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The human cranium from Bodo, Ethiopia: evidence for speciation in the Middle Pleistocene?

The cranium found at Bodo in 1976 is derived from Middle Pleistocene deposits containing faunal remains and Acheulean artefacts. A parietal recovered later must belong to a second individual, probably representing the same taxon. The cranium includes the face, much of the frontal bone, parts of the midvault and the base anterior to the foramen magnum. It is clear that the Bodo hominids resemble *Homo erectus* in a number of characters. The facial skeleton is large, especially in its breadth dimensions. The braincase is low and decidedly archaic in overall appearance. Individual bones are quite thick. Behind the projecting supraorbital torus, the frontal profile is flattened. The midline keel and bregmatic eminence are characteristic of *H. erectus*. Frontal narrowing is less pronounced than in crania from Olduvai and Koobi Fora but slightly greater than in some Sangiran specimens. The parietal displays a prominent angular torus. Whether the inferior part of the tympanic plate was substantially thickened cannot be checked, but in the placement of its petrous bone and the resulting crevice-like configuration of the foramen lacerum, the Bodo hominid resembles *H. erectus*. Other traits seem more clearly to be synapomorphies uniting Bodo with later Middle Pleistocene populations and recent humans. Cranial capacity is substantially greater than expected for *H. erectus*. Among traits related to this size increase may be counted the broader midvault with signs of parietal bossing, a high contour of the temporal squama and perhaps some details of cranial base anatomy. Derived features of the frontal bone and face likely include division of the brow at mid-orbit and its attenuation laterally. The "crista nasalis" falls vertically from rhinion so as to give the nasal aperture an erect appearance, characteristic of modern humans. Another synapomorphy is the positioning of the incisive canal relative to the hard palate. Sorting the Middle Awash specimens is difficult. The cranium is incomplete, and individuals are always variable in their anatomy. Nevertheless, it seems most reasonable to group Bodo with Broken Hill and similar Middle Pleistocene specimens from Africa and Europe. This entire assemblage can be referred to *Homo heidelbergensis*. It is clear that *H. heidelbergensis* overlaps in time with late populations of *H. erectus*. The Middle Awash hominids may be approximately contemporary with the people at Ternifine (Tighenif) and upper Bed IV at Olduvai Gorge. The Bodo deposits probably antedate even the first signs of occupation at Zhoukoudian and are far older than sites such as Longtandong (Hexian) in China. The evidence is consistent with an episode of speciation occurring in Africa or western Eurasia and subsequent dispersal of *H. heidelbergensis*. This event occurred while more archaic people still inhabited much of the Far East.

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Introduction

Human fossils from the Bodo localities south of Hadar in the Middle Awash region of Ethiopia include a cranium collected in 1976, a left parietal bone picked up in 1981, and a piece of distal humerus. The three specimens were situated in the same stratigraphic horizon and are geologically contemporary. They are derived from Middle Pleistocene deposits containing faunal remains and stone artefacts. Hard sandy matrix initially found adhering to the orbits and nasal cavity and partly filling the interior of the braincase suggests that the cranium lay face down in the sediments, and probably the back of the specimen was exposed first by weathering and subsequently lost. A preliminary reconstruction of the face and adjacent

structures was carried out by Conroy *et al.* (1978). Following cleaning and realignment of these pieces, which were sent on temporary loan to Berkeley in 1982, the cranium was reassembled and later returned to the National Museum in Addis Ababa. The 1981 parietal fragment, also a surface find, must belong to a second individual, likely to represent the same taxon as the first. The 1990 humerus has still to be described and is not considered here.

The cranial parts have been the subject of several previous reports (Conroy *et al.*, 1978; Asfaw, 1983), and the presence of cutmarks in the facial region has been documented by White (1985, 1986). Recently Adefris (1992) has completed a more detailed anatomical study. The face and braincase are striking for their size and robust construction. Observers have commented on the thickened brows, great interorbital distance and wide nasal aperture, massive zygomatic bones, and broad, deep palate. In some features, such as the breadth and heavy buttressing of the face and very thick vault bones, there is a resemblance to *Homo erectus*. Conroy *et al.* (1978) suggest parallels to Chinese and Indonesian hominids, as well as to African specimens such as OH 9. Other traits are said to give the Bodo cranium a more modern appearance, and it has been likened particularly to the fossils from Broken Hill (now Kabwe) and Petralona. The latter are usually described as “archaic” *Homo sapiens*. Although no firm consensus has emerged, many workers have assumed that the Middle Awash people are on balance slightly more similar to our own species than to *H. erectus*.

This rather general assessment is here checked and extended. The present author has examined the specimens with several questions in mind. One is whether key characters diagnostic of *H. erectus* may be present. If such evidence is sparse, and the Bodo hominids cannot be linked securely to *H. erectus*, do they instead share with Broken Hill or other fossils a set of derived features that will permit attribution to another species? Should the latter be identified as *H. sapiens*? The present author’s hope in undertaking this research is to comment on the transition or speciation “event” giving rise to the first populations recognizable as more advanced than *H. erectus*. How this process occurred is poorly understood, but it is possible that the transition took place in Africa, rather than in the Far East or more generally across all parts of the Old World.

Geological setting of the Bodo discoveries

Localities at Bodo and elsewhere in the Middle Awash region were explored between 1975 and 1978 by members of the Rift Valley Research Mission in Ethiopia (RVRME), organized by J. E. Kalb. Pieces of the 1976 cranium were found scattered on the surface at a site adjacent to one of the seasonally dry tributaries of the Awash River. Following discovery of these fragments, excavations were carried out in order to expose the local stratigraphy, and a number of additional fossils and artefacts were collected. In 1981, a team led by J. Desmond Clark returned to the Middle Awash for 2 months, to continue archaeological surveys, conduct test excavations, and obtain larger samples for biostratigraphic analysis (Clark *et al.*, 1984). During this period, the Bodo parietal bone was picked up, ca. 400 m from the site of the original hominid. From 1982 to 1989, no further fieldwork was undertaken, but in 1990 research in the study area was resumed, under the direction of Clark and T. D. White.

Deposits yielding the hominid fossils were designated informally as the Upper Bodo Sand Unit (UBSU) by Kalb *et al.* (1980) and subsequently referred to the Bodo Member of the Wehailu Formation by Kalb *et al.* (1982*b*). These conglomerates and sands contain numerous assemblages of mammalian bones and Acheulean artefacts. Fauna collected by the RVRME has been compared with that from Bed IV at Olduvai and the Ologesailie

Formation (Kalb *et al.*, 1982*a*). If the UBSU is approximately equivalent to the upper part of the Ologesailie Formation, then an early Middle Pleistocene date is most likely. Geochemical correlations and radiometric results obtained for tuffaceous horizons indicate that the upper members of the Ologesailie Formation are older than previously thought, with an age between 0.7 and 0.5 Ma (Bye *et al.*, 1987; Deino & Potts, 1990).

Recent work has emphasized the locally complex nature of the Middle Awash lithostratigraphic succession. As a consequence of faulting and lateral changes in sediment composition, it is often difficult to establish correlations between beds exposed in different areas, and the Berkeley team no longer uses the nomenclature established by the RVRME. Nevertheless, biostratigraphic assessments based on extensive collections of vertebrate fossils confirm a Middle Pleistocene age for the sands containing the Bodo hominids. New radiometric dates reported by Clark *et al.* (1994) support this biochronology. The UBSU is part of a 15–20 m thick series of deposits now designated informally as unit u–t. Prior to faulting in the area, these sediments appear to have been in place atop a lower unit u, which contains a tuff that has been dated using the laser-fusion method. Samples of this vitric horizon obtained at different localities give argon–argon ages of 0.74 and 0.55 Ma, and pooling of results yields a weighted mean age for unit u of 0.64 Ma. Clark *et al.* (1994) consider that the evidence from fauna, archaeology, and laser-fusion determinations is consistent with an age of ca. 0.6 Ma for the Bodo hominids.

Anatomy of the cranium

As presently reconstructed, the Bodo cranium consists of the facial skeleton including the entire left orbit and interorbital region, some of the right orbit, the left cheek, all of the nasal cavity, the nasoalveolar clivus, most of the palate, and some broken roots but not the crowns of the maxillary dentition (Figure 1). Much of the frontal bone is present, although there are gaps in the squama. Parts of both parietals and the left temporal including the medial aspect of the glenoid cavity are intact, and the cranial base is reasonably complete anterior to the foramen magnum. All in all, the specimen is well preserved and can provide a lot of information. Of the 1981 parietal, only the posteroinferior quadrant is available. Nevertheless, this bone helps to fill in some of the anatomical detail otherwise missing from the 1976 individual. Descriptions of both hominids have been published elsewhere, so the present author's account will emphasize the morphology of specific regions, treated from a comparative standpoint.

The face

Below the prominent glabellar region, nasion is deeply depressed. The entire interorbital pillar is massively constructed, as noted by other workers. The nasofrontal and frontomaxillary sutures together describe a nearly horizontal course, angling downward just at the lacrimal crests. Width of the nasal bridge as measured between these crests is about 28 mm. The nasal bones themselves are narrow superiorly, having a combined breadth of only 9 mm. These elements become progressively broader as they descend. Superiorly, there is some blunt keeling at the internasal junction. Here the adjacent surfaces of the maxillae are flat or even slightly hollowed, so as to give the nasal saddle a tent-like cross section. Keeling is not evident inferiorly, where the bridge is more rounded.

In side view, the nasal profile is concave over most of its length, although the bones seem to dip slightly at their tips (Figure 2). The lateral margin of the piriform opening is nearly vertical



Figure 1. Anterior and oblique facial views of the Bodo cranium. The broad frontal is slightly keeled posteriorly and carries supraorbital tori that are especially thickened centrally. A projecting glabellar region, wide interorbital pillar and deep zygomatic bones give the entire face a massive appearance, similar to that of *Homo erectus*. Other features including the vertical border of the nasal aperture seem to be apomorphies shared with later Middle Pleistocene hominids and *Homo sapiens*.

and joins the floor of the aperture at a point directly below the terminus of the overhanging nasal roof. This is the condition characteristic of modern humans. It differs from the morphology of *H. erectus*, where the piriform margin (“crista nasalis”) slopes forward, as described by Weidenreich (1943). The clivus appears relatively flat. Some bone is missing from the surface of the maxillary alveolar process, and restoration would result in prognathism associated with the roots of the anterior teeth. But it is not likely that there was any pronounced convexity of this contour in the midline.

At the entrance to the nose, there is a blunt ridge which demarcates the external surface of the clivus from the inclined nasal floor. This ridge, corresponding to the spinal crest of McCollum *et al.* (1993), is not continuous with the lateral margin of the aperture but passes behind it on either side, to subside into the maxillary wall. Centrally, there is a large rugged spine, partly broken away. This feature extends posteriorly as an incisive crest but has not been fully cleared from matrix still filling the interior of the nasal cavity. The rim of the aperture itself is sharp rather than rounded, and lateral crests do not encroach onto the nasal sill. Again because of damage, it is difficult to ascertain whether a canine jugum was well developed, but this pillar could not have been especially prominent and did not reach far upward. The bone bordering the nose is flattened. Even superiorly, there is little or no eversion of these surfaces.

No canine fossa is apparent. The maxillary wall is generally inflated, but just below the infraorbital foramen there are traces of a shallow groove. This groove is quickly lost in an area of missing cortex. Probably an elongated vertical furrow comparable to that described by Weidenreich (1943) for *H. erectus* was not present. In keeping with the robust construction of



Figure 2. Lateral views of the crania from Bodo and Broken Hill. The two Middle Pleistocene specimens are probably similar in endocranial volume. They resemble one another in overall proportions of the braincase and in numerous anatomical details.

the face, the cheek itself is very deep. Minimum height taken on the maxilla is 33.5 mm, while the distance between the infraorbital margin and the masseter attachment exceeds 34 mm. Total height of the zygomatic bone is at least 60 mm.

The lower margin of the orbit is thin medially, where it approaches the lacrimal fossa. This rim is blunted laterally, and here the contour of the cheek is convex. Between the orbital margin and the zygomaxillary suture, there is an area of swelling, reaching outward to round off the entire malar "angle". Several of the parallel striations observed by White (1986) pass over this region. The anteroinferior aspect of the cheek is retracted slightly, so that the

masseteric origin is set directly below, rather than forward of, the border of the orbit. Posteriorly, there is damage to this surface, and the temporal process of the zygomatic bone is missing. There is no sign of any malar tubercle. The zygomaticoalveolar crest springs from a position above the M^1 roots. This pillar follows a low curve, becoming nearly horizontal at its lateral extent. The incisure itself can be described as shallow rather than strongly flexed.

The palate must have been long and moderately deep. The alveolar process is partly complete on the left side, where the broken roots of M^1 to M^3 are still in place. Enough of the hard palate is preserved anteriorly to show that the opening to the incisive canal is situated 6–8 mm behind the septum separating the central incisor sockets. The intervening space is filled by a narrow midline groove. The canal is blocked with matrix but appears to follow a nearly vertical path upward toward the nasal floor. Its orientation differs from that characteristic of *H. erectus* as described by Weidenreich (1943), where the canal passes posteriorly and is inclined relative to the alveolar plane.

The frontal region

The Bodo frontal bone is very broad and supports massive supraorbital structures. Glabella is rounded and strongly projecting. To either side, the superciliary elements trend upward, and it is here that maximal thickening occurs. Vertical thickness readings taken near the center of the orbit are close to those obtained for (some) *H. erectus*. The more lateral segments of the brow are set off from these central arches by faint depressions, in which the supraorbital foramina are situated. There is little supratatorial hollowing, although several shallow pits are present near the frontal midline. One of these is narrow and oval in form, and here the tabular bone seems to have been pushed inward rather than eroded. White (1986) suggests that there are signs of healing in these regions. Postorbital constriction is moderate. The temporal lines are slightly crested anteriorly and follow a low course toward the coronal suture. At the margin with the parietals, they are about 108 mm apart. In facial view, the middle portion of the frontal squama is rounded, while posteriorly there is a midline keel. This blunt ridge produces a strong eminence at bregma. Thickness of the vault measured at this landmark is 13 mm.

The midvault

The parietal bones are incomplete. On the left, the anterior portion is preserved, and both the coronal suture and some of the squamosal margin are present. Although its termination at pterion is difficult to locate, the coronal chord can be measured and is ca. 100 mm long. The corresponding arc is 111 mm. On the right, more of the parietal has been pieced together from fragments. The sagittal suture can be traced posteriorly, and here keeling is reduced. Only faint parasagittal ridges are apparent. The surface adjacent to the midline is flattened, but laterally there is significant development of a parietal tuber. Probably the maximum breadth of the vault would fall at this level, rather than lower at the supramastoid crests. On this point, Adefris (1992) disagrees. She finds biparietal width to be less than the bitemporal dimension, but her reasoning, like my own, is based on estimates rather than direct measurements. Most of the temporal bone is missing on one side.

Unfortunately, parietal length cannot be determined very accurately. Even on the right side, much of the sagittal border has been lost, and only a few millimeters of the lambdoid margin can be identified. These lambdoid serrations are situated about 12 mm behind the downcurving (and heavily weathered) temporal line and probably lie in the vicinity of, but posterior to, asterion. Bone thickness at this point is 9 mm.

Although the mastoid angle is missing, details of the anatomy of this region can be obtained from the separate parietal fragment described by Asfaw (1983). This specimen represents a second individual, collected from the same sandy deposits (UBSU) yielding the original cranium. It displays a number of archaic features. At asterion, the bone is very thick. There is a prominent, elongate angular torus, and the extension of the supramastoid crest onto the parietal surface is more marked than in Broken Hill and various specimens attributed to *H. erectus*. These traits suggest that the individual documented by the 1981 fragment may well be more robust than the first. Nevertheless, the piece provides information that is relevant to any discussion of the morphology of the Bodo hominids.

The greater wing of the sphenoid and some of the temporal bone are preserved on the left side of the braincase. The surface of the sphenoid is hollowed (and eroded) but not deeply excavated to form a channel for fibers of *musculus temporalis*. The squamous temporal is cracked and pitted. Clues concerning its original form are supplied by the parietal, which bears a fan-like area of roughening accompanied by striations. These striations indicate overlap by the temporal, pieces of which have now broken away. The area of overlap is quite extensive, as is the case also for the separate parietal fragment (Asfaw, 1983). From these traces, it is apparent that the squamosal suture followed a high course, dropping steeply downward posteriorly. This arched configuration is characteristic of humans more advanced than *H. erectus*. In the latter, the proportions of the temporal bone are distinctive, and the suture describes a rather straight path downward toward the parietal incisure.

Only the medial part of the mandibular fossa is intact, again on the left side. The ectoglenoid process and adjacent bone are missing, but a little of the zygomatic root is present posteriorly, over the auditory opening. This section of the root forms a projecting shelf, suggesting that the supramastoid crest was also strongly developed. The fossa itself is relatively shallow, and the surviving aspect of the articular eminence is flattened. Whether this eminence was prominent or bar-like laterally can no longer be determined. The entoglenoid process is simply a lip, present at the sphenotemporal suture. Here the sphenoid is damaged, but the pattern of breakage suggests that a spine extended inferiorly, as in recent *Homo*. The postglenoid process is large and flange-like. Nearly all of the tympanic plate has been lost, and the terminal piece that is still in place between the carotid canal and the sphenoid spine shows little detail. The bone has been eroded, and there is now no trace of any conical tubercle (the "process supraturbarius" of Weidenreich, 1943). A separate temporal fragment from the right side carries a little more of the tympanic plate, which is moderately thickened. Some of the petrous pyramid is preserved, and its apex seems mostly to fill the space between the basioccipital and the sphenoid greater wing. If these spacial relationships have not been distorted, then the foramen lacerum is narrow and restricted.

Comparisons to *H. erectus*

Any discussion of the affinities of the Bodo cranium should include comparisons to *H. erectus*, based on descriptive (non-metric) traits as well as measurements. It is important to note that *H. erectus* is here considered to have a geographic distribution including Africa as well as Asia. As described by Le Gros Clark (1964), Howell (1978), and Howells (1980), the hypodigm is made up of specimens from Java, Zhoukoudian and other sites in China, Ternifine (now Tighenif) in Northwest Africa, Olduvai Gorge, the Turkana basin, and probably Swartkrans in South Africa. This view has been challenged, on grounds that the oldest African crania lack key features developed by the Asian populations. These differences have prompted Andrews

(1984) and Tattersall (1986) to recognize two species and to suggest that *H. erectus* must be restricted geographically to the Far East. Groves (1989) and Wood (1991, 1994) concede that Dubois's species may be present in Africa but argue that the hominids from the Turkana basin should indeed be set apart from later *H. erectus*, on the basis of facial measurements and perhaps some aspects of temporal morphology. Wood now refers the Koobi Fora specimens to *Homo ergaster*. The present author agrees that there is variation among the various assemblages, but the fossils from the Turkana basin, Olduvai and other sites exhibit essentially the same set of traits as do those from the Far East (Rightmire, 1990). Characters said to be unique to the Asian populations are variable in their expression, and in fact most of them can be identified in the earlier East African material (Kennedy, 1991; Bräuer & Mbua, 1992; Bräuer, 1994). Probably just one polytypic species should be recognized.

H. erectus as broadly defined does possess a number of anatomical distinctions. The braincase is low in outline, with thickened walls. Endocranial capacity ranges from about 800 cc to over 1100 cc. Brows are projecting, even in smaller specimens likely to be females. The frontal may be keeled in the midline, and there is substantial postorbital constriction. The parietal bone is relatively short and carries an angular torus at its mastoid angle. The back of the cranium is sharply flexed, and there is always some expression of a transverse torus. Special features of the skull base include anteroposterior narrowing of the mandibular joint to produce a medial crevice and thickening of the tympanic plate. Where they are preserved, the facial parts are heavily constructed, but the bone surrounding the nose is thin and plate-like, and there is a low nasal bridge. Lower jaws and teeth are large by modern standards. As judged from the remarkably complete skeleton found at Nariokotome (Walker & Leakey, 1993), the pelvis is relatively narrow, and the femoral neck is long. These and other traits serve generally to describe *H. erectus* and to distinguish this species from modern humans.

Insofar as comparisons can be carried out, it is clear that the Bodo hominids resemble *H. erectus* in a number of craniofacial characters. The braincase is low and decidedly archaic in overall appearance. Individual vault bones are quite thick, both for the 1976 cranium and in the case of the 1981 parietal. For the latter, maximum asterionic thickness exceeds the values recorded for many other Middle Pleistocene individuals. The supraorbital torus is projecting and heavily constructed, especially in its central parts. Behind the brow, there is some supratatorial hollowing, and the frontal profile is flattened. The midline keel and bregmatic eminence are characteristic of *H. erectus*, as noted by Stringer (1984). Postorbital constriction expressed as the ratio of least frontal breadth to the biorbital chord is 80.7 mm (Table 1). Frontal narrowing is thus less pronounced than in crania from Olduvai and Koobi Fora but slightly greater than in Sangiran 17.

The full length of the parietal is not preserved, so proportions of the midvault cannot be assessed accurately. The parietal does display a prominent angular torus. As observed by Asfaw (1983), this feature and the supramastoid crest extension accompanying it are associated more frequently with *H. erectus* than with later hominids. Because of damage, some key aspects of mandibular fossa morphology are obscured. Whether the inferior part of the tympanic plate was substantially thickened and carried a petrosal spine and/or a process supratubarius cannot be checked. However, in the placement of its petrous bone and the resulting crevice-like configuration of the foramen lacerum, the Bodo cranium resembles *H. erectus*.

The facial skeleton is large, especially in its breadth dimensions. Width as measured across the orbits is greater than in other specimens listed in Table 1, but it is surpassed by the midfacial breadth. This is apparent even though the right cheek is missing, and the bizygomatic diameter cannot be reconstructed. These facial proportions differ from those of

Table 1 Measurements (mm) for the Bodo cranium and selected hominids of Early to Middle Pleistocene age

	Bodo	Broken Hill	Ndutu	Omo 2	Petralona	KNM-ER 3733	OH 9	Sangiran 17
Whole vault								
Basion-nasion length	107 ?	108	105 ?	—	110	107	119 ?	115 ?
Basion-prosthion length	121 ?	116	—	—	116	118	—	129 ?
Basion-bregma height	131 ?	127	—	—	126	111 ?	110 ?	114 ?
Maximum cranial breadth	148 ?	145	144 ?	147	165	142	150	161
Maximum biparietal breadth	148	145 ?	—	142 ?	151	131	139	142
Facial skeleton								
Nasion-prosthion length	88	90	—	—	91	81	—	75 ?
Malar (cheek) height	33.5	29	—	—	39	34	—	37
Biorbital chord	130	125	—	114 ?	126	109	123	115 ?
Nasion Subtense	22	26	—	—	23	12	23	—
Nasion angle*	142	135	—	—	140	155	139	—
Midorbital chord	76† ?	76	72†	—	75	73	—	—
Naso-orbital subtense	17 ?	20	—	—	17	15	—	—
Naso-orbital angle†	132 ?	124	—	—	131	135	—	—
Bimaxillary chord	134† ?	107	—	—	120	101	—	116 ?
Subspinale subtense	28 ?	33	—	—	36	17	—	—
Prosthion subtense	43 ?	?	—	—	>45	41	—	—
Orbit breadth	47.5	48	—	—	44	44 ?	—	38 ?
Orbit height	39	38	—	—	34	35	—	40 ?
Interorbital breadth	35 ?	28	23	—	36	26 ?	30 ?	—
Nasal breadth	43 ?	30	27	—	37	36 ?	—	—
Nasal height	62	57	—	—	68	53	—	—
Palate breadth	48 ?	46	—	—	50	—	—	—
Frontal bone								
Supraorbital torus thickness								
central	16	23	—	13.5 ?	21	8	19	17
lateral	7.5	16	10.5	8	14	9	14	13
Minimum frontal breadth	105	98	—	108	110	83	88	95
Maximum frontal breadth	119	118	112 ?	120 ?	120	110 ?	—	119
Frontal breadth index§	88.2	83.0	—	90.0 ?	91.6	75.4 ?	—	79.8
Biorbital chord	130	125	—	114 ?	126	109	123	115 ?
Postorbital constriction index††	80.7	78.4	—	94.7	87.3	76.1	71.5	82.6 ?
Frontal sagittal chord	125	120	—	—	110	104	—	118 ?
Frontal sagittal arc	144	139	—	—	129	119	—	—
Frontal subtense	23	21	—	—	20	18	—	—
Frontal angle	139	141	—	—	140	139	—	—

Broken Hill, Ndutu, Omo 2 and Petralona are usually considered to represent "archaic" Homo sapiens, whereas KNM-ER 3733, OH 9 and Sangiran 17 are referred to Homo erectus.

*Nasion angle measures prominence of nasion relative to the biorbital chord. Larger angles suggest transverse frontal flatness. Equivalent to NFA of Howells (1973).

†Measurement obtained by doubling the distance from the landmark on one side to the midline of the face.

‡Naso-orbital angle measures projection or height of the nasal profile relative to the lower margin of the orbits.

§Frontal breadth index is calculated as the ratio of minimum frontal breadth to maximum frontal breadth.

††Postorbital constriction index is calculated as the ratio of minimum frontal width to biorbital chord length.

both Broken Hill and early African *H. erectus* as represented by KNM-ER 3733, where the bimaxillary chord is relatively short. Bodo is more similar to Sangiran 17. General massiveness of the face is evident also in the width of the interorbital pillar and the height of the cheek, although these measurements do not align Bodo more closely with *H. erectus* than with advanced hominids of the Middle Pleistocene. By itself, the absence of a canine fossa does not help to sort the specimen, as a vertical furrow comparable to that found on the maxillary wall in (Asian) *H. erectus* cannot clearly be identified.

Although Bodo seems to share numerous characters with *H. erectus*, not all of these similarities carry equal weight in the assessment of relationships. Some traits are primitive, in the sense that they have a wider distribution among hominid species and cannot be treated as specialized or apomorphic for *H. erectus*. This is so, for example, in the case of the low vault profile, postorbital narrowing of the frontal bone, and robust construction of the midface, all of which are present in some members of the genus *Australopithecus* as well as early *Homo*. Other traits are more likely to be diagnostic for *H. erectus*. There is some divergence of opinion on this point, and slightly different lists have been advanced by Andrews (1984), Groves (1989), Rightmire (1990) and Wood (1991). Of the features generally agreed to be important, several are displayed by the Bodo hominids. These include midline keeling of the frontal squama (continuing at least to bregma), a strong angular torus on the parietal, and thickening of the individual bones of the braincase. The brow is also prominent, although it shows less development laterally than medially, and therefore, does not meet all of the specifications given by the authors cited above. On the strength of this evidence alone, however, it is difficult to reach a decision concerning the affinities of the Middle Awash people. Characters such as the angular torus or an elevated nasal saddle, considered to define *H. erectus* relative to earlier *Homo* or australopiths, are expressed also in individuals usually described as "archaic" *H. sapiens*. Clearly these shared specializations cannot be used to exclude Bodo from the latter group.

Resemblances to later Middle Pleistocene hominids

As noted by Conroy *et al.* (1978) and subsequently by other workers, Bodo is similar in overall size and robusticity to specimens from Middle Pleistocene localities such as Broken Hill and Petralona (see Figure 2). Cranial capacity has been estimated by Adefris (1992), using external dimensions of the vault. Basibregmatic height, the porion-bregma arc and two measures of breadth are treated (separately) in regression analysis to predict a brain volume well in excess of 1400 cc. Here very different estimates are simply averaged, without regard for the uncertainties associated with each. On other grounds, capacity is then adjusted upward to over 1500 cc. For various reasons, this figure is almost surely too large. A more accurate determination, made from the partial endocast, is likely to fall close to 1300 cc (R. L. Holloway, personal communication). This result is still substantially greater than expected for *H. erectus*, and expansion of the brain seems to be a character linking Bodo generally to more advanced humans.

Despite its flattened profile, the frontal bone is longer than that of other specimens (Table 1). It is also wide. Least frontal breadth exceeds that of *H. erectus*, and proportions of the squama as expressed by the ratio of minimum to maximum widths are most like those of Omo 2 and Petralona (Figure 3). Although the midvault and occiput are incomplete, it is likely that the braincase is as broad at the level of the parietal bosses as at the asteria or near the auditory openings. This expansion of the parietal walls relative to the bitemporal width is characteristic of *H. sapiens*. On the left side, the squamosal suture describes a high arch as in more modern

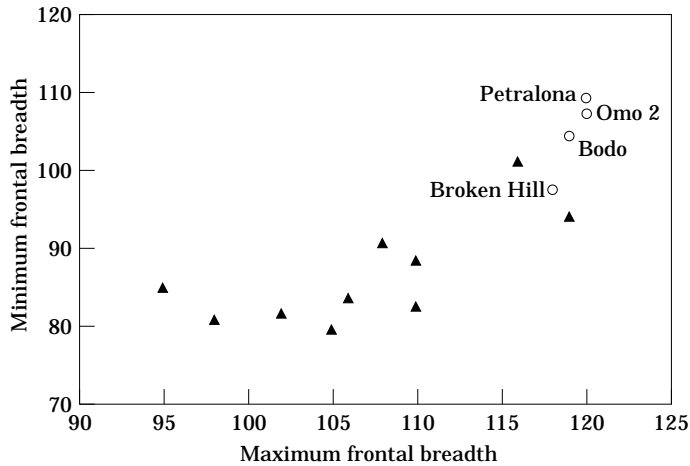


Figure 3. Shape of the frontal bone as assessed by the ratio of least postorbital width to maximum breadth. The Bodo cranium falls close to other Middle Pleistocene hominids usually referred to "archaic" *Homo sapiens* but is distant from most representatives of *Homo erectus*. Measurements from Table 1 and Rightmire (1990). (▲), *Homo erectus* (Africa and Asia); (○), "archaic" *Homo sapiens*.

humans. Some aspects of cranial base anatomy also depart from the condition common in *H. erectus*. The glenoid cavity is relatively shallow, and the entoglenoid process is small. The lip-like construction of this process resembles that of Broken Hill. As in the latter individual, a sphenoid spine probably projected inferiorly, without contributing directly to the wall of the mandibular fossa.

The supraorbital torus is divided into a medial glabellar segment including the superciliary arches, and lateral portions set off from these arches by furrows associated with the supraorbital foramina. The entire brow and particularly its lateral segments are somewhat less thickened than in Broken Hill and Petralona. Viewed from the side, the border of the piriform aperture is oriented vertically and does not slope forward as in *H. erectus*. The aperture itself is very broad, but at its entrance the spinal crests are situated in about the same way as in Broken Hill, and a central spine is well developed. Rounding of the angle of the cheek, a feature of the Bodo face, is also prominent in Broken Hill. In the latter, the area of swelling is more localized. Although Habgood (1989) refers to this structure as a malar tuberosity, it is positioned behind the zygomaxillary suture and does not extend inferiorly as in the Zhoukoudian hominids (Weidenreich, 1943; see also Pope, 1991). Rooting of the zygomaticoalveolar pillar and form of the incisive foramen constitute additional similarities to Broken Hill and Petralona. On the hard palate, the incisive foramen is located anteriorly, and the canal itself appears to pass directly upward toward the nasal floor, as in modern humans.

As before, it should be emphasized that many of these features are subject to variation. Some are simply not useful for sorting the Bodo specimen in relation to taxa of Pleistocene *Homo*. Proportions of the mandibular fossa provide an example, as the cavity is not always deep in archaic hominids, nor is it uniformly shallow in later populations. Probably the same caution applies to shape of the nasal aperture and rooting of the zygomaticoalveolar crest above M^1 . Other traits seem more clearly to be synapomorphies uniting later Middle Pleistocene populations with recent humans. One is increased cranial capacity, and Broken Hill, Omo 2 and Petralona as well as Bodo have brains larger than expected for (late) *H. erectus*.

Elsewhere, I have suggested that this pattern cannot be attributed to continuation of any linear trend established in more archaic populations, and Bodo along with other African and European specimens may document an episode of relatively rapid brain expansion (Rightmire, 1990). Among traits related to this size increase may be counted the broader midvault with signs of parietal bossing, a high contour of the temporal squama and perhaps some details of cranial base anatomy. Whether Bodo exhibits rounding of the occiput and changes in occipital proportions comparable to those seen in early *H. sapiens* cannot be determined, as the back of the skull is not preserved.

Apomorphic features of the frontal bone and face likely include division of the brow at mid-orbit and its attenuation laterally. Here again, however, there is much individual variation, and distinctions between groups of archaic *Homo* are not always very clear. Some workers emphasize form of the supraorbital torus as diagnostic at the species level, while others see few differences. A more useful trait is the orientation of the lateral border of the nose. In Bodo as for Broken Hill, the "crista nasalis" falls vertically from rhinion so as to give the aperture an erect appearance, characteristic of modern humans. Another synapomorphy is the positioning of the incisive canal relative to the hard palate.

Affinities of the Bodo hominids

From the forgoing, it is apparent that Bodo is similar not only to *H. erectus* but also to hominids from later Pleistocene localities. The impression that the cranium is "intermediate" in its anatomy is quite striking. In fact this condition is better documented for Bodo than in the case of other specimens considered to resemble both (late) *H. erectus* and (early) *H. sapiens*. An example is provided by the assemblage from Ngandong in Java, often cited as linking the archaic people from Sangiran with more recent populations of Australia (Wolpoff *et al.*, 1984). Several of the Ngandong braincases have expanded capacities, and the frontal may be less constricted than is usual at Sangiran or at Zhoukoudian. In most respects, however, these individuals are very much like other ancient hominids from Asia. This assessment holds not only for overall shape of the vault but for many discrete characters as well (Rightmire, 1994). The Ngandong fossils should be viewed not as "transitional" in form but rather as an integral part of the *H. erectus* hypodigm.

A different conclusion follows from analysis of the Bodo material. The Middle Awash specimens do share features with *H. erectus*, but several of these traits are primitive and cannot be considered diagnostic for the species. Of the (*erectus*-like) characters that are derived, some (e.g., the angular torus) are present also in Broken Hill and Petralona. In general, it is clear that the Bodo cranium cannot be excluded from a population that is advanced anatomically in comparison to *H. erectus*. This finding is strengthened when brain size is considered. It is further supported by the observation that Bodo shares with Broken Hill a number of facial traits found in more modern humans.

Sorting the Middle Awash specimens is difficult. This is so partly because the cranium is incomplete, and key regions such as the occiput and portions of the base are damaged or missing altogether. A further complication is the fact that individuals are always variable in their anatomy and cannot be expected to display all of the characters carried by other conspecifics. Nevertheless, it seems most reasonable to group Bodo with Broken Hill and similar specimens from Middle Pleistocene sites in Africa and Europe. Such hominids are rightly described as archaic, in the sense that they retain numerous (mostly plesiomorphic)

features common in *H. erectus*. At the same time they exhibit important changes in their anatomy, expressed in the contour of the parietals, shape of the temporal bone, the cranial base, and particularly in the morphology of the nose and palate.

“Archaic” H. sapiens?

These Middle Pleistocene people from Africa and Europe should be set apart from *H. erectus* at the species level. Many workers feel that the fossils are best characterized as “archaic” *H. sapiens* (Stringer *et al.*, 1979; Rightmire, 1983; Bräuer, 1984, 1992; Clarke, 1990). This way of classifying them emphasizes broad similarities to later groups such as the Neanderthals and also living humans. Within the species, several grades are frequently distinguished on the basis of morphology. For example, Bräuer (1992) recognizes “early archaic” specimens such as Bodo and Broken Hill, “late archaic” people at Florisbad and Laetoli, and more modern populations. For sub-Saharan Africa, Bräuer interprets this record as demonstrating continuity through time, so his levels are linked in an evolutionary progression. In other cases, where both Africa and Eurasia are considered, the relationships among grades are often left unspecified. The utility of such schemes is limited. An alternative is to assign the fossils to subspecies (Bonde, 1989). The Middle Pleistocene people of sub-Saharan Africa have been partitioned from other assemblages in this way, while the Neanderthals from Europe and western Asia are commonly referred to *H. sapiens neanderthalensis*. Just how many subspecies should be named is not certain, however, as the criteria by which such groups can be identified have never been fully agreed upon. Whether this category should be used to denote time-successive as well as geographic subdivisions within a species is unclear.

The case for Homo heidelbergensis

Given the difficulties associated both with grades and subspecific designations, and the observation that Middle Pleistocene hominids are in fact very different from modern humans, it can be argued that at least two separate species are required (Tattersall, 1986, 1992; Groves & Lahr, 1994). The problem of recognizing species in the fossil record is of central importance to any effort aimed at reconstructing the history of primates and other organisms. Extinct taxa must be identified in a way that is biologically reasonable, although just how this is to be accomplished is a question on which there is likely to be disagreement (see papers in Kimbel & Martin, 1993). Using anatomical characters and measurements as a guide, fossils can be sorted by morphological similarity, even if it may never be established that these phenotypes represent biological species as defined for living groups. Careful reading of the present evidence suggests that the European and African specimens are generally similar enough to be grouped together, and if the mandible from Mauer is placed with Petralona and Arago Cave, Broken Hill, Elandsfontein, Lake Nduku and Bodo, the entire assemblage can be referred to *H. heidelbergensis* (Rightmire, 1988, 1990; Stringer, 1993; Groves, 1994).

This species was named by Schoetensack (1908), to accommodate the jaw found a year earlier in the basal sands and gravels complex of the Grafenrain pit near Mauer. Schoetensack was impressed with the primitive character of his specimen but recognized that it must be human, as the canines are reduced in size and the tooth crowns generally display the proportions expected for modern populations. Later authors have continued to emphasize the primitive appearance of the mandible, and Howell (1960) pointed to its massive construction, multiple mental foramina, very thick symphysis lacking any indication of a chin, well developed alveolar planum, and superior transverse torus as characters shared by other archaic representatives of *Homo*. However, Howell was careful to note that the specimen can

be distinguished by features including ramus breadth, great anterior depth of the corpus, and relatively moderate size of the dentition, both from Asian *H. erectus* and also from the Ternifine hominids. He argued that

“the evolutionary history of (Middle Pleistocene) European people must have been quite different from that of the northwest African and eastern Asian populations”

and added that the Mauer mandible is

“very likely specifically distinct”

from any Asian lineage. He left open the relationship of this isolated fossil to later European groups, including the Neanderthals. I agree with this assessment. But while there are (still) obvious difficulties with linking the Mauer fossil to individuals such as Petralona, for which no lower jaw has been recovered, some provisional sorting of broadly contemporary materials from the Middle Pleistocene can be attempted. When constituted in the way outlined above, the hypodigm of *H. heidelbergensis* confirms that this species retains a number of archaic characters, although it is undoubtedly a close relative to *H. sapiens*.

Some authorities advocate instead an expanded use of the taxon *H. neanderthalensis* to include Mauer, Petralona and Arago as well as later hominids from Europe and southwest Asia that display a full suite of Neanderthal characters. This view is strengthened by discoveries from the Sierra de Atapuerca in northern Spain (Arsuaga *et al.*, 1993). The assemblage excavated from the Sima de los Huesos includes several crania that show the midfacial protrusion, arched supraorbital torus and occipital proportions characteristic of Neanderthals. The age of ca. 0.3 Ma obtained from a speleothem overlying the fossils is currently under review, but it can tentatively be claimed that the Sima material extends the Neanderthal lineage well back into the Middle Pleistocene.

A problem with this interpretation concerns the role played by archaic African populations. Broken Hill and Bodo, for example, are similar in many ways to Petralona but cannot easily be grouped with Europeans of the Late Pleistocene. It is now clear that the African crania exhibit few if any of the apomorphic traits that define Neanderthals. This holds not only for Bodo and other specimens from the sub-Saharan region but also for North African assemblages such as that from Jebel Irhoud in Morocco (Hublin, 1993). Probably none of these people can be linked with the Neanderthals, who are best viewed as members of a lineage restricted geographically to western Eurasia. A similar question of affinities must be raised in respect to the hominids resident in the Far East at sites such as Yunxian, Jinniushan and Dali. As reviewed recently by Pope (1992), Wu & Bräuer (1993) and Etlar (1994), the Chinese record does not contain nascent Neanderthals, but the origin of these populations and their relationships to contemporary western groups remain obscure.

Implications for human evolution in the Middle Pleistocene

If *H. heidelbergensis* is accepted as a species exhibiting a combination of archaic and specialized traits not found in *H. erectus*, the Neanderthals, or recent *H. sapiens*, and if Bodo is assigned to this taxon, then several important conclusions may be drawn. One is that hominids distinct from *H. erectus* evolved early in the Middle Pleistocene, if not before. Given the geographic distribution of the fossils, this speciation “event” could have occurred in western Eurasia or in Africa. Dating for many European localities remains problematical. Some authorities

continue to argue that assemblages containing crude stone artefacts document a human presence in France and central Europe in the Early Pleistocene, perhaps before 1.0 Ma ago. Such claims have been strongly questioned (Roebroeks, 1994). However, a lithic industry composed mainly of flakes and lacking hand axes, cleavers or picks has been recovered recently at Gran Dolina in the Sierra de Atapuerca (Spain), from a level that may date to the time of the Brunhes-Matuyama magnetic boundary (Carbonell *et al.*, 1995; Parés & Pérez-González, 1995). These artefacts are accompanied by human fossils. At least four individuals are represented by teeth and skeletal fragments, including part of a frontal bone. For the latter, some of the squama and supraorbital region are preserved, and Carbonell *et al.* (1995) suggest that this piece differs in its morphology from *H. erectus*. These important discoveries will require further study, but current evidence points to the Gran Dolina hominids as perhaps the most ancient known in western Europe. The mandible from the Mauer Sands (Germany) and a newly described tibia from Boxgrove (U.K.) are also likely to be old, and both may be about 0.5 Ma in age (Zöller, 1991; Roberts *et al.*, 1994). For the moment, a reasonable hypothesis is that people first occupied Europe at the onset of the Middle Pleistocene, after they were able to survive in heavily forested environments. Coincidental changes in the composition of the predator community and increased availability of ungulates as food might also have encouraged hominids to move westward during this period (Turner, 1994).

Such a scenario implies that *H. heidelbergensis* may have evolved elsewhere, in southwest Asia or in Africa. There is no doubt that hominid populations were established well before 1.0 Ma ago at 'Ubeidiya in the Jordan Valley and perhaps also at Dmanisi in the Georgian Caucasus, but presumably the 'Ubeidiya people and more certainly the Dmanisi mandible are best described as *H. erectus* (Bar-Yosef & Goren-Inbar, 1993; Gabunia & Vekua, 1995). The frontal bone with facial parts from Zuttiyeh in the Levant is usually compared to early Neanderthals or the Skhul/Qafzeh people (Simmons *et al.*, 1991), although Sohn & Wolpoff (1993) find an affinity to Far Eastern *H. erectus*. No matter how this question is resolved, the Acheulo-Yabrudian levels at Zuttiyeh are probably of later Middle Pleistocene antiquity (Bar-Yosef, 1993), and the frontal is, therefore, too recent to bear on the origins of *H. heidelbergensis*.

Hominid localities more relevant to this issue include Elandsfontein in the southwestern Cape Province of South Africa. Along with the human skullcap found in 1953, deflation surfaces (or "bays") at Elandsfontein have yielded Acheulean artefacts and a very large fauna. Dating of this assemblage is complicated by the fact that it may contain taxa of somewhat different ages, and several of the bovid species are unknown elsewhere. Comparisons with Olduvai Gorge and other African sites imply that the bones were accumulated between 0.7 and 0.4 Ma ago (Klein & Cruz-Urbe, 1991). At Broken Hill in Zambia, faunal elements possibly associated with the more complete hominid cranium suggest that this material may date from the same broad interval (Klein, 1994). This is true also for the Ethiopian Middle Awash sites, where radiometric results confirm an early Middle Pleistocene age. As determined by Clark *et al.* (1994), the deposits (UBSU) containing the Bodo hominids are approximately 0.6 Ma old. These fossils from Africa presently provide some of the most secure evidence for first appearance of the new species.

It is clear that *H. heidelbergensis* overlaps in time with late *H. erectus*. The Middle Awash hominids may be roughly contemporary with the people at Ternifine (Tighenif) in Algeria, who are generally taken to be *H. erectus* (but see Dean, 1993), and they are more ancient than specimens from the Atlantic coast of Morocco that are usually (if again somewhat

ambiguously) attributed to this species. The Bodo localities are about the same age as upper Bed IV at Olduvai, where OH 12 and OH 28 seem to document the presence of *H. erectus* in early Middle Pleistocene deposits. It can be argued that these examples are equivocal, but the record for Asia leaves little room for question. The UBSU probably antedates even the first signs of occupation at Zhoukoudian and is (far) older than sites such as Longtandong (Hexian) in China. The date of last appearance for *H. erectus* in China is not firmly established but is likely close to 0.23 ma, if layers 3 and 4 at Zhoukoudian Locality 1 are taken as a guide (Zhou & Ho, 1990). In Java also, the species may have persisted until late in the Pleistocene. Uranium-series dates for samples of animal bone collected at Ngandong suggest this (Bartstra *et al.*, 1988), although the age of the Ngandong hominids remains controversial. The survival of archaic people in the Far East thus contrasts markedly with the pattern of evolutionary change apparent elsewhere, as noted by Dean & Delson (1995). The evidence is consistent with an episode of speciation occurring in populations of *H. erectus* restricted to Africa or western Eurasia, and subsequent dispersal of *H. heidelbergensis*. Following emergence of the new species, *H. erectus* continued living in Java and China. These latter groups were supplanted relatively late in the Pleistocene by people exhibiting a suite of advanced characters.

If *H. heidelbergensis* is a contemporary to Asian *H. erectus*, then another important question concerns the relationship of this species to European Neanderthals, late Middle Pleistocene hominids such as Yunxian, Jinniushan and Dali from China, and more modern humans. Here several hypotheses can be entertained. A first possibility [Figure 4(a)] is that recent *H. sapiens* is closely related to the Neanderthals, and both are more similar to *H. heidelbergensis* than to the archaic people of Asia. Modern humans and Neanderthals may in fact be descended from *H. heidelbergensis*, while the Chinese fossils probably represent more distant members of this clade. The second tree [Figure 4(b)] again assumes that recent people should be grouped with Neanderthals, on the strength of numerous shared apomorphic traits. These taxa are linked in a sister relationship to the East Asian hominids, which are taken to be less "derived" in comparison to *H. heidelbergensis*. Such a scheme is compatible with the ideas advanced by Groves & Lahr (1994), who lump Dali and Jinniushan with *H. heidelbergensis* while cautioning that the Chinese fossils differ somewhat from European and African specimens sorted to this species. A third and less likely reading of the evidence [Figure 4(c)] places *H. heidelbergensis* as a close relative to the Neanderthals, on the assumption that both taxa possess special features not shared with recent *H. sapiens*. A fourth branching sequence [Figure 4(d)] links modern humans with archaic Asians, in a part of the tree separate from that containing *H. heidelbergensis* and the Neanderthals. This last view would presumably be favored by Li & Etlar (1992), who find that facial traits characteristic of geographically diverse populations of *H. sapiens* can be traced back to the more ancient crania from Yunxian in China. Figure 4(d) is also compatible with the scenario proposed by van Vark (1995), who detects large differences between *H. heidelbergensis* and other groups. The Neanderthals alone may represent an extinct product of this lineage in Europe.

My own opinion is that the first or second of these hypotheses [Figures 4(a) or 4(b)] is most likely to hold up under close scrutiny, but choosing among such trees (or others) is not easy at present. It will be important to identify characters that have changed during this Middle Pleistocene episode of human evolution and to determine their polarities wherever possible. This has been done with some success for the Neanderthals of Europe, who are known to display a number of specialized features of the face and braincase. Other groups must now be studied in more detail. However, application of Hennig's principle may be problematical, where the taxa considered are all quite closely related. Here it will likely be difficult to define

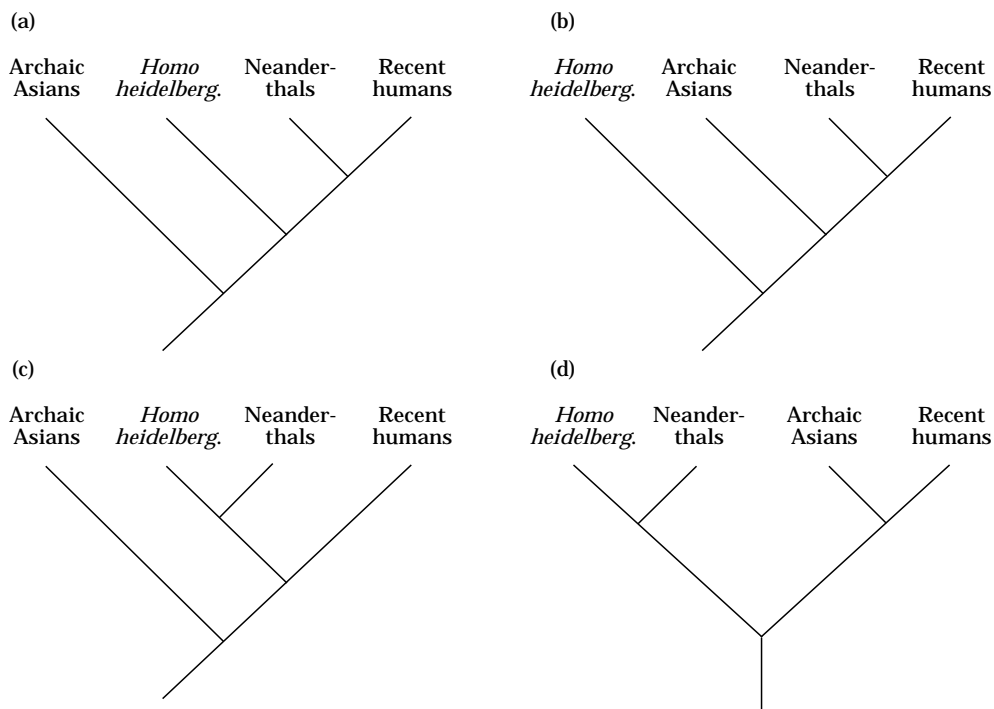


Figure 4. Trees illustrating alternative hypotheses concerning the relationship of *Homo heidelbergensis* to later Middle Pleistocene hominids from Asia, the Neanderthals, and recent humans. See text for discussion.

traits that are clearly apomorphic. An alternative is to take into account overall similarity between groups, as assessed by measurement. In this case, where all available information must be brought to bear on the question of relationships of *H. heidelbergensis*, both approaches should be utilized.

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