# Later Middle Pleistocene *Homo*

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## Abstract

Hominin fossils are known from Middle Pleistocene localities in Africa, Europe, South Asia, and the Far East. It is recognized that these individuals display traits that are derived in comparison to the condition in *H. erectus*. However, the skulls retain numerous primitive features that set them apart from modern humans.

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Faces are massively built with strong supraorbital tori, frontals are flattened, and vaults remain low with less parietal expansion than in *Homo sapiens*. The hominins from Bodo, Broken Hill, and Elandsfontein in Africa are quite similar to their Middle Pleistocene contemporaries in Europe. Crania and jaws from Arago Cave and Petralona, and the spectacular assemblage from Sima de los Huesos, are particularly informative. In sum, this evidence suggests a speciation event in which *H. erectus* gave rise to a daughter lineage. At or before the beginning of the Middle Pleistocene, new populations spread through Africa and western Eurasia and perhaps also to the Far East. How the fossils should be treated taxonomically is currently uncertain. One view emphasizes gradual anagenetic change, while others advocate speciation occurring repeatedly throughout the Pleistocene. In the perspective favored here, differences between the Middle Pleistocene hominins can be attributed to geography, time, or intragroup variation. Many, if not all, of the European and African specimens can be accommodated in one species distinct from Neanderthals and modern humans. If the Mauer mandible is included in this hypodigm, then the appropriate name is *H. heidelbergensis*. This species is probably ancestral to both the Neanderthals in Europe and the earliest representatives of *H. sapiens* in Africa.

## Introduction

Humans evolved in Africa and were confined to that continent for much of their early history. The first dispersals from Africa into Eurasia occurred near 2 million years ago (Ma). These migrants were probably representatives of *Homo erectus* (sometimes called *Homo ergaster*). Traces left by these hominins have been recovered from the site of ‘Ubeidiya in the central Jordan Valley and at Dmanisi in the Georgian Caucasus. Some early occupations were likely transitory and did not result in permanent settlements. However, groups of *H. erectus* were able to travel relatively quickly across southern Asia to the Far East, where they were established both in Java and in China by 1.7–1.6 Ma. The first penetration westward into Europe apparently came much later. There are indications that humans were moving into the Mediterranean region prior to 1 Ma, but the initial populating of Europe north of the major mountain barriers is documented only after about 700 thousand years ago (Ka). The biological identity of the first Europeans is unclear, but it is agreed that these hominins differ from *H. erectus*. Many of the ancient fossils are presently assigned to the species *H. heidelbergensis* (named originally from a mandible found near Heidelberg in Germany). *Homo heidelbergensis* or perhaps other closely related species are known also from Middle Pleistocene localities in Asia and Africa (Fig. 1). These people seem to have been more advanced in behavior than their predecessors, and there is evidence that *H. heidelbergensis* was able to make relatively sophisticated stone tools, hunt larger and more dangerous game animals, and perhaps engage in cooperative social activities.

**Fig. 1** Map giving the locations of Middle Pleistocene localities where important hominin fossils have been discovered

## The Middle Pleistocene of Africa

In Africa, fossils from the early Middle Pleistocene are clearly different from *H. erectus* in cranial capacity (approximately equal to brain size), width of the frontal bone, proportions of the occipital region, and anatomy of the underside of the skull. Where it is preserved, the face is still heavily constructed, but the brows, nasal profile, and bony palate more closely resemble the condition seen in later humans. In many instances, the hominins are found with stone tools that are more carefully shaped than the choppers and relatively crude hand axes associated with *H. erectus*. From Bodo in Ethiopia to Elandsfontein in South Africa, a shift toward the manufacture of thinner, more finely flaked bifacial tools is documented in the Middle Pleistocene, and it is reasonable to link this change in behavior to a speciation event in which *H. erectus* gave rise to a daughter lineage exhibiting increased relative brain size (encephalization).

### Bodo

One important specimen came to light in 1976 at Bodo, in the Middle Awash region of Ethiopia (Fig. 1). The Bodo cranium and later a broken parietal from a second

**Fig. 2** Facial and oblique views of the cranium from Bodo, Ethiopia. The projecting glabellar region, wide interorbital pillar, and massive zygomatic (cheek) bones give the face an archaic appearance similar to that of *H. erectus*. Other traits including the vertical border of the nasal aperture are interpreted as apomorphies shared with later humans

individual were found in conglomerates and sands containing mammalian bones and Acheulean tools (Kalb et al. 1980; Clark and Schick 2000; Gilbert et al. 2000). Fauna from the Bodo site has been compared to that from Bed IV at Olduvai Gorge and Olorgesailie in Kenya, and an early Middle Pleistocene date is indicated. $^{40}$Ar/$^{39}$Ar measurements reported by Clark et al. (1994) support this biochronology, and the evidence points to an age of about 600 Ka for the Bodo hominins.

The face and the anterior part of the Bodo braincase are preserved (Fig. 2). There are some cut marks on the facial bones, and these indicate intentional postmortem defleshing, as documented by White (1986). It can be established that Bodo is like *H. erectus* in some features. The massive facial bones, projecting brow, low frontal with midline keeling, parietal angular torus, and thick vault give the specimen a pronounced archaic appearance. In other respects, the cranium is more specialized (derived) in its morphology. Brain size is close to 1,250 cm$^3$ and is thus substantially greater than expected for *H. erectus*. Frontal bone proportions, the high-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 opens into the front of the hard palate (Rightmire 1996). These are derived (apomorphic) conditions present in the face of recent *Homo*.

## Broken Hill and Elandsfontein

Another African specimen is the cranium from Broken Hill (now Kabwe) in Zambia, discovered by miners in 1921. Quarrying for lead and zinc ore had already removed most of a small hill, when the miners broke into the lower part of an extensive cavern. Published reports do not all agree on this point, but apparently the cranium was picked up by itself, not in clear association with other hominin remains. The fossil is in remarkably good condition. The face is massive, with some of the heaviest brows on record. The frontal is flattened with slight midline keeling, and the vault is low in profile. Shortly after it was found, the fossil was attributed to the (new) species *H. rhodesiensis* (Woodward 1921). In its overall morphology, however, Broken Hill resembles *H. erectus*, and indeed, it has been classified this way on more than one occasion. At the same time, there are apomorphic features shared with later humans. The temporal squama is high and arch shaped, and the upper scale of the occipital is expanded relative to its lower nuchal portion (where the neck muscles are attached). Several discrete characters of the temporomandibular joint region are specialized. These include a raised articular tubercle and a sphenoid spine. More changes are apparent in the face, where the lateral border of the nasal aperture is set vertically, and the palatal anatomy is like that of later people (Rightmire 2001).

Another cranium quite similar to that from Broken Hill comes from the farm Elandsfontein, near Saldanha Bay on the Atlantic coast of South Africa. At Elandsfontein, there is an expanse of sandveld that has long been a focus of attention for paleontologists. Dunes migrate across this area, and in between the dunes, there are swales resulting from deflation. Whether the ancient horizons exposed in these “bays” are stratified land surfaces or simply mark the (seasonal) fluctuations of the water table is unclear. Given either of these interpretations, it is evident that during the mid-Quaternary, the region supported wetlands and water holes, with plenty of grass (Deacon 1998). Animals, many of them bovids or other large herbivores, were attracted to the water. The fauna includes numerous archaic elements such as a dirk-toothed cat, a sivathere, and a giant buffalo. Altogether, some 15 of 48 mammalian species collected at the site have no historic descendants. Comparisons conducted by Klein and Cruz-Uribe (1991) imply that the bones were accumulated between 700 and 400 Ka, but more recent sorting of the fauna suggests an older interval, between 1 Ma and 600 Ka (Klein et al. 2006).

Much of the work at Elandsfontein has been surface prospecting, and it was during one such visit in 1953 that investigators picked up pieces of a human skullcap. The reconstructed Elandsfontein cranium is composed of the frontal and parietal walls and some of the occiput. The bones are cracked and heavily weathered, but the braincase is not distorted. There are some similarities to *H. erectus*, but certainly the better match is with Broken Hill. These two Middle Pleistocene specimens are alike not only in overall proportions but also in many anatomical details. The Elandsfontein brow is almost as thick as that of Broken Hill, and the frontal contours are the same. Radiographs show that the frontal sinus is large and complex, reaching well up into the squama in both cases (Seidler et al. 1997; Rightmire unpublished observations). The South African frontal bone gives a breadth index of 91.9 and is thus slightly less constricted than that of Broken Hill, for which the ratio of least width to greatest breadth is 83.0. Sagittal and coronal measurements of the parietal are similar in the two individuals as is the length and orientation of the upper scale of the occipital. Unfortunately, the Elandsfontein base is missing, and there is no face. These are just the regions where one would expect to find additional apomorphies setting the South African hominin apart from *H. erectus*.

## Lake Ndutu

A fourth Middle Pleistocene specimen is known from Lake Ndutu. This seasonal soda lake is located at the western end of the Main Gorge at Olduvai, in northern Tanzania. Excavations conducted near the lake margin in 1973 produced an encrusted human cranium, along with other fossils and numerous artifacts (Mturi 1976). Initially, the stone assemblage included mostly spheroids, cores, and flakes, but hand axes were picked up during later visits to the site. All of this material is thought to be derived from archaeological horizons in a greenish sandy clay, tentatively correlated with the upper Masek Beds at Olduvai.

When it was found, the cranium was severely damaged and encased in a clay matrix. The process of cleaning and reconstructing the fossil has been described by Clarke (1990). These efforts were generally successful, but the face is quite incomplete, as is the frontal bone. There are gaps in the parietals as well. The braincase is relatively small, with a capacity of only about 1,100 $cm^3$. Just a fragment of the supraorbital region is preserved, and the torus is projecting, if not especially thickened. Bossing of the parietals is emphasized in Clarke's reconstruction. This has perhaps been overdone with plaster, but the walls of the vault appear to be more convex than would be the case for *H. erectus*. Also, the upper plane of the occiput is vertical, above the moundlike transverse torus. The morphology of this torus is in keeping with other characters suggesting that Ndutu could be female, in comparison to males such as Bodo or Broken Hill.

## Florisbad

Several additional fossils are more fragmentary and therefore somewhat less informative. An example is the cranium from spring deposits at Florisbad in South Africa, consisting only of facial parts, the frontal bone, and pieces of the parietals. Early studies compared the hominin to recent populations, but it is important to emphasize that Florisbad is far from modern in its morphology. Glabella (in the midline above the nasal root) is projecting, as is the brow on either side. The facial bones as repositioned by Clarke (1985) suggest that the nasal cavity is large and the cheek is flattened, without obvious infraorbital hollowing. The face is less heavily constructed than that of Broken Hill but otherwise not dissimilar. A human upper molar tooth from Florisbad has been dated by ESR to 259 Ka (Grün et al. 1996).

## The Omo Localities and Herto

Several sites in the Omo region of southern Ethiopia, explored initially in 1967, have recently been revisited. Human remains are known from Member I of the Kibish Formation, now considered to be 200–100 Ka in age (Assefa et al. 2000). Omo 2 is an isolated surface find from PHS, lacking archaeological associations. This partial cranium is low in contour and decidedly massive in its construction, with a blunt frontal keel and a strongly angled occiput. Other likely primitive features include the shape of the deep mandibular cavity lacking any distinct articular tubercle and the absence of a sphenoid spine. Nevertheless, the vault is large overall. The frontal bone is broad and relatively unconstricted, and the parietal walls show some outward curvature (limited to the regions below the temporal lines). The supraorbital torus is extensively damaged, and none of the face is preserved.

Omo 1 was excavated at the KHS site, dated to 195 Ka (McDougall et al. 2005), from which there is now a large collection of Middle Stone Age artifacts. This individual is represented by only small portions of a skull, but much more of the postcranial skeleton is present. The cranium as reconstructed by several workers is globular in form, with expanded parietals and an occipital that is more rounded than that of Omo 2. To the limited extent that these can be checked, cranial superstructures (crests and tori) are not strongly expressed. The anterior part of the mandible shows clear signs of chin formation. Given these important markers of modern morphology, there is general agreement that Omo 1 should be regarded as early *H. sapiens*.

An important question, still not firmly resolved, is whether the Omo 1 skeleton can be grouped with the more archaic Omo 2 remains or whether these individuals should be placed in separate populations. The morphological differences between the two crania are very substantial. Indeed Omo 2 has been compared to specimens such as Broken Hill or Elandsfontein, even though the frontal is rather less narrowed behind the orbits. If the Omo fossils are approximately the same age, then there are two possibilities. Omo 2 may be a remarkably robust individual, within a highly variable but essentially modern population. Alternatively, this specimen can be regarded as representative of an archaic, late-surviving lineage, present alongside anatomically modern humans. However, if Omo 2, picked up on the surface, is actually older than implied by recent dating for the PHS site, then it is easier to argue that the cranium is sampled from an earlier portion of the lineage ancestral to *H. sapiens*.

Specimens from Herto in the Middle Awash region confirm the presence of *H. sapiens* in northeastern Africa late in the Middle Pleistocene. Three fossilized crania recovered in 1997 show cut marks associated with postmortem defleshing and are associated with a stone tool assemblage that can be characterized as late Acheulean or Middle Stone Age. The bones and artifacts are dated radioisotopically to between 160 and 154 Ka (Clark et al. 2003). One of the adult crania

(BOU-VP-16/1) is intact, with a brain size estimated as 1,450 $cm^3$ (White et al. 2003). This individual is ruggedly built, with a very prominent, bilaterally arched glabella, a long vault, and a distinctly flexed occipital. The parietal walls are convex rather than inward sloping, and the index of neurocranial globularity (Lieberman et al. 2002) calculated as ca. 0.54 for BOU-VP-16/1 is high enough to be within the range expected for anatomically modern humans. A second adult cranium is less complete, and there is a child estimated as 6–7 years in age. As a group, the Herto individuals are very robust but display morphologies that place them close to recent populations. White et al. (2003) have referred the fossils to a new subspecies of *H. sapiens*.

## Middle Pleistocene Hominins from Europe

Skulls very similar to those from Africa have been found in western Eurasia. Several of the principal localities lie close to the Mediterranean Sea, but it is apparent that humans were also able to reach Britain and central Europe, relatively early in the Middle Pleistocene (Fig. 1).

### The Cranium from Petralona

Petralona lies near the city of Thessaloniki in northern Greece. The exact provenience of the hominin fossil found within cave deposits containing the bones of numerous extinct animals is uncertain, but the Middle Pleistocene antiquity of this material is not in doubt. The cranium itself is exceptionally well preserved (Fig. 3)

**Fig. 3** Lateral and facial views of the cranium from Petralona, Greece. This European hominin resembles Middle Pleistocene specimens from Africa. The Petralona and Broken Hill individuals are especially similar in measurements relating to facial proportions and vault shape

and would have enclosed a brain close to 1,230 $cm^3$ in volume (Stringer et al. 1979). Supraorbital tori are about as massive and projecting as in Broken Hill, while CT scans show that the frontal sinuses are greatly expanded. These air cavities extend posteriorly toward bregma and also laterally, where they are separated from the sphenoid sinuses only by thin bony partitions (Seidler et al. 1997). The frontal bone itself is relatively shorter and broader than in Broken Hill. The ratio of least to greatest frontal breadths is 91.6; postorbital constriction is thus less pronounced than in Broken Hill but comparable to that estimated for the Elandsfontein specimen. Petralona also differs from Broken Hill in having a wider cranial base and a less prominent torus crossing the occipital bone. However, the two hominins are alike in many other aspects of vault shape, in orientation of the infraorbital region, and in several measures of facial projection (Rightmire 1998, 2001; Friess 2010; Harvati et al. 2010, 2011).

## Arago Cave

Much the same conclusion applies to the less complete cranium from Arago Cave in France dated to about 450 Ka. The partial cranium numbered Arago 21 has a face that is largely intact but damaged as a result of its long interment in compacted cave sediments. The frontal bone, interorbital pillar, nose, and cheeks show numerous cracks, and areas of localized crushing are present. The discoverers have been able to correct some of this damage in a reconstruction, but significant distortion remains. Nevertheless, it is evident that Arago 21 is somewhat smaller than Petralona or Broken Hill in brow thickness, upper facial width, and facial length. Height of the bony orbit and the subnasal part of the maxilla are especially reduced, and the nasal saddle seems to be less elevated relative to the orbital margins. Apart from these differences, Arago 21 is similar in its proportions to the Broken Hill cranium from Africa (Rightmire 2001).

Some workers discern resemblances to Neanderthals. Hublin (1996) and Arsuaga et al. (1997) note that the infraorbital surface of the Arago 21 maxilla is flattened and the cheek bones are obliquely oriented, as in Neanderthals. Also, there is forward protrusion of the face at subspinale (in the midline, just below the nasal opening), and the nasal aperture is bounded inferiorly by a sharp rim. These observations must be tempered by the fact that cracking and plastic deformation make it difficult to assess key aspects of morphology. The wall of the Arago 21 maxilla is generally flattened or even inflated in the manner characteristic of Neanderthals, but the cheek is slightly hollowed laterally, below the orbit. This feature cannot be due entirely to damage. Also, it is not clear that the zygomatic bone is swept back (obliquely oriented) so noticeably as in later European populations. In facial forwardness at subspinale [as measured by the zygomaxillary angle of Howells (1973)], Arago 21 at 113° is in the Neanderthal range, and Petralona at 118° shows almost as much protrusion. But the value for Broken Hill is only 116°, so a low zygomaxillary angle does not align Arago 21 and Petralona with Neanderthals 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 hominins (section "Sima de los Huesos, Atapuerca") have a pattern of cresting on the nasal floor resembling that in Broken Hill or Bodo.

In addition to the partial cranium, the cave at Arago has yielded several mandibles, of which two have been described. Arago 2 is the more complete, missing only the angle and ascending portion from the left side. This specimen has sustained damage anteriorly, where the symphysis and left corpus are cracked. Arago 13 is a large hemimandible (right side), in relatively good condition. Both specimens present a mix of archaic and more modern characters. Development of the lateral prominences, marginal tori and tubercles, and internal symphyseal buttresses is comparable to that observed in *H. erectus*, although the alveolar planum is steeper and less shelflike in the Arago individuals. Arago 2 displays definite incurving of the symphyseal face below the alveolar border. Here, the elements of a mental trigone are present, while in Arago 13, signs of "chin" formation are less clear. Both jaws have retromolar fossae. However, in Arago 13, this fossa is restricted, and the crown of $M_3$ is partly obscured by the leading edge of the ramus when the specimen is viewed from the side.

The Arago mandibles are important not only because they reveal information about a Middle Pleistocene hominin population but also because they can be compared to the jaw from Mauer, near Heidelberg in Germany. Assigned a radiometric age of 609 Ka (Wagner et al. 2010), the Mauer fossil is likely to be one of the oldest recovered in Europe. It has often been described as primitive, with a massive body and very thick symphysis lacking any mental eminence. At the same time, the broad ramus, increased symphyseal height, and moderate size of the teeth suggest a morphological pattern different from that of *H. erectus*. The mandible was referred to the (new) species *H. heidelbergensis* by Schoetensack (1908). As the Arago jaws resemble the Mauer specimen, it is possible to link the French assemblage with the same taxon. Similarities of the Arago 21 face to Petralona (or Broken Hill) in turn provide a formal basis for including other European (or African) individuals in *H. heidelbergensis*.

## Sima de los Huesos, Atapuerca

The species *H. heidelbergensis* is increasingly well documented by the spectacular finds from Atapuerca in northern Spain. Excavations in the Sima de los Huesos have produced hominin remains, representing virtually all parts of the skeleton, that their describers have attributed to *H. heidelbergensis*. In addition to skulls, there are many postcranial bones, and it is clear that at least some of the Sima (male) individuals were tall and robust (Arsuaga et al. 1999a). Somewhat surprisingly, sexual dimorphism is comparable to that expressed in recent populations. The cave also contains the bones of bears and a few other carnivores, but there are no herbivores that might represent food waste. With one exception, there are no stone artifacts. A single hand axe fashioned from red quartzite was discovered in 1998. Investigators working at the Sima have argued that the skeletons were deposited in this pit by other humans and that the unique hand axe documents symbolic behavior (Carbonell and Mosquera 2006). First application of U-series dating to a speleothem present in the lower part of the stratigraphic sequence suggested a date of >350 Ka (Bischoff et al. 2003). More recent sampling from the same speleothem points to an age for the fossils of ca. 530 Ka (Bischoff et al. 2007).

Two of the Sima adults provide estimates for brain size. At close to 1,100 $cm^3$, SH 5 is rather small, but SH 4 with a capacity of 1,390 $cm^3$ is one of the largest of all Middle Pleistocene specimens. The crania are primitive in some respects, and the massive face of SH 5 is surmounted by a prominent browridge. Vault bones are thickened, and both sagittal keeling and an angular torus are variably developed. The braincase is broadest in the supramastoid region or just above the ear openings. As do their European and African contemporaries, the Sima hominins also exhibit derived traits in the face, shape of the squamous temporal, proportions of the occipital bone, and structure of the cranial base.

An important question is the extent to which these people resemble the later Neanderthals of Europe. As described by Arsuaga et al. (1997), the midface of SH 5 seems to anticipate the distinctive morphology associated with Late Pleistocene Europeans. The infraorbital surface and the side wall of the nose meet at a shallow angle, so as to produce a slight concavity. The cheek region is thus not “inflated” in the extreme manner of Neanderthals, but it can be interpreted as intermediate in form. Also in the Sima sample, continuity of the supraorbital tori at glabella is said to be reminiscent of Neanderthals, and the broad nasal bones are set in a relatively horizontal orientation. At the rear of the cranium, the suprainiac area is large but not very depressed. This trait and the shape of the occipital torus may also foreshadow the Neanderthal condition. How these features are evaluated (whether any of them can be judged to be true Neanderthal apomorphies) will determine how the Sima hominins as well as Arago and Petralona are related to populations outside of Europe and how these regional paleodemes should be treated in phylogenetic schemes.

## The TD6 Assemblage from Gran Dolina, Atapuerca

Additional evidence bearing directly on the first peopling of Europe is accumulating from another site in the Atapuerca region. Excavations at Gran Dolina have uncovered stone core-choppers and flakes, animal bones, and human remains dating to the end of the Early Pleistocene. An age slightly in excess of 780 Ka for the TD6 level containing the fossils now seems to be established (Falguères et al. 1999). Cranial specimens include a juvenile face, an adult cheek bone, part of a subadult frontal with some of the brow, and a piece of the cranial base on which most of the joint cavity for the mandible is preserved. There are also broken lower jaws with teeth, along with vertebrae, ribs, and bones of the hand and foot.

Arsuaga et al. (1999b) argue that the TD6 people are not *H. erectus*. Morphology of the hollowed cheek region, vertical orientation of the nasal aperture, features of the hard palate, form of the developing (but already substantially thickened) brow, a wide frontal, the shape of the temporal bone at the side of the vault, and the apparently modern mandibular joint all suggest that the Gran Dolina fossils are different from *H. erectus* and more like later humans. Also, there can be little doubt that this population is distinct from the later Neanderthals. The hollowed cheek (bearing a "canine fossa") points toward this conclusion, and neither in the juvenile nor in the adult faces is there much sign of the specialized Neanderthal condition. One partial mandible is generalized in its morphology, while the teeth resemble those of European and African Middle Pleistocene hominins.

Given this complex of traits, the Gran Dolina material may represent a new species. The name *H. antecessor* was proposed by Bermúdez de Castro et al. (1997). However, the number of fossils is still quite small, and several of the craniodental remains are fragmentary and/or subadult. A fair question is whether there is presently enough evidence to separate the TD6 assemblage from other penecontemporary fossils already on record. In particular, it must be asked whether the Gran Dolina bones and teeth differ from those of other early Europeans such as Mauer, Arago, and the Sima de los Huesos. Much attention has been focused on the development of a "canine fossa" in the midface. Hollowing is indeed apparent in the cheek of the TD6 juvenile, but a fossa is less obvious in the TD6 adult. This feature is variable in its expression in other populations, and the significance of this pattern is unclear. In the mandible, teeth, and postcranial bones, there seem to be few traits that differentiate the Gran Dolina hominins from Europeans of the Middle Pleistocene.

## South Asia and the Far East

One South Asian locality deserving mention is the Narmada Valley in central India (Fig. 1). Part of a cranium was found there in 1982, embedded in a conglomerate containing animal bones and a scattering of Acheulean artifacts. Dates for this material are poorly constrained, but it is probably of Middle Pleistocene age (Sonakia and Biswas 1998). Unfortunately the skull is damaged and lacks most of the face. Narmada has been described by its finders as *H. erectus*, but it is better compared to *H. heidelbergensis* (Kennedy et al. 1991). In its overall morphology, the cranial vault is not very different from the African and European hominins already discussed.

Early humans occupied China before 1.6 Ma (Zhu et al. 2004). This part of Asia has been a focus of research in paleoanthropology for quite a long time. Apart from the famous discoveries of *H. erectus* at Zhoukoudian, there are important sites dating to the later Middle Pleistocene. One is Dali and another is Jinniushan, both of them in northern China. The Dali cranium was found in river terrace deposits with stone flakes and fauna. The Jinniushan skeleton was recovered from cave fill containing animal bones but no artifacts. ESR and U-series dates obtained from animal teeth suggest ages of perhaps 300–200 Ka.

Dali is much of a cranium, damaged on the right side and at the base. The alveolar process and palate have been crushed upward. The specimen is otherwise undistorted and carries a lot of information. It has most often been described as "archaic" *H. sapiens*, intermediate in form between *H. erectus* and recent humans. Indeed, there are similarities to *erectus*, and these include the heavy brow, a long low vault that is broad across the base, and the sharply angled occiput. The temporomandibular joint cavity is offset laterally, and the cranial bones are thickened. These traits are best described as primitive retentions. At the same time, Dali exhibits other advanced features that link it to later populations. There is not much postorbital constriction, and the parietal walls are vertical rather than inward sloping. Both the high temporal squama and the proportions of the occiput depart from the *erectus* condition. The face is particularly short and non-prognathic (Wu and Athreya 2013).

The Jinniushan cranium has been reconstructed several times, and there are gaps in the face, the frontal region, and the base. The brow is somewhat less massive than in Dali, but there is an eminence behind bregma, and the occiput is flexed. In other respects, the specimen differs from *H. erectus*. Brain volume is close to 1,300 $\mathrm{cm}^3$. The border of the nasal aperture is vertical (rather than angled forward), and the nasal sill is crested. On the palate, the incisive canal opens anteriorly (just behind the incisor roots) as in recent humans.

In many anatomical details, both Dali and Jinniushan are like other Middle Pleistocene hominins from Africa or Europe. Comparisons based on facial measurements show that the Chinese specimens resemble Broken Hill to about the same extent as does Arago 21 (Rightmire 2001). There are some differences relative to Broken Hill, particularly in upper facial height (reduced in Dali and Jinniushan) and flattening below the nose (more pronounced in Jinniushan). Also, the Dali cheek exhibits a "canine fossa." This feature has been taken as a basis for regarding the Chinese fossil(s) as distinct from western populations, but in fact hollowing of the infraorbital surface can be documented for faces outside of the Far East. Finds from Gran Dolina suggest that this feature may appear in Europe at the beginning of the Middle Pleistocene (section "The TD6 Assemblage from Gran Dolina, Atapuerca"). The recognition of such variation will make it harder to argue for isolation of the major Old World geographic provinces.

## Brain Size, Encephalization, and Speciation

Many of the Middle Pleistocene hominins have brains that are enlarged relative to those of *H. erectus*. For 10 of the more complete crania including Bodo, Broken Hill, Petralona, two of the Sima de los Huesos adults, Dali and Jinniushan, average capacity is 1,206 $\mathrm{cm}^3$. For 30 *H. erectus* individuals, the mean volume is only 973 $\mathrm{cm}^3$. This difference is substantial, and it can be determined that a number of the Middle Pleistocene specimens actually lie beyond the limits predicted for an average *H. erectus* of comparable antiquity. Apparently, the change in brain size is not simply a consequence of larger body mass (Rightmire 2004).

Encephalization quotients (EQ) can also be obtained for a number of the specimens. This entails first estimating body mass from orbital height (following Aiello and Wood 1994) and then deriving EQ from the relationship of brain weight to body mass established for mammals by Martin (1981). Here, there are various complications. Apart from the error associated with any weight estimate, there is the fact that the regression equations of Aiello and Wood (1994) are based on several species. Because EQ is a function of body mass predicted for individuals using an interspecific equation, comparisons of the EQ values determined for fossils may be misleading (Smith 2002). In any event, six *H. erectus* crania from Africa and Asia are complete enough to supply the necessary measurements, and the average EQ is 3.61 (Rightmire 2004). This result is comparable to that reported by Ruff et al. (1997), who employ mean estimates of brain and postcranially based body masses to compute EQ values of 3.40 and 3.46 for temporally defined (Early Pleistocene to early Middle Pleistocene) assemblages.

During the balance of the Middle Pleistocene, a rise in EQ is apparent. Bodo and Broken Hill remain within the range observed for *erectus*, but other individuals have higher values and the average for eight specimens is 5.26. The magnitude of this increase is greater than that determined by Ruff et al. (1997) for humans of mid-Quaternary age. These authors use unmatched brain and body weights (means for samples of disassociated crania and postcrania) as a basis for their EQ calculations, and this may account for some of the difference in results. Also, orbit height may tend to underestimate body mass in comparison to predictor variables drawn from the postcranial skeleton. Nevertheless, there is evidence for a shift in brain size at or just before the onset of the Middle Pleistocene.

This increase in encephalization seems to be linked to an episode of speciation. It is generally assumed that the larger brain and accompanying changes to the vault and face distinguish *H. heidelbergensis* from *H. erectus*. Here, an important question must be raised. Differences in frontal proportions, the parietal arc, form of the temporal squama, and rounding of the occiput may be related to the expanding brain, as may the increase in cranial height. As a consequence, traits such as parietal length and occipital curvature are not independent, and it will be incorrect to claim that each of these measurements adds new information useful in phylogenetic analyses. If this is the case, it may not be reasonable to recognize one or more new species, primarily on the strength of an increase in cranial capacity. Examined critically, the morphological evidence may not justify the recognition of so many taxa within *Homo* (Lieberman and Bar-Yosef 2005).

Correlation analysis provides information about the interactions of brain volume with vault form in Pleistocene *Homo* (Rightmire 2012, 2013). It can be determined that the expanding brain influences vertex height and probably also parietal sagittal length. However, brain size fails to influence vault breadth within either *H. erectus* or the Middle Pleistocene hominins. Instead, the cranial base has a major effect on variations in width. Endocranial volume is not associated with the frontal flattening that is so characteristic for *H. erectus*. In *H. erectus*, and in individuals such as Bodo and Petralona, the massive face seems to override the brain as a determinant of frontal form. Encephalization does not explain the occipital rounding that distinguishes Broken Hill, Omo 2, and the Sima crania. Evidently, apart from greater vertex height, few of the vault characters considered diagnostic for *H. heidelbergensis* can be attributed directly to changes in the brain. Traits that are independent can be used to document speciation.

## Phylogenetic Hypotheses

Discoveries of new fossils, reassessments of specimens found earlier, and advances in the application of dating techniques show that hominins differing from *H. erectus* appeared in southern Europe before 780 Ka and in Africa at about the same time. One reading of the record suggests that these European and African groups share a number of derived features of the cranial base and vault. Other similarities to later humans are apparent in the facial skeleton (orientation of the nasal aperture, location of the palatal incisive canal) and perhaps the mandible (symphyseal height increased relative to the posterior corpus, incipient mental eminence). Postcranial bones known principally from the Sima de los Huesos in Spain suggest that the European hominins were heavily built, perhaps reflecting adaptation of body form to a temperate environment. In sum, the anatomical evidence can be interpreted as supporting a claim that all of the earlier Middle Pleistocene fossils belong to a single lineage (Fig. 4a). This species can be called *H. heidelbergensis*. Later in the Middle Pleistocene, some populations dispersed northward within Europe, where they were subject to long episodes of extreme cold. During glacial advances and retreats occurring over several hundred thousand years ago, these hominins continued to adapt to harsher (cold/dry) conditions and evolved the specialized craniofacial characters and body build of the Neanderthals. In this same interval of time, other representatives of *H. heidelbergensis* in Africa were becoming more like modern humans. Fossil finds from Irhoud in Morocco, the Omo in southern Ethiopia, Herto in the Middle Awash region, and Laetoli in Tanzania document this evolutionary progression toward *H. sapiens*.

Alternatively, it can be argued that *H. antecessor* is the ancestor to all later humans (Fig. 4b). This species is considered to be descended from (African) *H. erectus* (Bermúdez de Castro et al. 1997). Rather soon after its first appearance in Spain, *H. antecessor* must have given rise to *H. heidelbergensis*. In this scenario, the *heidelbergensis* lineage was confined exclusively to Europe, where its members gradually acquired the large nose, more projecting facial skeleton, and other morphology of the Neanderthals. This is the accretion hypothesis of Dean et al. (1998). Also, *H. antecessor* is presumed to have evolved an African offshoot, represented at localities such as Bodo, Broken Hill, and Elandsfontein. Although these Middle Pleistocene hominins are acknowledged as morphologically similar to (perhaps even capable of exchanging genes with) their European contemporaries, they are not assigned to *H. heidelbergensis*. Instead, the African fossils are lumped

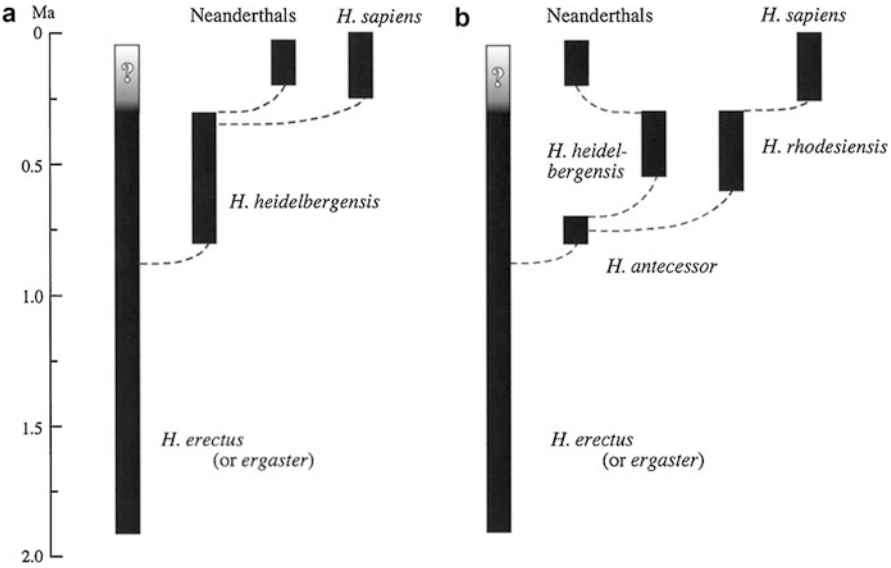

**Fig. 4** Alternative evolutionary trees showing the relationships among *H. erectus*, Middle Pleistocene hominins, Neanderthals, and modern humans. Bars depict the time range estimated for each species. Broken lines indicate likely links of ancestors with descendants. Hypothesis (**a**) shows *H. heidelbergensis* to be descended from *H. erectus*. This species must have dispersed widely across Africa and western Eurasia at the beginning of the Middle Pleistocene, and some populations may also have reached the Far East. Here *H. heidelbergensis* is depicted as the antecedent to both Neanderthals in Europe and recent humans all across the old World. In a different interpretation (**b**), *H. antecessor* is recognized as the direct descendant of *H. erectus*. In turn, *H. antecessor* evolved into European *H. heidelbergensis*, and this species gave rise (only) to the Neanderthals. African *H. rhodesiensis* is considered to be ancestral to *H. sapiens*

in a separate species, for which the nomen *H. rhodesiensis* is available. Whether this taxonomic view can be accepted will depend largely on the outcome of excavations that are continuing in the TD6 levels at Gran Dolina. It will be important to expand the sample of fossils documenting the earliest European settlers.

Another question is whether the far eastern specimens can be accommodated within one of these systematic frameworks. The answer is a tentative yes, although the evidence is sparse. Dali and Jinniushan do share a number of apomorphic traits with the western hominins. But there are some differences, and the face has been a focus of contention. Dali has a short face, and this would be true even if damage to the maxilla were corrected. Jinniushan also has a short clivus (the subnasal portion of the maxilla), and it is oriented vertically. In Dali, there is hollowing of the cheek below the orbit, and such excavation is not present in the African crania. Much has been made of this facial morphology, but in fact there is individual variation (see section "Brain Size, Encephalization, and Speciation"). The significance of the Dali "canine fossa" should not be overemphasized. It is possible to argue that the later Middle Pleistocene hominins of China document an eastward excursion of *H. heidelbergensis*, where this species is taken to be the link between *H. erectus* and all later humans. Dating is not very firm, but probably fossils such as Dali and Jinniushan are younger than those in Africa. This may suggest that *H. heidelbergensis* was a late arrival in the eastern part of Asia.

## Current Debates

A differing interpretation arises from ongoing analyses of the discoveries at the Sima de los Huesos. As noted above, the Sima skulls exhibit traits expected to occur (very) early in the evolution of the Neanderthal lineage (Arsuaga et al. 1997). Recently, it has been emphasized that the Sima de los Huesos teeth are remarkably like those of "typical" Neanderthals (Martinón-Torres et al. 2012). The upper incisors display conspicuous labial convexity and a distinctive shovel shape, while the upper premolars present a bulging of the buccal aspect of the crown. The $M^1$s possess an enlarged hypocone, giving the crown a rhomboidal outline characteristic of Neanderthals. The $P_3$s have a symmetrical contour. Here, the talonid is reduced or absent, so that the remaining cusps occupy a small area near the lingual border of the crown. This Neanderthal-like morphology is more pronounced in the Sima sample than in other Middle Pleistocene hominins. Indeed, Martinón-Torres et al. (2012) claim that the Sima specimens are "more Neanderthal" in form than the Mauer or the Arago dentitions. They suggest that the Sima may constitute a source population for Neanderthals, while Mauer and Arago document the presence of a morphologically distinct lineage. Such a conclusion is favored by Stringer (2012), who envisions two species coexisting in the European Middle Pleistocene. The second species (*H. heidelbergensis*) includes fossils presumed to predate the evolutionary emergence of *H. neanderthalensis*, as well as specimens such as Petralona from later time periods.

## Archaeology and Behavior in the Middle Pleistocene

Controversy over the number of Middle Pleistocene lineages in Eurasia and Africa will likely continue. Nevertheless, it is becoming clear that the hominins were more encephalized than *H. erectus*. Also, there is evidence from archaeology that these people were developing new behavior. Later Acheulean artifacts are known from numerous African sites, including Bodo, Olorgesailie, Isimila, Lake Ndutu, the Cave of Hearths, Elandsfontein, and Duinefontein 2. In general, later Acheulean hand axes can be characterized as thinner, more symmetrical, and bearing many more flake scars than their earlier counterparts. In some sites, relatively small hand axes are accompanied by flake tools resembling those of the Middle Stone Age (Klein 2000). While it is dangerous to expect universal associations of *Homo* species with particular industrial traditions, informative patterns may be uncovered (Foley and Lahr 1997). In virtually all mid-Quaternary African contexts, where diagnostic human bones are found with later Acheulean artifacts, the maker is *H. heidelbergensis* (or *H. rhodesiensis*). One may conclude that this species was capable of producing a tool kit more sophisticated than that utilized routinely by *H. erectus*.

In western Eurasia, hominins equipped with Acheulean tools were present by the onset of the Middle Pleistocene (780 Ka) at Gesher Benot Ya'aqov in Israel (Goren-Inbar et al. 2000). Farther to the west in Europe, there are no Acheulean sites from the beginning of the Middle Pleistocene, but Boxgrove in Britain is likely to be 500 Ka in age. This locality has yielded thin, extensively flaked flint bifaces, along with bones of horses and rhinoceroses bearing cut marks. The animals may well have been hunted and butchered. In addition, there is the shaft of a human tibia. The dimensions of this bone at midshaft are large, and the Boxgrove individual was probably quite massive. This hominin has been attributed to *H. heidelbergensis* by Roberts et al. (1994). Signs of later Acheulean toolmakers are known from Torralba and Ambrona in Spain, where the artifacts are again found with large herbivores, including elephants and horses (Freeman 1994). Acheulean artifacts occur also at several sites in France and Italy. At Castel di Guido in central Italy, finely flaked bifacial tools were produced from elephant bone (Villa 1991). At some other earlier Middle Pleistocene localities, including Arago Cave, the stone industries contain small chopping tools and flakes but no hand axes (De Lumley et al. 1984). The reasons for this difference are unclear, but the availability of suitable raw materials, the constraints imposed by different types of stone, and the context in which tools were manufactured must all be considered, along with the possibility that distinct cultural behaviors or styles are represented.

An isolated but particularly significant example of the skills acquired by mid-Quaternary Europeans comes from Schöningen in Germany. Eight carefully crafted wooden throwing spears have been uncovered near a former lake, where they are associated with flint tools and chips (Thieme 1997, 2005, 2007). Scattered through the same horizon are the remains of numerous horses. Many of the bones are cut-marked, and some of the animals must have been processed for meat and marrow extraction (Roebroeks 2001). More convincingly than other early European assemblages, the Schöningen discovery points to systematic hunting of large animals. Stalking and killing of agile or dangerous prey requires experience and practice, and it is reasonable to hypothesize that the people were cooperating with one another in these efforts. Increased levels of social cooperation and exchange of knowledge would have become the norm. And if the hunters at Schöningen (also at sites such as Boxgrove and Arago) were able to obtain large amounts of meat, they would likely have shared or exchanged food with other groups, perhaps at established meeting places (Roebroeks 2001). Certainly our understanding of the behavior of the early Europeans remains quite incomplete, but it is apparent that bands of *H. heidelbergensis* were not only skilled at flaking stone but also capable of interacting regularly in the pursuit of game and other social activities.

## Conclusion

Middle Pleistocene crania from Bodo, Broken Hill, Elandsfontein, and Lake Ndutu in Africa are quite similar to penecontemporaneous fossils from Europe. Craniodental remains and jaws from Petralona and Arago Cave are particularly informative, and the assemblage from Sima de los Huesos is spectacular. If this grouping is expanded to include the Mauer mandible, then it can be argued that *H. heidelbergensis* was a geographically dispersed paleospecies.

A question is whether additional specimens from China can be accommodated within this taxon. Dali and Jinniushan share a number of apomorphic traits with the western hominins, but there are differences, and the face has been a focus of contention. Dali has a short face, and there is hollowing of the cheek below the orbit. Probably the significance of the Dali "canine fossa" should not be overemphasized. Later Middle Pleistocene populations of China may document an eastward excursion of *H. heidelbergensis*, where this species is taken to be the link between *H. erectus* and all later humans.

*Homo heidelbergensis* differs from *H. erectus* in absolute as well as relative brain size. Correlation analysis provides information about the interactions of brain volume with vault form. It can be determined that the expanding brain influences vertex height and probably also parietal sagittal length. Traits that vary independently from brain volume have greater taxonomic utility and include anterior frontal broadening, perhaps the high, arched outline of the temporal squama, and lateral expansion of the parietal vault. Encephalization does not explain the occipital rounding that distinguishes Broken Hill, Omo 2, and the Sima crania, nor does it account for the greater elevation of the lambda-inion chord. Traits of the cranial base also serve to diagnose *H. heidelbergensis* in relation to *H. erectus*. Morphology of the temporomandibular joint generally resembles that in *H. sapiens*, as is the case for the tympanic and petrous portions of the temporal bone. There is no reduction in overall face size in comparison to *H. erectus*, and the facial skeleton seems to be "hafted" to the braincase in such a way as to accentuate anterior projection. But reorientation of the nasal aperture and forward placement of the incisive canal within the palate suggest that the face of *H. heidelbergensis* may be more nearly vertical, as in *H. sapiens*.

Later Acheulean artifacts are known from many mid-Pleistocene African localities, and in general, the hand axes can be characterized as thinner and more symmetrical than earlier examples. In some sites, relatively small hand axes are accompanied by flake tools resembling those of the Middle Stone Age. While it is dangerous to expect universal associations of *Homo* species with particular industrial traditions, in virtually all African contexts where diagnostic human bones are found with later Acheulean artifacts, the maker is *H. heidelbergensis*. One may conclude that these people were more advanced in behavior than their predecessors. There is evidence that *H. heidelbergensis* was able to make relatively sophisticated stone tools, hunt larger and more dangerous game animals, and perhaps engage in cooperative social activities.

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