defined in this way is common in later Pleistocene Neanderthals but absent in the Mauer jaw, the Arago individuals, and *Homo erectus* (Franciscus and Trinkaus, 1995). Rosas and Bermúdez de Castro (1998b) acknowledge this fact but argue that a space may be present internally, between M_3 and the triangular torus of the ramus, even when no lateral gap is expressed. For Mauer, the distance measured from M_3 to the lingula is indeed large, approaching the maximum values recorded for Neanderthals. At the same time, it is clear that this internal dimension is quite variable, and the ranges for Neanderthals, earlier European fossils and diverse other hominids show substantial overlap.

A second trait is the location of the mental foramen on the wall of the mandibular corpus. Rosas and Bermúdez de Castro (1998b) evaluate this feature by measuring a chord from the foramen to M_3. In *Homo erectus* and earlier *Homo*, this distance is relatively large, indicating anterior placement of the foramen. For Mauer, the chord is shorter, as it is in the Arago jaws and the Sima specimens. A posterior situation of the foramen seems to characterize the European Middle Pleistocene hominids as well as later Neanderthals. However, data presented by Rosas and Bermúdez de Castro (1998b) show that the foramen to M_3 distance is also reduced in assemblages of anatomically modern individuals. This feature cannot be said to be apomorphic only for a Neanderthal lineage,

restricted to Europe. Instead, a relatively short chord serves to distinguish recent humans, Neanderthals, the Arago fossils and Mauer from earlier taxa including *Homo erectus*, *Homo habilis* and some australopiths.

Given this degree of doubt concerning the expression of specialized Neanderthal traits in either the Arago face or the Mauer mandible, and the often recognized similarities of Arago and Petralona to Broken Hill or Bodo, there is little basis for separating the early Europeans from their Middle Pleistocene contemporaries in Africa. In my view, all of these hominids can be referred to one taxon, and the appropriate name for this group is *Homo heidelbergensis*.

6. The TD6 assemblage from Gran Dolina

Additional information bearing directly on the first peopling of Europe is accumulating from northern Spain. The site of Gran Dolina in the Sierra de Atapuerca has produced core-choppers and flakes, a rich fauna, and human remains dating to the end of the Early Pleistocene (Carbonell et al., 1995). An age slightly in excess of 780 ka for the TD6 level containing the fossils now seems to be established (Falguères et al., 1999; Parés and Pérez-González, 1999). Cranial specimens of particular interest include the ATD6-69 juvenile face, an adult cheek bone (ATD6-58), part of a frontal including the right supra-orbital region (which may represent the same subadult individual as the face), some of the right sphenoid and squamous temporal on which most of the glenoid fossa is preserved, and the mastoid portion of another temporal bone. There are also a mandible, teeth and postcranial elements.

Arsuaga et al. (1999) argue that the ATD6 people are not *Homo erectus*, and their discussion is quite persuasive on this point. Morphology of the midface in which the infraorbital region is depressed, the vertical orientation of the lateral margin of the nose, a relatively forward location of the incisive canal in the palate, form of the developing (but already substantially thickened) brow, the large estimate for minimum frontal breadth, apparent development of an articular tubercle bounding the glenoid surface anteriorly, and the high, arched superior border of the temporal squama all suggest that the Gran Dolina fossils are derived in comparison to *Homo erectus* and more like (some) later humans (see Table 1).

Also, there can be little doubt that this population differs from the Neanderthals. The ATD6-69 infraorbital region is clearly hollowed (a "canine fossa" is present), and this surface is flexed where it merges with the nasal wall. There is no sign of the specialized Neanderthal condition in which the relatively flat infraorbital plate is angled forward. In ATD6-69 and the Gran Dolina adult cheekbones, the zygomaticoalveolar crest appears to be arched, rather than straight as in later Pleistocene

"archaic" Europeans. The partial mandible (ATD6-5) is said to be generalized in its morphology (Rosas and Bermúdez de Castro, 1999), while the teeth resemble those of African and European Middle Pleistocene hominids (Bermúdez de Castro et al., 1999).

Given these distinctions, the Gran Dolina material may represent a new species. The name *Homo antecessor* has been proposed by Bermúdez de Castro et al. (1997). However, the hypodigm associated with this taxon is still small, and a number of the craniodental remains are fragmentary and/or subadult. A fair question is whether there is presently enough evidence to separate the ATD6 assemblage from other penecontemporary fossils already on record. In particular, it must be asked whether the Spanish bones and teeth differ from those of other early Europeans such as Mauer, Arago, Bilzingsleben, and Steinheim. Much attention has been focused on the development of a "canine fossa" filling the maxillary zygomatic process. Hollowing is indeed expressed in the midface of the Atapuerca juvenile, but a fossa is less obvious in the ATD6-58 adult, as noted by Arsuaga et al. (1999). And in the mandible, teeth and postcranial skeleton, there seem to be few features that would differentiate the Gran Dolina hominids from the ancient Europeans of the Middle Pleistocene. By the reasoning advanced here, the latter may reasonably be grouped with contemporary Africans as *Homo heidelbergensis*.

7. Discussion

If these (currently intractable) taxonomic issues are put aside, it is still possible to outline an evolutionary role for the populations succeeding *Homo erectus*. The tree of Fig. 4 has a geographic component, and there is a time scale to one side. Several splitting events (marked with an S) are indicated. After dispersing through Africa into Europe (and possibly the Far East), the taxon recognized here as *Homo heidelbergensis* could have been the stem from which both Neanderthals and modern people are derived. Speciation to *Homo sapiens* probably took place later in the Middle Pleistocene, as depicted in the figure. This event is documented by fossils such as Florisbad, Laetoli, (some of) the Omo material, and Jebel Irhoud. Especially the cranium from Laetoli in Tanzania is less archaic than Broken Hill or Bodo and shows features that link it to more recent populations (Rightmire, 1989). More evidence for continuity comes from Late Pleistocene sites such as Klasies River Mouth in South Africa, along with Skhul and Qafzeh in Israel. Here the picture is quite convincing, as Klasies and the Levantine caves were occupied by anatomically "close-to-modern" people during the Last Interglaciation (Vandermeersch, 1981; Singer and Wymer, 1982).

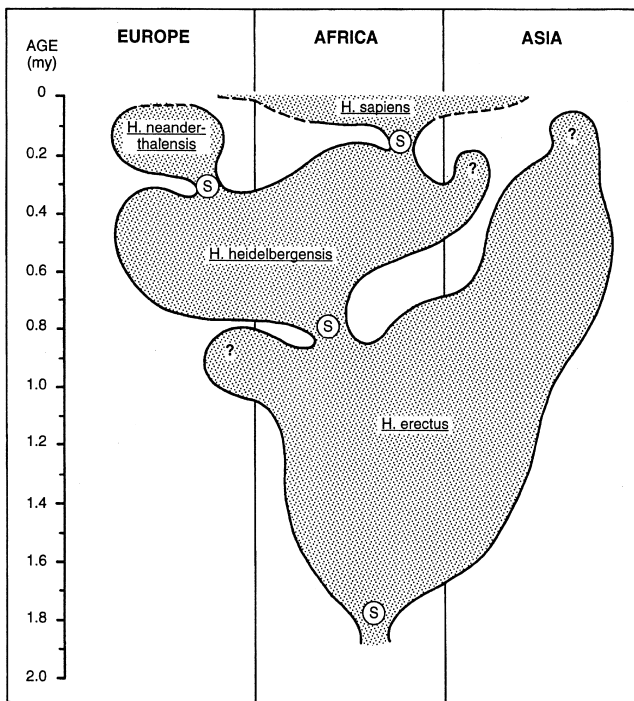Of course, there is uncertainty about human phylogeny in the Pleistocene, and the pattern of dispersal(s)

Fig. 4. Tree illustrating the evolution of Quaternary humans. *Homo heidelbergensis* is depicted as the descendant of *Homo erectus*. After evolving in Africa, *Homo heidelbergensis* spread into Eurasia during the Middle Pleistocene. A European branch of the species then gave rise to the Neanderthals, while an African deme is ancestral to modern humans. Four speciation events are indicated (S).

from Africa to Eurasia must still be clarified. There is much additional material to consider, including the important new cranial finds from Dmanisi and continuing discoveries in the Sierra de Atapuerca. South Asia continues to pose questions, although the Narmada assemblage points to a human presence in India, perhaps early in the Middle Pleistocene. In China, sites such as Dali and Jinniushan have yielded "archaic" crania that are clearly more advanced than *Homo erectus*. These Far Eastern individuals possess some of the same derived features as do the hominids from Africa and Europe, although their facial morphology may differ from that of *Homo heidelbergensis*. Fitting these diverse fossils into our family tree will be a challenge.

Acknowledgements

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