

Homo in the Middle Pleistocene: Hypodigms, Variation, and Species Recognition

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It is generally accepted that modern humans evolved in Africa. This consensus has emerged in the last two decades, as molecular evidence has been coupled with findings from paleontology and prehistory. Patterns of DNA variation in living populations, morphology of fossils, and archeological traces can all be read to show that our species has deep roots in Africa and began to disperse into other regions only late in the Pleistocene. There are still questions about the timing of these dispersals and the extent to which modern people replaced or exchanged genes with other, more archaic groups, but new problems are now coming more clearly into focus. These relate to the ancestry of *Homo sapiens* in the Middle Pleistocene. In this essay, I emphasize the evidence available from Middle Pleistocene localities in Africa and Europe, exploring variation among individuals, composition of hypodigms, species-level taxonomy, and evolutionary relationships of the hominin populations. One obvious difficulty is that the fossils are scarce. For the most part, only incomplete crania are available from African localities. The record is more comprehensive for the Sima de los Huesos in Spain, but principally crania and jaws are known from other European sites. This means that skull traits and measurements must provide the basis for sorting individuals to groups and building differential diagnoses. For much of the material, dating is still poorly controlled, although a few of the most important assemblages can now be placed more securely within a Middle Pleistocene chronological framework. Despite these constraints, it is possible to point toward tentative solutions.

In Africa, fossils have been collected at localities from Bodo and the Omo Basin in Ethiopia to Elandsfontein in the southern Cape. It is recognized that these individuals

differ from *Homo erectus* in brain size and other aspects of morphology. Also, there are indications that the people were capable of making relatively sophisticated stone tools, hunting large herbivores, and probably controlling fire to prepare food. However, the skulls retain numerous primitive features that set them apart from recent humans. Faces are massively built with strong supraorbital tori; frontals are flattened, and vaults remain low with less parietal expansion than is evident in *Homo sapiens*.

The hominins from Africa are quite similar to their early Middle Pleistocene contemporaries in Europe. The spectacular assemblage of skulls and postcranial bones from Sima de los Huesos (Atapuerca) is

particularly informative, and there are other important specimens from Arago Cave in France, Mauer and Steinheim in Germany, and Petralona in Greece. Considered as a whole, the evidence from Africa and Europe suggests a speciation event in which *Homo erectus* gave rise to a daughter lineage. At or before the beginning of the Middle Pleistocene, these new populations spread across Africa and into western Eurasia. It is possible that additional splitting occurred subsequently, as the hominins in Europe became increasingly isolated from other groups. In any case, it is very likely that a lineage established in Africa produced the first populations resembling modern humans.

How the fossils from Africa and Europe should be treated taxonomically is currently uncertain. A traditional approach assigning the fossils to earlier (“archaic”) and later grades within *Homo sapiens*¹ has generally given way to hypotheses postulating species different from our own. One view recognizes two species in Europe (in addition to the later Neanderthals), both of them distinct from mid-Pleistocene Africans.² Alternatively, just two lineages may be identified. A Neanderthal branch may be traced back nearly to the beginning of the Middle Pleistocene in Europe, while an African lineage, clearly distinct from *Homo erectus*, may exhibit morphology that aligns it with anatomically modern humans. Still another perspective holds that morphological differences among the most ancient European and African specimens are minor and can be attributed to geography and intragroup variation. Here many

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Key words: cranial form; *Homo heidelbergensis*; Neanderthals; systematics; phylogeny; human evolution

TABLE 1. Measurements (mm) for Middle Pleistocene Crania From Africa and Europe

	Bodo	Omo 2	Ndutu	Broken Hill	Elandsfontein	Arago	SH 4	SH 5	Steinheim	Petalona
Entire neurocranium										
Capacity	1250	–	1100	1280	–	1166	1390	1125	1100	1230
Glabella-opisthocranion	–	–	183	209?	202?	–	201?	185	–	208
Basion-bregma height	131	–	–	129	–	–	131	125	104?	126
Maximum breadth	148	147	144	145?	–	–	164	146	–	165
Maximum biparietal breadth	148	142	–	145	138	–	–	–	–	151
Biauricular breadth	–	131	128	138?	–	–	155	139	109?	150
Facial skeleton										
Nasion-prosthion	88	–	–	90	–	80	–	85	–	90
Basion-prosthion	121	–	–	117	–	–	–	121	–	116
Basion-nasion	107	–	105	110	–	–	109	109	–	110
Biorbital chord	130	114?	–	124	–	114	115	112	100?	126
Nasion angle	142	–	–	134	–	145	138	137	142?	140
Midorbital chord	76	–	72	76	–	75?	–	–	62?	75
Naso-orbital angle	132	–	–	124	–	139?	–	–	120?	131
Bimaxillary chord	134	–	–	107	–	110	–	118	–	120
Subspinale angle	134	–	–	116	–	113	–	111	–	118
Prosthion angle	114.6	–	–	90	–	99	–	–	–	<106
Orbit breadth	47.5	–	–	48	–	46	–	43	40	45
Orbit height	39	–	–	39	–	30	–	33	32	34
Cheek height	33.5	–	–	29	–	30	–	33	26	38
Nasal breadth	43	–	27	30	–	29?	–	38	–	37
Nasal height	62	–	–	57	–	56?	–	57	–	68
Clivus length	–	–	–	29	–	21	–	–	–	22
Palate breadth	48	–	–	48	–	41	–	44	–	50
Palate length	–	–	–	57	–	–	–	55	–	51
Frontal bone										
Supraorbital torus thickness	16	13.5	–	22	19	12.5	11	14	16	21
Minimum breadth	105	108	–	98	103	105	117	106	–	110
Postorbital constriction index	80.7	94.7	–	79.0	–	92.1	101.7	94.6	–	87.3
Maximum breadth	119	120	112	118	112	–	126	118?	–	120
Frontal breadth index	88.2	90.0	–	83.0	91.9	–	92.8	89.8	–	91.6
Frontal sagittal chord	125	–	–	120	116	–	115	106	98	110
Frontal sagittal arc	144	–	–	139	>130	–	126?	114	–	129
Frontal angle	139	–	–	140	–	–	140	145	–	140
Parietotemporal region										
Parietal sagittal chord	–	119	–	112	110	98	111	105	96	106
Parietal sagittal arc	–	125	–	120	122	105	118	112	103	114
Lambda-asterion chord	–	94	83	91	–	99?	95	85	88	88
Lambda-asterion arc	–	103	91	100	–	110?	–	–	99	99
Mastoid length	–	33?	27	29	–	–	–	–	–	–
Occipital bone										
Biasterionic breadth	–	129	113	129?	–	–	132	116	102?	120
Occipital sagittal chord	–	106	87	89	–	–	94	92	–	92
Occipital sagittal arc	–	136	111	–	–	–	125	114	–	128
Occipital angle	–	106	111	–	–	–	106	114	–	97
Lambda-inion chord	–	70	61	60	58	–	67	61	62	65
Inion-opisthion chord	–	55	45	54	–	–	46	49	–	55
Occipital scale index	–	78.5	73.7	90.0	–	–	68.6	80.3	–	84.6

of the fossils are placed together in one taxon. If the Mauer mandible is included in the hypodigm, then the appropriate name for this species is *Homo heidelbergensis*, which has been posited as ancestral to both the Neanderthals in Europe and the earliest representatives of *Homo sapiens* in Africa.^{3,4}

MORPHOLOGY OF KEY SPECIMENS

In Africa, fossils from the early Middle Pleistocene are clearly different from *Homo erectus* in vault size and form. 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. An important exemplar in this regard is the cranium from Bodo, in the Middle Awash region of Ethiopia. Measurements are given in Table 1. The Bodo cranium, and later a broken parietal from a second individual, were found in conglomerates and

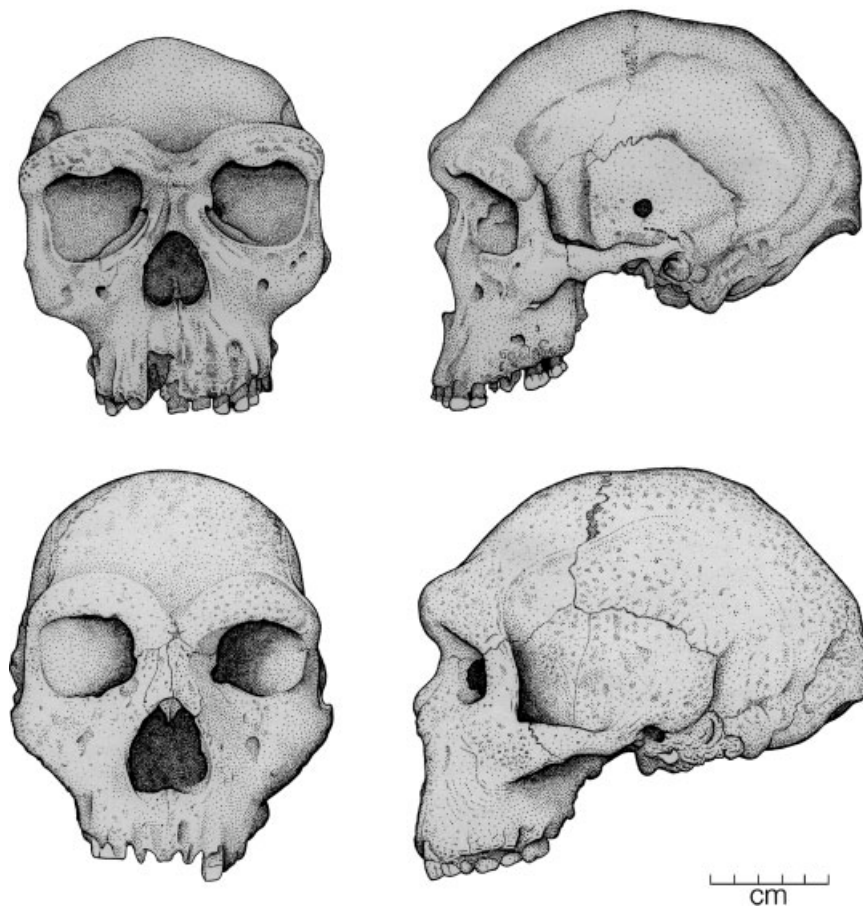


Figure 1. Hominins from Broken Hill (above) and Petralona. The two crania resemble one another in many aspects of form. Supraorbital tori are projecting and vertically thickened. Facial heights and breadths are comparable, but the Petralona interorbital pillar and cheek are particularly massive, while the Broken Hill maxilla is lengthened below the nose. The vaults have similar sagittal profiles, although there are small differences in frontal proportions and configuration of the occipital torus. Brain sizes are larger than expected for *Homo erectus*, and the cranial bases share several features that appear to be derived (similar to the condition in later *Homo*).

sands containing mammalian bones and later Acheulean tools.⁵⁻⁷ 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. ⁴⁰Ar/³⁹Ar measurements support this biochronology, and the evidence points to an age of about 600 thousand years (Ka) for the Bodo hominins.⁸ It is apparent that Bodo is like *Homo 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 derived in its morphology.

Brain size is close to 1,250 cm³ and is thus substantially greater than expected for *Homo erectus*. Frontal proportions, the high arched shape of the squamous temporal, and traits of the cranial base are like those of more modern humans. Although the face is very broad with a prominent glabellar region, 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.⁹ These are apomorphic conditions expressed also in the face of recent *Homo*.

Another African cranium is known from Broken Hill (now Kabwe) in Zambia, where it was 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 (Fig. 1). 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 Broken Hill fossil was

Shortly after it was found, the Broken Hill fossil was attributed to the new species *Homo rhodesiensis*.¹⁰ In its overall morphology, however, Broken Hill resembles *Homo erectus*, and indeed it has been classified this way on more than one occasion. At the same time, it shares apomorphic features with later humans.

attributed to the new species *Homo rhodesiensis*.¹⁰ In its overall morphology, however, Broken Hill resembles *Homo erectus*, and indeed it has been classified this way on more than one occasion. At the same time, it shares apomorphic features 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. 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.¹¹

A 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 sand transported by wind from the Atlantic shore. This site 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 horizons exposed in these "bays" are stratified land surfaces or simply mark 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.¹² Animals, many of them bovids or other large herbivores, were attracted to the water. One ancient calcareous surface, known as Elandsfontein Main, has provided thousands of animal bones, along with later Acheulean artifacts. The highly diverse fauna includes numerous archaic elements such as a dirk-toothed cat, a siva-there, 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-Urbe¹³ implied that the bones were accumulated between 700 Ka and 400 Ka, but more recent sorting of the fauna suggests an older interval, between 1 million years (Ma) and 600 Ka.¹⁴

The reconstructed Elandsfontein skullcap is composed of the frontal and parietal walls and some of the occipital. The bones are cracked and heavily weathered, but the braincase is not distorted. There are some similarities to *Homo 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 (Table 1). 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.¹⁵ The South African frontal bone gives a breadth index of 91.9. This bone 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 *Homo erectus*.

A fourth Middle Pleistocene specimen is on record 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.¹⁶ 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 archeological 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 clay matrix. Clarke¹⁷ has described the process of cleaning and reconstructing the fossil. 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 cm³. Just a fragment of the supraorbital region is preserved. 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 *Homo erectus*. Also, the upper plane of the occiput is vertical, above the mound-like transverse torus. The morphology of this structure is in keeping with other characters suggesting that Ndutu could be female,

in comparison to males such as Bodo or Broken Hill.

Several sites in the Omo region of southern Ethiopia, initially explored in 1967, have recently been revisited. Human remains are known from both the PHS and KHS localities in Member I of the Kibish Formation, now considered to be close in age to 195 Ka.¹⁸ Omo 2 is an isolated surface find from PHS, lacking archeological 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 features likely to be primitive 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; none of the face is preserved.

Omo 1 was excavated at the KHS site, 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 *Homo 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 fron-

tal 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 is 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 *Homo sapiens*.

Additional specimens are on record from sites of broadly Middle Pleistocene antiquity, including Singa, Eyasi, Laetoli (Ngaloba), and Florisbad. Some of these individuals are quite fragmentary. The Florisbad orbit, nasal area, and cheek have been reconstructed several times, and there is continuing uncertainty as to some morphological details. Nevertheless, the facial parts and frontal bone appear to be less heavily constructed than is the case for Broken Hill. The Laetoli 18 maxilla and braincase are more complete than the Florisbad or Eyasi materials. Like Omo 1, LH 18 displays features that suggest a link to *Homo sapiens*. As a group, these relatively late fossils seem to differ from the other Middle Pleistocene hominins and are not considered here.

Skulls similar to those from Africa are documented from 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. One of the regions that has proved to be most informative with respect to hominin evolution is Atapuerca in northern Spain. Excavations in the Sima de los Huesos have produced fossils representing virtually all parts of the skeleton. 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.¹⁹ Somewhat surprisingly, overall size differences assumed to reflect sexual

dimorphism are comparable to those expressed in recent populations.²⁰ The cave also contains the bones of bears and a few other carnivores, but there are no herbivores that might represent food waste. With the exception of a single hand axe fashioned from red quartzite, which was discovered in 1998, there are no stone artifacts. Investigators working at the Sima have argued that the skeletons were deposited in this pit

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by other humans and that the unique hand axe documents symbolic behavior.²¹ First applications of U-series dating to a speleothem present in the lower part of the stratigraphic sequence suggested a date of >350 Ka.²² More recent sampling from the same speleothem has produced high-resolution U-series dates averaging 600 Ka. A conservative minimum estimate for the age of the fossils is now said to be 530 Ka.²³

Two of the Sima adults provide estimates of brain size (Table 1). At close to 1,100 cm³, SH 5 is rather small, but SH 4, with a capacity of 1,390 cm³, 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 auditory openings. Like their African contemporaries, the Sima hominins exhibit derived traits. These are evident in the face, the shape of the squamous temporal arch, proportions of the occipital bone, and the structure of the cranial base.

A key question is the extent to which the ancient SH hominins resemble later Pleistocene Europeans. As described by Arsuaga and coworkers,²⁴ the midface of SH 5 seems to anticipate the distinctive morphology associated with Neanderthals. 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 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. Careful evaluation of these features will help in determining how the Sima hominins are related to other populations of Europe and Africa, as well as how these regional paleodemes should be treated in phylogenetic schemes.

Petalona lies near the city of Thessaloniki in northern Greece. The exact provenience of the hominin fossil found within a cave containing the bones of numerous extinct animals is uncertain, but the Middle Pleistocene antiquity of this material

is not in doubt. The Petralona cranium is exceptionally well preserved and would have enclosed a brain close to 1,230 cm³ in volume.²⁵ Supraorbital tori are about as massive and projecting as in Broken Hill (Fig. 1), 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.¹⁵ The frontal bone itself is relatively shorter and broader than that in Broken Hill. The ratio of least-to-greatest frontal breadths is 91.6; postorbital constriction is thus less pronounced than it is 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, height, breadth, and massive construction of the upper face and cheek, and in several measures of facial projection (Table 1).

Much the same conclusion applies to the less complete cranium from Arago Cave in France, dated to ca. 350 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 (Fig. 2). 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 (Table 1). The 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 (the naso-orbital angle is relatively large). Apart from these differences, Arago 21 is similar in its proportions to the Broken Hill cranium from Africa.¹¹

Some workers discern resemblances to Neanderthals. Hublin²⁶ and



Figure 2. The Arago 21 facial skeleton and frontal bone. Although quite complete, the face exhibits numerous cracks and there is considerable distortion. The supraorbital tori are less thickened than those in Broken Hill, the breadth across the orbits is reduced, and the subnasal clivus is very short. Nevertheless, the cheeks are relatively massive, as is the case for Petralona. Warping of the maxilla makes it difficult to assess the morphology of the midfacial region, but it appears that the walls of the nasal aperture may be inflated in the manner characteristic of later Neanderthals.

Arsuaga and coworkers²⁴ 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) as noticeably as in later European populations. In facial forwardness at subspinale, as measured by the zygomaxillary angle of Howells,²⁷ Arago 21 at 113° is in the Neanderthal range. 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 exclusively with Neanderthals rather than with other Middle Pleistocene specimens. The sharp inferior margin of the Arago nasal opening is indeed reminiscent of that in Neanderthals. However, there is variation in this feature. The inferior margin of the nasal opening of Petralona is less like that of the Neanderthals. In other archaic Europeans, including the SH hominins, these



Figure 3. The Arago 2 mandible. The jaw is damaged anteriorly and all of the left ramus is missing. The relatively delicate corpus and small teeth have been taken as evidence that Arago 2 is a female, while the more massive Arago 13 hemimandible is probably a male. Elements of a mental trigone (the bony "chin") are present, while internally the alveolar plane slopes steeply downward and is less shelf-like than in most *Homo erectus*. On the right side, the root of the ramus rises from a relatively posterior location, suggesting forward positioning of the dentition (not evident in Arago 13).

margins 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 two mandibles. Arago 2 is the more complete, missing only the angle and ascending portion from the left side (Fig. 3). 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 derived morphology. Development of the lateral prominences, marginal tori and tubercles, and internal symphyseal buttresses is comparable to that observed in *Homo erectus*, although the alveolar planum is steeper and less shelf-like in the Arago individu-

als. 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 M₃ is partly obscured by the leading edge of the ramus when the specimen is viewed from the side.

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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 tentative age of ca. 500 Ka, the Mauer fossil is likely to be one of the oldest recovered in Europe.

because they can be compared to the jaw from Mauer, near Heidelberg in Germany. Assigned a tentative age of ca. 500 Ka, 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 (Fig. 4). At the same time, the broad ramus, increased symphyseal height, and moderate size of the teeth suggest a morphological pattern different from that of *Homo erectus*. Schoetensack²⁸ referred the mandible to the (new) species *Homo heidelbergensis*.

Because 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 *Homo heidelbergensis*.

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



Figure 4. The Mauer mandible, discovered in sands and gravels of the Grafenrain pit near Heidelberg, Germany. The jaw is massively constructed, lacks any sign of chin formation, and is usually said to resemble "archaic" representatives of *Homo*. However, the high anterior corpus, wide ramus, and relatively moderate size of the teeth distinguish the specimen from *Homo erectus*. The fossil was attributed to *Homo heidelbergensis* by Otto Schoetensack in 1908.

be established.²⁹ 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 and coworkers³⁰ argued that the TD6 people are not *Homo erectus*. Morphology of the hollowed cheek region, vertical orientation of the nasal aperture, features of the hard palate, the form of the developing but already substantially thickened brow, a wide frontal, the shape of the temporal bone, and the apparently modern mandibular joint all suggest that the Gran Dolina fossils are different from *Homo 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. Moreover, 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 *Homo antecessor* was proposed by Bermúdez de Castro and colleagues.² 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 known from the Sima de los Huesos, Mauer, and Arago. 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.

VARIATION IN CRANIAL DIMENSIONS

It is evident from the preceding discussion and the measurements in Table 1 that many of the mid-Pleistocene specimens are similar in overall form. The African crania possess primitive features but display derived traits of the vault and face that set them apart from *Homo erectus*. The

... in light of the numerous similarities shared by all of the mid-Pleistocene fossils, a reasonable hypothesis is that they can be sorted to one group. This null hypothesis suggests that intragroup differences are small, thus permitting recognition of just one paleospecies.

European hominins also differ from *Homo erectus* and appear relatively modern in many of the same features that characterize Bodo or Broken Hill. Some European individuals have morphology that can be described as “incipiently” Neanderthal-like. However, in light of the numerous similarities shared by all of the mid-Pleistocene fossils, a reasonable hypothesis is that they can be sorted to one group. This null hypothesis suggests that intragroup differences are small, thus permitting recognition of just one paleospecies.

Rejecting this proposition will require demonstrating that variation

within the mid-Pleistocene hypodigm is greater than can be allowed, following some reasonable criterion. There is a question, of course, as to how great the differences must be in order to show that more than one taxon is present. Traditionally, paleontologists have used modern populations as a guide. Variation in the ancient sample is compared to that in one or more reference groups, typically *Homo sapiens* and/or representatives of *Pan*, *Gorilla*, *Pongo*, or one of the cercopithecoid genera. Various methods have been devised for comparing levels of variation within and between samples. Some are inappropriate, but a size-independent statistic that has been demonstrated to be useful in paleontological situations is the coefficient of variation (CV). Where the number of individuals is small, the CV may be modified as $(1 + 1/4N) \times (100s/\bar{X})$, following Sokal and Braumann.³¹ The resulting unbiased statistic is V^* .

In Table 2, values for both CV and V^* are provided for variables including cranial capacity, vault length, basibregmatic height, several cranial breadths, supraorbital torus thickness, upper facial dimensions, and the hard palate. Some of these measurements relate to the neurocranium and the skull base, for which intraspecific variation is expected to be low in hominoids.³² Dimensions of the upper face tend to be more variable. The palate, like the lower jaw, is subject to relatively high magnitudes of mechanical strain and is therefore likely to exhibit the most variation, arising as a consequence of differences in individual body size and sex dimorphism. In general, those variables that consistently show little within-species variation are considered to have greater utility as indicators of taxonomic heterogeneity (higher taxonomic valence).

In Table 2, the mid-Pleistocene hominins, treated as a group, are compared to both *Homo erectus* (*sensu lato*) and *Homo sapiens*. Here *Homo erectus* is considered to be a geographically widespread species, with representatives in Africa and Asia. Crania included in the analysis are drawn from Olduvai Gorge, Koobi Fora, Nariokotome, Daka

TABLE 2. Relative Variation in Dimensions of the Cranial Vault, Base, and Facial Skeleton for Archaic *Homo* and Recent Humans

	Mid-Pleistocene <i>Homo</i>			<i>Homo erectus</i>			<i>Homo sapiens</i>	
	N	CV	V*	N	CV	V*	Males	Sexes Combined
							CV	V*
Cranial capacity	8	8.4	8.6	32	14.0	14.1	~13.7	–
Glab-opisthocranion	6	5.7	5.9	20	7.6	7.7	3.2	4.0
Basion-bregma ht.	6	8.2	8.5	9	7.9	8.1	3.7	4.7
Max br.	7	6.0	6.2	22	6.5	6.6	3.6	4.5
Max. biparietal br.	5	3.5	3.7	24	6.8	6.9	–	4.1
Max. frontal br.	8	5.2	5.3	19	10.4	10.5	4.1	5.0
Min. frontal br.	8	3.8	3.9	22	15.8	16.0	–	–
Biauricular br.	7	8.9	9.2	24	7.7	7.8	4.1	4.2
Biauricular br.	7	11.2	11.6	19	5.3	5.4	3.6	4.6
Supraorbital torus thick.	9	23.8	24.4	8	26.5	27.3	–	–
Nasion-prosthion	5	4.9	5.1	5	5.8	6.1	5.9	6.6
Biorbital chord	8	8.1	8.3	9	10.7	11.0	3.4	5.5
Midorbital chord	6	8.9	9.3	5	15.1	15.8	–	–
Bimaxillary chord	5	8.9	9.3	7	8.1	8.4	4.7	–
Orbit br.	6	6.7	7.0	7	9.1	9.4	4.0	4.2
Orbit ht.	6	10.8	11.2	7	11.2	11.6	5.8	6.7
Cheek ht.	6	13.2	13.7	7	15.5	16.0	9.3	11.2
Nasal br.	6	18.4	19.1	7	12.4	12.8	6.8	8.1
Nasal ht.	5	8.4	8.8	6	5.0	5.2	5.3	6.7
Palate br.	5	7.8	8.2	5	12.4	13.0	4.9	7.1

(Bouri), Buia, Dmanisi, Trinil, Sangiran, Sambungmacan, Ngandong, Gongwangling, Zhoukoudian and Hexian. The data given for *Homo sapiens* relate to recent people. Values of V* for mixed-sex samples are taken from Wood and Lieberman³² or calculated from measurements for 40 modern Italian crania supplied by R. Kruszynski. CVs for males only are computed from the grand means and within-group standard deviations reported for 17 populations by Howells.²⁷

For *Homo sapiens*, most measurements of length, height, and width of the neurocranium exhibit low levels of variation. CVs for males range from 3.2 to 4.1, while V* for a mixed sample reaches 5.0. Biauricular breadth also has a low coefficient. As expected, dimensions of the upper face tend to be somewhat more variable, with the figures for orbit height (V* = 6.7), nasal breadth (V* = 8.1), cheek height (V* = 11.2), and palate breadth (V* = 7.1) being especially elevated. Cranial capacity displays a higher level of variation, even within samples restricted entirely to male individuals.

In the case of the mid-Pleistocene hominins and *Homo erectus* (*sensu lato*), the same neurocranial and fa-

cial dimensions are associated with generally greater values of CV and V*. However, such comparisons are not straightforward. Methods for testing whether measures of relative variation are significantly different in fossil and modern reference populations have been explored carefully,^{33,34} making it clear that few are reliable. Ratios of squared CVs can be used as an F-test if the data are normally distributed. Also, a weighted-scores method developed by Fligner and Killeen³⁵ has been shown to be quite powerful if N is greater than seven.³⁴ Here it is very likely that there are departures from normality and, for most variables, the mid-Pleistocene sample is quite small. Given these constraints, it is probably best to comment on the CV or V* values without attempting to draw any conclusions as to statistical significance.

Perhaps the most revealing comparisons are between the two Pleistocene assemblages. In both groups, supraorbital torus thickness is highly variable. This region exhibits the largest CV and V* values in Table 2, and the degree of supraorbital development does not seem to carry high taxonomic valence.³⁶ Measurements of the upper facial skeleton, includ-

ing the midorbital chord, orbit height, nasal breadth, and cheek height, are quite variable in *Homo erectus*, as is palatal breadth. Relative variation in orbital, nasal, and cheek dimensions is also high in the mid-Pleistocene group, suggesting that these features are not a good guide to taxonomic heterogeneity. Upper facial height is associated with a reduced value for CV (and V*) in both assemblages, and here the archaic hominins are comparable to modern humans. As expected, neurocranial dimensions are less variable. Apart from absolute volume and frontal widths, measurements of the braincase display lower coefficients. Biauricular breadth is more variable in the mid-Pleistocene population than in *Homo erectus*, but most of the CV (and V*) values relating to the vault are of about the same magnitude in both groups. An overall impression obtained from Table 2 is that dimensions of the neurocranium, upper facial height, and some facial breadths exhibit comparable between-sample relative variability. In many instances, the coefficients are highest in *Homo erectus*. So there is no metric evidence to suggest that the mid-Pleistocene assemblage is more variable than one widely

TABLE 3. Relative Brain Size, Vault Proportions, and Cranial Angles in Archaic *Homo* and Recent Humans

	Mid-Pleistocene <i>Homo</i>			<i>Homo erectus</i>			<i>Homo sapiens</i>		
	N	Mean	Range	N	Mean	Range	World Wide	Zulu Males	Zulu Females
Relative brain size index ^a	6	3.0	2.7–3.3	6	2.6	2.5–2.9	3.3	–	–
Cranial height/length index ^b	4	63.7	60.5–67.5	7	60.8	55.0–67.2	72.7	72.2	71.7
Cranial breadth/height index ^b	5	119	112–130	7	126	116–141	105	100	102
Globularity index ^b	4	49.3	42.8–53.3	7	46.7	42.8–52.6	55.4	52.3	52.7
Postorbital constriction index	7	90.0	79.0–101.7	8	80.1	71.5–91.1	–	96.3	98.0
Frontal breadth index	7	89.6	83.0–92.8	14	84.4	75.4–91.8	–	84.5	83.9
Frontal angle	5	140.8	139–145	7	140.5	138–146	129.2	126.3	125.1
Occipital angle	5	106.8	97–114	10	101.5	95–108	118.8	121.6	119.8
Occipital scale index	6	79.2	68.6–90.0	13	97.2	68.1–119	–	67.2	–

^a Relative brain size is calculated as the cube root of cranial capacity/orbit height, following Rightmire.⁴⁹

^b Indices describing vault proportions are calculated from glabella-occipital length, maximum cranial breadth, and basibregmatic height. Globularity = (breadth × height)/length² (following Lieberman, McBratney, and Krovitz.⁴¹).

accepted as the basis for recognizing a single hominin species.

STRUCTURE OF THE BRAINCASE

If the hypothesis that the African and European crania can be placed in one hypodigm is not rejected, then another question is how, or to what extent, this group differs from other, closely related taxa. As has been noted, the mid-Pleistocene hominins differ from *Homo erectus* in a number of discrete traits. In this section, additional comparisons are presented with the purpose of identifying aspects of cranial form that discriminate among the archaic and recent groups. Emphasis is placed on measures of the cranial vault, as these are the features that tend to display low levels of intragroup variation. Dimensions of the upper facial skeleton and lower jaw are frequently more variable, and are therefore less likely to provide information useful for defining species.

Several indices that can be calculated for the more complete crania, as well as ratios describing frontal and occipital proportions, and angles registering sagittal curvature, are listed in Table 3. One index measures relative brain size. A simple method for expressing size in relative terms (without the intermediate step of calculating body mass) uses the ratio of the cube root of volume to orbital height (where the result is multiplied by 100). This index varies from 2.50 to 2.95 for six representatives of *Homo erectus*. Bodo and Broken Hill also have values in the range

observed for the *erectus* group. Both of the African fossils have large orbits; this drives their ratios downward even though absolute brain volumes are substantially increased. Somewhat higher values occur among the European crania. Especially for Steinheim and Arago, where the orbit is quite small, relative brain size is inflated in comparison to that in *Homo erectus*. The mean index of 3.04 for six Middle Pleistocene individuals differs significantly from the mean of 2.68 calculated for *Homo erectus* ($t = 2.95$, $P = .014$). Application of the nonparametric Mann-Whitney U test gives the same result ($z = 2.16$, $P = .030$). However, the range for the mid-Pleistocene group overlaps with that in modern humans. As measured on a worldwide basis,³⁷ *Homo sapiens* has a mean brain volume of 1349 cm³. Coupled with average orbit height for males and females given by Howells,²⁷ this result yields a relative size index of 3.3.

Height/length and breadth/height indices document the expected trends. *Homo erectus* crania are relatively low and broad, while the *Homo sapiens* braincase tends to be higher, with reduced maximum breadth. There are large differences between the means, and little overlap. The mid-Pleistocene group is intermediate in form but generally closer to *Homo erectus*. A third index quantifying overall cranial globularity clearly distinguishes both *Homo erectus* and mid-Pleistocene humans from *Homo sapiens*. Anatomically modern people have rounded crania,

and this feature is held to be diagnostic for the species.^{38–40} Using a closely similar statistic, Lieberman, McBratney, and Krovitz⁴¹ find that there is, in fact, no overlap in ranges between *Homo sapiens* and a sample of “archaic” *Homo sp.*, including Neanderthals, along with Bodo, Broken Hill, and Petralona. Thus it can be argued that neurocranial globularity is an important structural autapomorphy evolved in anatomically modern humans. However, it is evident from Table 3 that this index is not efficient in discriminating among the Pleistocene assemblages.

Frontal narrowing is expressed in two indices. The ratio of least to maximum frontal breadths is ca. 84 in both *Homo erectus* and *Homo sapiens*, but is slightly higher in the mid-Pleistocene group. The ratio of least frontal breadth to the biorbital chord is more informative. Values for *Homo erectus* are low, indicating frontal narrowing. For the mid-Pleistocene hominins, the mean index of postorbital constriction is 90.0. Relative broadening of the frontal is apparent for many of these individuals. Although a few crania, including Broken Hill and Petralona, fall within the range observed for *Homo erectus* in this feature, there is an approach to the condition in *Homo sapiens*. However, the forehead remains relatively flat, while in modern people the frontal angle is much reduced, reflecting pronounced sagittal curvature.

The contour at the rear of the braincase is measured by the occipital angle. This angle is low (average

ca. 101°) for ten *Homo erectus* crania, confirming that the occiput is strongly flexed. An increase in the angle for the mid-Pleistocene assemblage suggests more rounding of the posterior vault, but the sample ranges overlap. In recent humans, the angle is much higher (ca. 120°), and here there is substantial separation relative to the archaic condition. The scale index measures the relative lengths of the upper and lower (nuchal) portions of the squamous occipital. A high index suggests that the nuchal area is expanded relative to the occipital plane above. For *Homo erectus*, the area of nuchal muscle attachment generally is extensive. This is confirmed by the mean index of ca. 97 and maximum value of 119 reported in Table 3. Proportions change in the mid-Pleistocene group, where the index drops by 18 points, but again there is overlap in sample ranges. In *Homo sapiens*, the upper scale dominates the nuchal surface. Thus the index is reduced.

The information in Table 3 can be summarized as showing that the mid-Pleistocene hominins are intermediate in cranial form between *Homo erectus* and *Homo sapiens*. *Homo erectus* has a low vault with a broad base, marked postorbital constriction, a flat frontal, and a flexed occipital with an expanded nuchal plane. These proportions are reflected in a low globularity index. Mid-Pleistocene skulls from Africa and Europe are relatively higher and less broad, although the position of maximum breadth is frequently low, near the supramastoid crests. Frontal narrowing is reduced, the occipital angle suggests more rounding of the posterior vault, and the upper scale is always larger than the nuchal plane. Both absolute volume and a simple index of relative brain size show increases in comparison to *Homo erectus*. *Homo sapiens* exhibits a more globular neurocranium, markedly departing from the other taxa in this feature. As has been amply documented in other studies, modern skulls are also distinguished by attenuation or loss of the supraorbital tori, reduction in size of the facial bones, retraction of the facial

skeleton, and formation of a bony chin.^{42–44}

Although the mid-Pleistocene hominins appear to be intermediate in their morphology, they nevertheless display some traits that are primitive (*erectus*-like) and others that are derived. This condition has sometimes been attributed, without further comment, to “mosaic evolution.”¹ However, it is important to note that Broken Hill, Bodo, the Sima specimens, Arago, Petralona, and the other crania consistently display a suite of characters that is unique. Brain size scaled to body mass differs significantly from that in *Homo erectus*. Overall vault form is *erectus*-like, but clear structural distinctions include reduced postorbital narrowing, occipital rounding, and a shift in occipital proportions. Another key variable is likely to be the cranial base angle (not included in this analysis). Individuals such as Broken Hill display more flexion of the anterior cranial base relative to the sphenoid clivus than is present in *Homo erectus*. Flexion of the base, along with increasing brain size, seems to provide a structural basis for both greater cranial globularity and reorientation of the facial skeleton.⁴¹ These changes culminate in the morphology evident in modern humans.

DISCUSSION

This review of the morphology of Middle Pleistocene hominins raises several points that can usefully direct a discussion of systematics and species-level taxonomy. First, the more complete specimens from Africa resemble their European contemporaries. There is variation within both groups, which presumably is attributable to sex dimorphism and differences among local populations. But Broken Hill is very much like Petralona in many of its features. All of the crania share a morphology that sets them apart from *Homo erectus* and differentiates them from modern humans. This pattern encompasses discrete anatomical details (thinning of the tympanic plate, a sphenoid spine), components of the cranium (nasal aperture, shape of the tempo-

ral squama, and occipital proportions), and relative brain size. Second, comparisons of CV and V* for several measurements suggest that variation within the mid-Pleistocene assemblage is not excessive relative to that observed in other taxa. Especially for some facial dimensions, values of CV and V* are higher than in samples of modern humans. However, magnitudes of variation within the mid-Pleistocene group are evidently not greater than in *Homo erectus* (*sensu lato*). On the strength of these findings, it can be proposed that the crania from Africa and Europe constitute a single, species-level hypodigm.

If all of the earlier Middle Pleistocene fossils, including the Mauer mandible, belong to a single lineage, then this species should be called *Homo heidelbergensis*. Also, it can be argued that later in the Middle Pleistocene, some populations of this species dispersed northward within Europe, where they were repeatedly subject to episodes of extreme cold. During glacial advances and retreats occurring over several hundred Ka, 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 *Homo heidelbergensis* in Africa were becoming more like modern humans. Fossils from Irhoud in Morocco, the Omo KHS locality in southern Ethiopia, Herto in the Middle Awash region, and Laetoli in Tanzania document this evolutionary progression toward *Homo sapiens* (Fig. 5a).

An alternative reading of the evidence has been advanced by Bermúdez de Castro and coworkers² Arsuaga and colleagues,³⁰ and authors of *The First Europeans*.²¹ Here the remains from Gran Dolina are attributed to *Homo antecessor*. This species is viewed as a descendant of African *Homo erectus* (Fig. 5b). *Homo antecessor* is presumed to have given rise to *Homo heidelbergensis*. In this scenario, the *heidelbergensis* lineage was confined exclusively to Europe, where its members gradually acquired the large nasal aperture, more projecting facial skeleton,

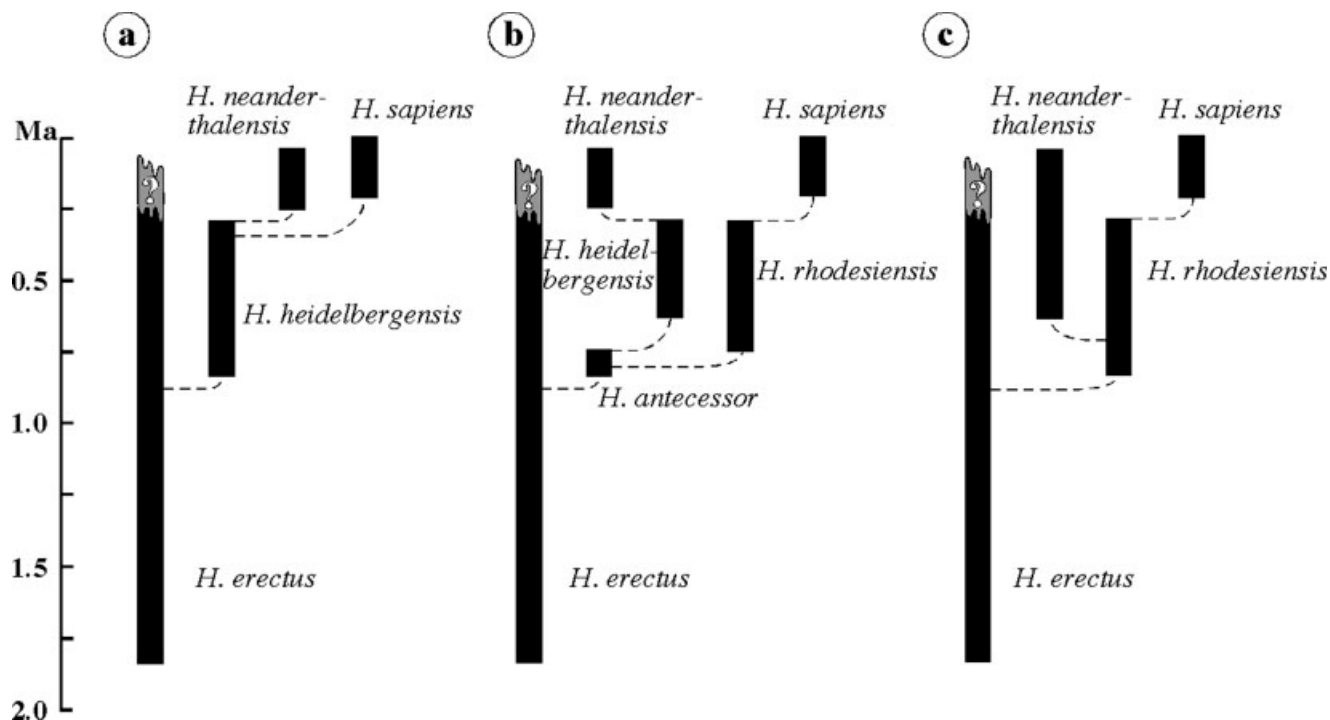


Figure 5. Alternative evolutionary trees showing the relationships among *Homo erectus*, Middle Pleistocene hominins, Neanderthals, and modern humans. Solid bars depict the duration (first appearance date and last appearance date) estimated for each species. Broken lines indicate likely links of ancestors with descendants. (a) Scenario showing *Homo heidelbergensis* to be descended from *Homo erectus*. After spreading widely across Africa and western Eurasia at the beginning of the Middle Pleistocene, *Homo heidelbergensis* was the antecedent to both European Neanderthals and recent humans. (b) Interpretation in which *Homo antecessor* is recognized as the descendant of *Homo erectus*. In turn, *Homo antecessor* evolved into *Homo heidelbergensis* in Europe and this chronospecies encompassed the Neanderthals. In Africa, *Homo rhodesiensis* was ancestral to *Homo sapiens*. (c) Hypothesis in which *Homo rhodesiensis* was the species from which all later hominins evolved. In Europe, a Neanderthal lineage can be recognized early in the Middle Pleistocene, whereas in Africa, *Homo rhodesiensis* was the antecedent to modern humans. Currently, the fossil evidence can be read to favor either tree (a) or (c); hypothesis (b) is problematical.

and other morphology of the Neanderthals. This is the accretion hypothesis.^{45,46} Also, rather quickly after its first appearance, *Homo antecessor* must 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 and perhaps even capable of exchanging genes with their European contemporaries, they are not assigned to *Homo heidelbergensis*. Instead, the African fossils are lumped in a separate species, for which the nomen *Homo rhodesiensis* is available.

Resolving the status of *Homo antecessor* will depend largely on the outcome of excavations that are continuing in the TD6 levels at Gran Dolina. Indeed, recent discoveries are prompting changes in the inter-

pretation offered earlier. Carbonell and colleagues⁴⁷ report that a hemimandible found in 2003 resembles Asian rather than African *Homo erectus*. The low corpus and relatively gracile morphology are said to be particularly like specimens from Zhoukoudian, suggesting the possibility of a phylogenetic link between Gran Dolina and China. Also, the new ATD6-96 jaw differs in some features from the more robust Middle Pleistocene European individuals. Thus, Carbonell and coworkers⁴⁷ now deny any role for *Homo antecessor* in the ancestry of *Homo heidelbergensis* (*sensu stricto*) and the Neanderthals. The extent to which these new claims can be supported is presently uncertain.

For the moment, the more important question is whether any of the other early European fossils display traits that tie them to a Neanderthal

lineage, thus justifying their exclusion from Middle Pleistocene populations in Africa. Analyses presented here and elsewhere⁴ show that crania from the Sima, Arago Cave, and Petralona are like Bodo and Broken Hill in indices of vault form, morphology of the cranial base, and massive build of the face. From a structural perspective, and when allowances are made for individual variation, there are essentially no differences that can be used to sort the fossils to distinct groups. Therefore, an argument for recognizing separate hypodigms must rest on the identification of discrete characters (Neanderthal apomorphies) that are expressed in ancient European specimens but absent in contemporary Africans.

Claims for Neanderthal-like features have been made in the case of the Mauer jaw,⁴⁸ the Arago material, and specimens such as Petralona

and Steinheim, which are less securely dated. The Mauer mandible has most often been regarded as “primitive” in its anatomy. In this massively constructed and chinless specimen with internal transverse tori and multiple mental foramina, it is difficult to discern any clear signs of Neanderthal affinity. The Arago face is cracked and subtly deformed. It can be demonstrated that there is midfacial protrusion, but a relatively low zygomaxillary angle is manifest also in Broken Hill. Cresting of the Arago nasal sill does seem to constitute a resemblance to later Neanderthals. By themselves, these observations are not very compelling. However, fossils from the Sima de los Huesos are much more numerous and remarkably well preserved. New dating places this population close to the beginning of the Middle Pleistocene (>530 Ka ago), and the Sima crania exhibit traits that might be expected to occur very early in the evolution of the Neanderthal lineage. In the supraorbital region, elevated nasal saddle, and the occiput, there is morphology that seems to distinguish the Sima specimens from penecontemporary Africans such as Bodo and Elandsfontein.

On the basis of this Atapuerca evidence, it can be argued more convincingly that the European hominins represent a unique hypodigm. If even the oldest Middle Pleistocene fossils display traits that link them with Neanderthals, then it will be appropriate to include all of these groups within a single lineage (Fig. 5c). Bermúdez de Castro and coworkers² acknowledged this as a possibility but elected to retain the nomen *Homo heidelbergensis*, recognizing that while this chronospecies has many primitive traits, it is directly ancestral to later Pleistocene populations. An alternative taxonomic scheme is to lump the European specimens (excepting Gran Dolina?) in *Homo neanderthalensis*, as advocated by Hublin.⁴⁶

If the European assemblages are dealt with in this fashion, then it is no longer possible to group the Sima or Arago people with African hominins, despite their obvious resemblances. All of the anatomical simi-

larities must be treated as shared primitive features or as examples of homoplasy. Here there is a conundrum. Mid-Pleistocene Africans are to be regarded as a distinct lineage, descended from a stem such as *Homo antecessor* or evolved directly from *Homo erectus*. If this group incorporates the find from Broken Hill, it can be called *Homo rhodesiensis*.¹⁰ The hypodigm is composed principally of skulls, and this material must supply the information used in any species definition. It is quite possible to distinguish *Homo rhodesiensis* from *Homo erectus* or from *Homo sapiens*, but much of this critical morphology mirrors that of the early Europeans. There is little, if any, basis for a full differential diagnosis.

Also, within such a systematic framework, where species are keyed to geographic regions, there is the question of how to view the Middle Pleistocene record of the Far East. Fossils like Dali differ from *Homo erectus* and display many of the same features that characterize early representatives of *Homo neanderthalensis* (*sensu lato*) and *Homo rhodesiensis*. The remains from China are not covered in this review, but it is essential that they be considered in any comprehensive discussion of the taxonomy for Pleistocene hominins.

In summary, there are two reasonable phylogenetic hypotheses that must be studied further. One holds that all of the European fossils make up a single lineage (Fig. 5c). Such a lineage can be traced back at least to the Sima population, present in the Atapuerca region near the beginning of the Middle Pleistocene. The appropriate species nomen is *Homo neanderthalensis*. This hypothesis will be strengthened if it can be demonstrated that the Sima individuals display “true” rather than “incipient” Neanderthal autapomorphies or if similar diagnostic morphology can be confirmed in other early European assemblages. An alternative view lumps both European and African fossils in the geographically widespread species *Homo heidelbergensis* (*sensu lato*) (Fig. 5a). Support for this hypothesis comes from an analysis of relative variation, suggesting that values of CV and V* in the

mid-Pleistocene assemblage are not excessive in comparison to those for *Homo erectus*. One way to falsify this hypothesis will be to show that there is significantly less metric variation in other hypodigms judged to document stable hominin taxa. Only if this second hypothesis is rejected and the first supported will it be necessary to consider the case for *Homo rhodesiensis*. There are problems with defining a Middle Pleistocene African species that is separate from European or East Asian lineages existing in the same time interval. These difficulties will be ameliorated if it can be demonstrated that Bodo, Broken Hill, and Elandsfontein, while resembling early Europeans, also possess autapomorphies and/or derived traits shared only with *Homo sapiens*. If *Homo* was undergoing speciation at the beginning of the Middle Pleistocene, then the task of identifying populations that lie at the roots of several closely related lineages will not be easy.

ACKNOWLEDGMENTS

For access to fossil materials in their care, I thank my friends and colleagues at The Natural History Museum in London, the Muséum National d'Histoire Naturelle in Paris, the Naturkunde Museum in Stuttgart, the University of Thessaloniki, the National Museum of Ethiopia, the National Museum of Tanzania, the National Museum in Bloemfontein, and the Iziko South African Museum of Cape Town. Robert Kruszynski kindly shared with me his measurements of recent human crania. Richard Klein offered valuable comments on a draft of the manuscript. Danielle Rogers helped with photographs and Anne Hull drew the illustration. The Boise Fund, the Leakey Foundation, and the Eckler Fund of Binghamton University (SUNY) provided grant support. For the invitation to attend the Stony Brook Workshop in Human Evolution, I am grateful to John Fleagle, John Shea, Frederick Grine, and Richard Leakey.

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