



Homo Erectus and Later Middle Pleistocene Humans

Author(s): G. Philip Rightmire

Reviewed work(s):

Source: *Annual Review of Anthropology*, Vol. 17 (1988), pp. 239-259

Published by: [Annual Reviews](#)

Stable URL: <http://www.jstor.org/stable/2155913>

Accessed: 30/12/2012 10:31

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Annual Reviews is collaborating with JSTOR to digitize, preserve and extend access to *Annual Review of Anthropology*.

<http://www.jstor.org>

HOMO ERECTUS AND LATER MIDDLE PLEISTOCENE HUMANS

G. Philip Rightmire

Department of Anthropology, State University of New York, Binghamton, New York
13901

INTRODUCTION

Apart from several Neanderthals unearthed in Europe, the earliest discoveries of human fossils were made in Java toward the close of the last century. After finding a skullcap and later a femur at Trinil, Eugene Dubois named *Pithecanthropus* (now *Homo erectus*) in 1894. Since then, many more bones have come to light, in Africa as well as Asia. Much has been learned from the fossils themselves, and a great deal of effort has been put toward obtaining stratigraphic, paleoecological, and cultural information from the more important sites. We now have a substantial understanding of the anatomy and behavior of *Homo erectus*. Lately, this species has become a focus of particular interest among paleoanthropologists, and fresh questions have been raised. Some of these concern the geographic distribution of the taxon and whether it should be recognized in Europe, or for that matter anywhere outside of the Far East. Another issue is how much *Homo erectus* has changed throughout its long history. Many workers prefer to describe this species as a grade, or loose collection of populations all evolving toward more modern humans. Others argue that *Homo erectus* can be distinguished morphologically from earlier or later groups. In this review, I comment on the anatomy of individual specimens to only a limited extent, although I list the key characters by which the taxon can be diagnosed. I emphasize points of controversy concerning the evolution of *Homo erectus* and its ties to later people.

GEOGRAPHIC DISTRIBUTION OF ARCHAIC *HOMO*

A number of the sites yielding remains of *Homo erectus* are located in China and Indonesia, and for more than 50 years after the first discoveries in Java,

this archaic form of *Homo* was known only from the Far East. However, in the last few decades, paleoanthropology in Asia has been partly overshadowed by developments in Africa. Human mandibles, other bones, and tools were collected at Ternifine in the mid-1950s, and spectacular finds followed at localities in eastern Africa, including Olduvai Gorge and East Turkana.

Discoveries of Homo erectus in Asia

Dubois' first specimen, a mandibular fragment, turned up at Kedung Brubus in 1890, and the famous Trinil skullcap was excavated from the banks of the Solo River in central Java in 1891. Digging continued at Trinil for another decade, but only a few more (postcranial) bones were recovered. It was not until later, in the 1920s, that more fossils were discovered far to the north, near Beijing in China. This site at Zhoukoudian proved to be immensely rich, and quantities of well-preserved skulls and teeth were eventually found in different levels of the cave deposits. Although nearly all of this Chinese *Homo erectus* material was lost during World War II, descriptions and photographs of the crania, jaws, and other fossils are fortunately on record, as a consequence of the efforts of the anatomist Franz Weidenreich (49–52). After the war, exploration of the cave produced a few new teeth, fragments of limb, and a mandible found in 1959. In 1966, the frontal and occipital portions of a cranium were uncovered and recognized as belonging to one of the individuals collected 1934. Excavations carried out more recently have yielded no further hominids but have addressed questions concerning the Zhoukoudian stone industry, paleoclimatic conditions, and dating (62). Studies of the cave sediments suggest that most of the deposits were accumulated during the Middle Pleistocene (29, 60).

Other important discoveries have also been made in China. A rather damaged cranium from Gongwangling and a more complete lower jaw from Chenjiawo have been referred to *Homo erectus* (57, 58). Assemblages of teeth are known from several localities, but perhaps the most significant find is a partial skull from Lontandong Cave, Hexian County, which came to light in 1980. This Hexian individual has been described briefly by Wu & Dong (61), who feel that it is best compared to later specimens of *Homo erectus* from Zhoukoudian. None of these hominids has been dated precisely. Faunal studies and paleomagnetic determinations suggest that all are approximately Middle Pleistocene in age, and even the oldest sites such as Gongwangling may lie close to the Brunhes-Matuyama boundary (33, 60).

In Indonesia, the tally of hominid discoveries has increased more dramatically. The Sangiran dome has proved to be the richest source of fossils. The famous B mandible was recovered there in 1936, and the first cranium turned up in 1937. This Sangiran 2 braincase is small, with an endocranial capacity

of only a little more than 800 ml. This suggests that the individual may be female, despite obvious thickening of the brow. Many features of Sangiran 2, including the low contour of the vault, some sagittal keeling, and the strongly flexed occiput, recall the morphology of the Trinil skullcap found by Dubois.

A maxilla with teeth, and the back portion of a thick-walled skull, were picked up at Sangiran in 1938 and 1939. This individual, numbered Sangiran 4, was referred first by Weidenreich to *Pithecanthropus robustus* and later by von Koenigswald to *Pithecanthropus modjokertensis*. On several subsequent occasions, the same species, now *Homo modjokertensis*, has been recognized from fragments thought to be derived from Pucangan horizons. Other material from Sangiran that may come from Pucangan levels includes mostly lower jaws. More fossils are known from the Kabuh sediments, and several of the latter crania are well preserved. The most complete is Sangiran 17, for which much of the facial skeleton is present. Altogether, some 40 individuals have now been recovered at Sangiran.

Other localities in central and eastern Java have yielded fewer fossils. Apart from Kedung Brubus and Trinil where the first discoveries were made, Modjokerto, Ngandong, and Sambungmachan have produced useful remains. The Modjokerto child, found in 1936, was the first specimen to be referred to *Homo modjokertensis*. Crania and postcranial parts recovered at Ngandong have been widely regarded as chronologically younger and anatomically less archaic than *Homo erectus*. However, both assumptions can be questioned. These crania share many features with *Homo erectus*, as has been documented by Santa Luca (42). At Sambungmachan, quite a complete braincase, unfortunately lacking the face, was discovered in 1973. This individual has been compared by Jacob (21) to the Ngandong assemblage, but again resemblances to the *Homo erectus* crania from Sangiran are apparent.

Northwest Africa, Olduvai, and the Turkana Basin

The first convincing evidence that *Homo erectus* lived in Africa as well as Asia was found at Ternifine (now Tighenif) in Algeria by Arambourg & Hoffstetter (2). Two nicely preserved mandibles were excavated in 1954, and a third jaw along with a cranial bone was picked up the following year. The deposits at Ternifine consist of clays and sands stratified in a small lake fed by artesian springs. The sequence apparently does not cover a long span of time. Although the sands are not suitable for paleomagnetic study, measurements made on clays near the bottom of the section show these sediments to be of normal polarity (15). This finding, coupled with the biostratigraphy of the site (14), is in keeping with an earliest Middle Pleistocene age for the deposits.

Additional remains are known from the Atlantic coast of Morocco, but it was at Olduvai Gorge in Tanzania that Louis Leakey discovered a large, heavy-browed braincase in 1960. Hominid 9, from the upper part of Bed II,

has an endocranial capacity of about 1070 ml (18). Given its size and robustness, this individual is best compared to specimens such as Sangiran 4 and Sangiran 17, or to the larger crania from Zhoukoudian. Such comparisons show clear similarities (35, 38). Another smaller and much fragmented cranium from Bed IV, several mandibles with teeth, and postcranial bones from Olduvai can also be attributed to *Homo erectus*.

Probably the oldest fossils representing this taxon have come from the Turkana basin in Kenya. An example is the fine cranium numbered ER-3733, which was found in the Koobi Fora region in 1975 (26). Here much of the facial skeleton is present, although the lower jaw is missing. Perhaps a female, this individual is similar in many respects to the smaller skulls from Indonesia. ER-3883 is most of another braincase, to which only the upper portion of the face is still attached. These specimens display some deformation but are nevertheless more complete than Olduvai Hominid (OH) 9 and many of the Asian hominids. Several mandibles and limb bones have also been recovered from the Koobi Fora exposures.

These deposits, which have accumulated on the eastern side of the Turkana basin, are thought to span about the same time interval as those to the north, in the well-studied Lower Omo Valley (6, 8). Of particular importance are the numerous, mostly waterlaid volcanic tuffs, which may be horizontally extensive. The same tuff can often be located in different areas. Such marker horizons allow correlation of sedimentary sequences for different localities within the Koobi Fora region and also help to tie these sections to others in the basin. One tuff, which is particularly important because of the stratigraphic proximity to it of fossils and stone tools, is known as the KBS Tuff at Koobi Fora and as Tuff H2 of the Shungura Formation. An age for this marker bed of about 1.88 million years is now well established (32). This part of the Turkana sequence is thus about as old as lower Bed I at Olduvai Gorge. Remains of *Homo erectus* occur in levels above the KBS Tuff, in the upper part of the Koobi Fora Formation.

Searches for fossils have been conducted on the west side of Lake Turkana as well. Among the most exciting finds is a *Homo erectus* skeleton discovered in 1984 on the bank of the Nariokotome River (5). Excavations at this site have produced few other mammalian bones, but an age for the deposits can be obtained through tuff chemistry. The hominid fossils occur in hardened silts within a stratigraphic sequence also containing several ash layers. One of these tuffs, which immediately underlies the *Homo erectus* remains, is similar in composition to tuffs sampled elsewhere in the basin. Correlations worked out by Brown & Feibel (4) suggest a date of about 1.6 million years for this horizon. Thus the new skeleton is a little less ancient than ER-3733 from Koobi Fora.

Nearly the entire skeleton of this individual is well preserved. WT-15000 is

subadult, and the dentition suggests an age of close to 12 years. Postcranial characters are consistent with an identification as male. All of the epiphyses are unfused, so the boy would certainly have grown further. Stature as estimated by regression relationships applicable to modern humans is already surprisingly great. The lower jaw has been recovered, and the cranium has been reconstructed from a number of pieces. Heavy tori and crests are not yet developed on the skull, but the brows are thicker than those of ER-3733. After some additional growth, the boy would likely have resembled other Turkana *Homo erectus*, although the cranium would probably have been more massively constructed.

Overview of Dating

Remains of *Homo erectus* have been recovered from sites that are widely dispersed geographically, and there is evidence that these collections differ greatly in absolute age. Some comparisons for Africa and Asia are provided in Figure 1. Fossils from the Turkana basin are among the oldest on record. ER-3733 and ER-3883 are from the upper part of the Koobi Fora Formation. The first cranium is likely to be more than 1.6 million years old. The second individual, from a slightly higher stratigraphic horizon, is somewhat younger. Cranial and postcranial remains attributed to *Homo erectus* are known also from Beds II, III, IV, and the Masek Beds at Olduvai Gorge. The Hominid 9 braincase from upper Bed II is about 1.2 million years old and therefore postdates the Turkana material by several hundred thousand years. The very incomplete cranium of OH 12 and the postcranial material of OH 28 are derived from Bed IV deposits. As is the case with the upper part of Bed II, these sediments cannot be dated directly by radiometric methods. However, estimates of 0.83 and 0.62 million years for the lower and upper boundaries of Bed IV have been obtained by measuring sediment thicknesses (17, 25).

Nearly all of these East African fossils are more ancient than those from Ternifine and the Atlantic coast of Morocco. The latter are probably close in age to the assemblages from Zhoukoudian in China. Dates for the Indonesian hominids are less certain. Recent studies of fauna collected from Dubois' early excavations suggest that Trinil is earlier than neighboring localities such as Kedung Brubus (13, 28). If this "new" biostratigraphy is correct, then *Homo erectus* at Trinil may be older than hominids associated elsewhere with a "Jetis" fauna. Comparisons with Sangiran indicate that elements of a Trinil fauna as currently defined occur in Grenzbank deposits, where they are roughly contemporary with the first humans at this locality.

At Sangiran, *Homo* is present mainly in the Kabuh Formation, while a few individuals may be derived from Pucangan levels. The locations of some of the discoveries are not known precisely. Recent attempts to clarify relative ages of the Sangiran hominids by analysis of bone fluorine content do seem

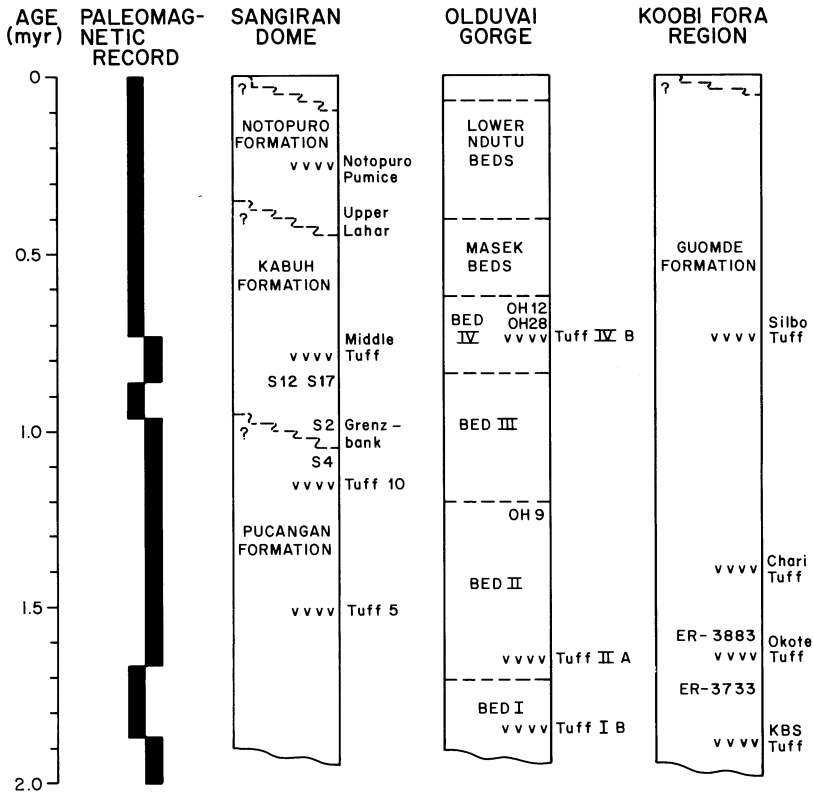


Figure 1 Pleistocene chronologies for Java and East Africa, based on tuff dates and paleomagnetic determinations. Positions of only a few of the more important fossils attributed to *Homo erectus* are shown. This species is present in the Turkana basin more than 1.6 million years ago, but its first appearance at Sangiran is considerably more recent.

promising. Matsu'ura (31) shows that Sangiran 4 may be from the uppermost Pucangan Formation, and he notes that the fluorine content of Sangiran 2 best matches that of material from Grenzbank or lower Kabuh levels. The Sangiran 12 and Sangiran 17 crania give fluorine measurements compatible with derivation from lower or middle Kabuh horizons. Some questions raised by magnetic polarity determinations and radiometric dates remain to be resolved, but it now looks as though most of the Sangiran hominids may be less than 1.0 million years old (33; see also Pope's review in this volume).

How Many Species?

Given the long span of time during which archaic humans lived in Africa and Asia, it is not surprising that there is variation among the different *Homo*

assemblages. This variation has prompted many workers to claim that more than one species is represented by the fossils. In Java alone, several distinct lineages have been recognized. Von Koenigswald referred the Modjokerto child and some of the Sangiran (Pucangan) specimens to *Homo modjokertensis*. Material from the Kabuh beds has usually been called *Homo erectus*, while the Ngandong crania are often grouped with *Homo sapiens*. Several other taxa have been named. However, Le Gros Clark noted more than 20 years ago that there is little basis for distinguishing among these groups, and newer studies of Sangiran teeth seem to strengthen this conclusion (16). In my opinion, there are no compelling reasons for recognizing more than one species of *Homo* at Sangiran. Questions about the Ngandong hominids are perhaps more difficult to answer, as there are serious doubts about the geological provenience and dating of the fossils. Santa Luca (42) finds unequivocally that the Ngandong people resemble other *Homo erectus* morphologically, and I am inclined to accept this view (G. P. Rightmire, in preparation).

Whether populations in Africa should be referred to *Homo erectus* is currently debated. There is some agreement that the jaws from Ternifine and the large braincase from Olduvai are very similar to Sangiran or Zhoukoudian specimens, but there is concern about the Turkana remains. It has been argued that the Koobi Fora crania lack several of the novel or derived characters that distinguish Asian *Homo erectus*. If this were so, then the Turkana hominids and perhaps (all) other African assemblages should be excluded from the taxon as defined in the Far East (1, 44, 59).

This position is countered by the observation that differences among the East African and Asian groups are not clear-cut. Key characters such as a heavy brow, midline keeling on the braincase, a bulge at the mastoid angle of the parietal bone, narrowing of the temporomandibular joint surface, a strong occipital torus, and thickening of the vault bones are variably expressed, in the Turkana and Olduvai fossils as well as at Sangiran or the Chinese localities (20, 40). If these apomorphies are present in the African record, then there are no grounds for identifying two species, which would in any case share so many other characters as to make separation difficult. A fair reading of the evidence is that all of the Lower Pleistocene and earlier Middle Pleistocene material may be attributed to *Homo erectus*.

DEFINING *HOMO ERECTUS*

If just one species of archaic hominid is present in Asia and in Africa, then all of the fossils should be surveyed in any attempt to provide a comprehensive description of *Homo erectus*. Since mostly skulls and teeth have been collected, it is not surprising that descriptions tend to emphasize these aspects of

anatomy. Some parts of the cranium are preserved less frequently than others, and the fragile facial bones are poorly represented in the *Homo erectus* inventory. Mandibles are relatively plentiful. Postcranial remains unfortunately are scarce at the Asian localities, although the limbs, girdles, and even the axial bones are becoming better known from several of the sites in eastern Africa. All in all, there is on record a substantial amount of material. The more important features of *Homo erectus* can be summarized as follows.

Descriptive Morphology

Crania are long and relatively low in outline, and the average endocranial capacity is close to 1000 ml. The facial skeleton, preserved for only a few individuals, is robust and projecting in its lower parts. The wall of the nasal opening is thickened below but is everted and plate-like superiorly. The nasal profile approaches that seen in later *Homo*. Brow ridges are heavy, even in smaller specimens that may be female. The frontal bone is flattened and may exhibit a keel or ridge in the midline. Least frontal breadth is low relative to the biorbital chord, so postorbital narrowing of the cranium is marked.

The parietal bone is short compared to that of recent humans, and the (superior) temporal line may produce a rounded bulge or torus at the parietal mastoid angle. The rear of the skull is sharply flexed. The occiput is relatively wide, and its upper part slopes forward. A transverse torus is most projecting near the midline, where it may be blunt or shelf-like. The cranium is broadest near the base, rather than at the level of the parietals. Crests associated with the mastoid process tend to be prominent, and the process itself is inclined medially.

In at least some individuals the skull base is flattened in comparison to the more flexed condition present in *Homo sapiens*. Other characters of the base also distinguish *Homo erectus* from later people. The glenoid fossa, which receives the condyle of the lower jaw, is narrowed to form a medial crevice, and a sphenoid spine is not developed. The tympanic bone is thickened inferiorly. The mandible is heavily constructed and often carries a broad ascending ramus. There is usually little indication of a bony chin.

Although there is variation in all of the assemblages, these as well as other traits noted by Weidenreich (49, 52), Le Gros Clark (27), and Howell (19) serve to describe *Homo erectus* in a general way. Nearly all of these features can be used to distinguish the archaic species from more modern humans. However, some of the same characteristics of vault form or mandibular anatomy may be found in earlier *Homo* from Africa or even in species of *Australopithecus*. Such widespread or primitive traits are not helpful if one wishes to define a taxon in a more formal way or assess its relationship to other groups. Constructing a diagnosis of *Homo erectus* requires further review of the fossil record.

Diagnosing the Taxon

During the last decade, several authors have attempted to list characters that may be derived (apomorphic) for *Homo erectus*. Delson et al (12) cite an earlier report of Macintosh & Larnach (30) to support their identification of six unique traits, including brow form, frontal narrowing, presence of an occipital torus, and a small mastoid process. More recently, Wood (59) has presented a set of some 30 characters, ranging from overall shape of the cranium to the anatomy of several small crests and ridges. Stringer (44) has also reviewed a long list of features said to be present in *Homo erectus*, in an effort to isolate autapomorphies. He finds that a dozen or so traits, expressed mainly in the Asian assemblages, are distinctive. Andrews (1) takes this as evidence that the name *Homo erectus* should be restricted to the Asian fossils, as I have already pointed out. Still another opinion is voiced by Hublin (20), who argues that few if any anatomical specializations can be considered unique to *Homo erectus*. Hublin suggests that these hominids constitute a grade rather than a distinct taxon, and he sees no reason to retain separate species status for any of the mid-Pleistocene populations of *Homo*.

Given this level of controversy, it is apparent that the search for characters diagnostic of *Homo erectus* must be conducted cautiously. It is reasonable to begin by listing aspects of anatomy that seem to be derived for both African and Asian groups, relative to earlier *Homo* from East Africa. Such traits include a brow that is thickened and backed by a flattened supratatorial shelf, keeling of the frontal squama, and expression of a parietal angular torus. The occiput is angled, and morphology of the transverse torus is distinctive, as noted by Wood (59). Shape of the glenoid cavity and structure of the tympanic plate may also be specialized in *Homo erectus*, and the vault bones are robust.

Crania of earlier *Homo* are quite different, being small and thin-walled in comparison to *Homo erectus*. Faces, preserved in a few cases, exhibit variation, but at least one individual from the lower part of the Koobi Fora Formation (ER-1470) has a face that is flattened rather than projecting. Brow ridges are never massive. Neither frontal keeling nor an angular torus is observed, and the occiput is rounded. There is no strong occipital torus. Other differences are less easily documented, because of damage to the specimens. The glenoid cavity is in fact similar in form to that of African *Homo erectus*, as noted by Hublin (20), although the postglenoid process tends to be relatively large in earlier *Homo*. The tympanic plate, often not intact, seems to be less thickened inferiorly.

If it is accepted that these features do distinguish *Homo erectus* from *Homo habilis*, then it must be asked whether any of the same specializations are shared with *Homo sapiens*. Certainly a trend toward increasing brain size is one example of such a synapomorphy, although cranial capacity is still

substantially lower in *Homo erectus* than in modern people. Other traits interpreted as derived from *Homo erectus* occur also in early representatives of *Homo sapiens*. It is well established that crania from Broken Hill and Lake Ndufu in Africa, or Petralona and Arago Cave in Europe, possess heavy brows, flattened frontals, an angled occiput, and in some cases thick vault bones. At the same time, these and other later Middle Pleistocene individuals do differ from *Homo erectus*. They exhibit a number of novel characters shared only with recent humans. This evidence has prompted many workers to group Broken Hill and Petralona with *Homo sapiens*.

Strictly speaking, traits shared by two species cannot be considered diagnostic of *Homo erectus*. Such specializations may be labeled synapomorphies, although it must be recognized that they have a distribution limited to the more "archaic" representatives of *Homo sapiens*. Other derived aspects of frontal and parietal form and occipital morphology, along with the anatomy of the cranial base, are useful for defining *Homo erectus*. Individually or as complexes, these traits should be listed in any species diagnosis. Many additional features that are clearly primitive, in the sense of being shared by *Homo erectus* with earlier *Homo* or australopithecines, need not be emphasized as diagnostic but do of course provide descriptive information. *Homo erectus* crania are built to a common plan, which differs from that seen in other species.

Rates of Evolutionary Change

Homo erectus can be described as a real taxon rather than an arbitrary grade. This paleospecies had ancestors and probably left descendants, but these groups can be distinguished morphologically. Populations that can be identified as *Homo erectus* flourished during a period of well over one million years. Whether this species evolved steadily or remained relatively stable throughout its long history is debated. Attention has focused particularly on brain size as an indicator of important change, and a pattern of increase continuing throughout most of the Pleistocene has been reported (3, 55). Wolpoff (55) finds that the average cranial capacity for a group of late *Homo erectus* is about 30% greater than that for an earlier assemblage, and he contends that this is clear evidence for gradualism.

However, Wolpoff's treatment of the record can be challenged. If we exclude from this analysis two crania that are juvenile or incompletely prepared and one that is not likely to be *Homo erectus* at all, the picture is altered sharply (41). Changes are not so dramatic as Wolpoff claims. This question can also be addressed through regression. When the fossils are assigned approximate dates, and endocranial volume is regressed against geological age, the rate (slope) of size increase is not significantly different from zero (36, 39). Certainly some individuals from the localities at Zhoukou-

dian or Ngandong have brains larger than those of early *Homo erectus* at Koobi Fora, but there is much variation, and a real trend is not easily discerned.

Other characters of the skull and dentition change slowly or not at all. Thickness of the brow ridge, for example, or an angle expressing flexion of the occipital bone, undergoes minor fluctuations throughout the duration of *Homo erectus*. Vault widths show more variation, and breadth taken across the base of the cranium does tend to increase in the later Asian populations. Height of the body of the mandible remains relatively stable, while jaw breadth decreases more regularly with time. For the lower molar teeth, no patterns are evident. Buccolingual breadths of M_1 and M_2 are about the same at Zhoukoudian as in the much older Turkana hominids, and there is no indication of any dramatic reduction in posterior tooth size (G. P. Rightmire, in preparation).

Toward the close of the Middle Pleistocene, there are signs that some of these traits begin to change more rapidly. It is during this period that populations of *Homo erectus* must have given way to the first representatives of *Homo sapiens*. How this evolutionary event occurred, and whether it took place gradually in several different geographic areas or perhaps in a more restricted region, are important problems. Fossils that inform us about later Middle Pleistocene developments are known from Europe as well as from Africa and Asia, but this material is still scattered and incomplete. Using it to reconstruct the history of our own species is difficult.

THE EVOLUTION OF MORE MODERN PEOPLE

The transition from *Homo erectus* to more modern humans must have occurred across much of the Old World, but this process has been described in very different ways. Many workers argue that there has been continuity in most geographic regions. Change is assumed to be gradual, and populations of late *Homo erectus* are succeeded by local *Homo sapiens* in an unbroken progression. Few if any groups become extinct. Here the distinction between the two species is seen as arbitrary or is ignored altogether.

An opposing view holds that archaic people were actually replaced as a new form of *Homo* evolved and spread across the landscape. In some and probably many areas, extinctions overshadow local continuity. If this version of later Pleistocene events is more or less correct, then the first representatives of the new species would be expected to share a common set of features. Traits characteristic of *Homo erectus* might not appear in later populations of the same geographic region, where instead novel trends in morphology might be established.

Fossils taken to support one or both of these scenarios are known from

Europe, where some of the more spectacular discoveries have come from Petralona in Greece and Arago Cave in France. Other localities such as Mauer, Bilzingsleben, and Vertesszöllös are likely to be equally ancient, although the remains recovered at these sites are less complete and consequently less informative. Dates are very approximate. Even the oldest of the European specimens (Mauer?) may be less than 450,000 years in age (10). Hominids that differ significantly from *Homo erectus* have turned up also in Africa, at Bodo in Ethiopia, Lake Ndotu near Olduvai Gorge, Broken Hill (now Kabwe) in Zambia, and Elandsfontein in South Africa. In China, important discoveries have been made at Dali and other sites. As in Europe, dating is very imprecise, although it can be established that the fossils cover a substantial span of later Middle Pleistocene time.

Africa and Europe

Following its discovery in 1973, the cranium from Lake Ndotu was described as *Homo erectus* (9). This individual is small, with relatively well-developed brows and thick vault bones, but other features of the occiput and cranial base establish ties to modern people. The Ndotu vault is in fact similar to others from Africa that have been called "archaic" *Homo sapiens* (37). In superior view, the cranium is somewhat more rounded than that of Broken Hill and is comparable to the braincase from Elandsfontein, located near Hopefield on the Cape coast. A resemblance of Ndotu to Elandsfontein is again apparent when the two are viewed from the rear. Both crania have walls that rise steeply from the supramastoid region and appear better filled than those of Broken Hill. Parietal bossing is emphasized in Clarke's reconstruction of Ndotu, which must be approximately correct. The parietal bones could probably be flattened, but these adjustments would have to be minor, and Clarke's comment that the Ndotu vault shows more bossing than expected for *Homo erectus* is accurate.

In details of occipital anatomy and architecture of the cranial base, Ndotu is especially like Broken Hill. The upper part of the occiput is vertical, rather than forward sloping as in *Homo erectus*. The glenoid cavity is deep and bounded in front by an articular bar or tubercle which is much more prominent than that of archaic *Homo*. The inner aspect of this cavity is damaged, and it is not possible to tell whether a spine is developed from the sphenoid bone. In Broken Hill, this sphenoid spine is not very projecting but is oriented in about the same way as in recent *Homo sapiens*. The inferior margin of the tympanic plate is thin and again resembles the condition characteristic of modern humans.

Petralona and Arago 21 are two of the best crania from Europe. Brows are large, especially in Petralona where the torus is almost as thickened as in Broken Hill. Division of the brow into separate arches is more noticeable in

the case of Arago 21, but here, as in Petralona and the African faces, glabella is strongly projecting. Facial skeletons are massively constructed, although the orbits are somewhat smaller than in Broken Hill. Petralona resembles the Zambian hominid in measurements of facial projection (43). Comparable figures cannot be obtained for Arago 21. The latter specimen is damaged, but there are signs that the wall of the maxilla to either side of the nasal opening is more inflated than in other individuals. In Broken Hill, projection of the face is prominent, but there is less involvement of the nose itself.

Neither the Petralona nor the Arago parietal is quite as large as that of Broken Hill. Nevertheless, parietal lengths fall toward the upper end of the range noted for *Homo erectus*, while widths are greater. Clearly the middle portion of the vault is expanded, as is suggested by an overall increase in endocranial capacity. Some features of the Petralona occipital and temporal bones are also shared with recent humans. Lower jaws recovered at Arago Cave present a mix of archaic and more modern characters. Development of lateral prominences, marginal tori, and internal buttresses is comparable to that seen in *Homo erectus*. A few other traits may be of more use in distinguishing the Arago people. These include a chin eminence and the presence of a large triangular space behind the last molar tooth. In the Arago jaws, the root of the ascending ramus is located relatively far posteriorly. This particular feature is found also in Neanderthals, but by itself it need not signify any special relationship of Arago to these later European populations.

How Many Lineages of Later Homo?

If the fossils from Africa and Europe are not *Homo erectus*, then it must next be established whether just one lineage or several are to be recognized in the later Middle Pleistocene. Here contrasting views have been expressed. One commentator is Wolpoff (54), who would include all of the hominids from Europe in a single, highly dimorphic group. To Wolpoff, it is unimportant whether the root of this lineage is termed *Homo erectus* or *Homo sapiens*. All of its members are said to be connected in an unbroken evolutionary stream with the Neanderthals and with modern humans. Stringer (43, 45) disagrees and notes that there are substantial differences between hominids such as Swanscombe and Biache, which clearly share apomorphic characters with the Neanderthals, and a more archaic assemblage including Arago and Petralona. These latter individuals show few if any of the specialized traits associated with Neanderthals of Europe and the Middle East. Instead, they may be lumped broadly with archaic humans from other geographic regions, including sub-Saharan Africa. Stringer et al (46) have suggested that fossils such as Petralona, Arago, Mauer, Broken Hill, and Bodo may represent a primitive grade of our own species.

Another perspective is provided by Tattersall (47), who argues that taxic

diversity within *Homo* has been seriously underestimated. Tattersall attributes this to the fact that paleoanthropologists have focused their attention on variation within species, when dealing with the fossil record. This application of within-groups variability as a yardstick, coupled with disregard for the observation that morphological distinctions among closely related species may be slight, has resulted in much lumping of the fossils. Tattersall notes that this situation is unfortunate, as legitimate species must be identified and described before the phylogeny of hominids can be investigated. As an example, he points to “archaic” *Homo sapiens*, taken by most workers to encompass nearly all Pleistocene discoveries that are neither anatomically modern nor representative of *Homo erectus*. This loosely defined assemblage must contain several distinct morphs, and Tattersall would recognize one or perhaps two species in Europe in addition to the highly specialized Neanderthals.

On the basis of my own observations and measurements, I am inclined to agree with Stringer, at least in part. It is reasonable to assign Ndutu, Broken Hill, Petralona, and the Arago remains to a single taxon distinct from *Homo erectus* and later Neanderthals, even if the Arago specimens display a few Neanderthal characters. There is no clear justification for separating the African and European assemblages. I also endorse Tattersall’s point that groups exhibiting the archaic morphology of Broken Hill or Petralona should be set apart from anatomically modern people. To lump all recent humans, Neanderthals, and an assortment of Middle Pleistocene fossils together in one taxon is to ignore important differences.

Stringer et al (46) have attempted to deal with this obvious diversity by allocating the hominids to a series of grades within *Homo sapiens*. By placing Broken Hill, Petralona, and other “primitive” specimens in *Homo sapiens* grade 1, these authors do recognize similarities linking the fossils, although such shared characters are not treated in detail. However, there is no explicit effort to define a unit appropriate to evolutionary study. The relationships of populations making up grade 1 are not clarified, and the members of this grade cannot be regarded as ancestral to those of a succeeding level. Such a scheme simply does not tell us very much, as I have argued before.

In earlier papers (34, 37), I have advocated the use of a subspecies label for archaic populations of Africa, so as to distinguish this group from the Neanderthals of Europe. If this procedure were to be followed consistently, it would now be necessary to swell such a subspecies to encompass not only Middle Pleistocene Africans but also Arago and Petralona. If the Mauer jaw were added, this group could be termed *Homo sapiens heidelbergensis*. However, this expansion of a paleontological subspecies to include fossils from very distant provinces is inappropriate. The criteria by which such taxa should be recognized have never been fully agreed upon, but subspecies are

generally taken to be restricted geographically. Whether this category should be used to denote time-successive subdivisions of a species is also debatable. In cases where many successive subspecies are named, there is real danger of obscuring divisions among lineages.

What is important is that the fossils are sorted into groups that can be described and studied as evolutionary units (not grades). Samples of later Middle Pleistocene humans from Africa and Europe are admittedly small, and most of these individuals are incomplete. Under the circumstances, it is difficult to make extensive comparisons or to reach definite conclusions concerning classification. However, it can be argued that this material is best placed in a species of its own. If some of the confusion surrounding designation of certain hominids as "archaic" relative to other members of the same species can be done away with, then relationships of *Homo heidelbergensis* to *Homo erectus*, the Neanderthals, and modern people can be assessed in a more straightforward fashion.

Although the fossils from Africa and Europe share some features with *Homo erectus*, they depart in other respects from the morphology detailed for archaic people. Characters that can be interpreted as derived for *Homo heidelbergensis* include increased width of the parietal bone, coupled with parietal bossing. Rounding of the rear of the vault is more noticeable for Ndutu and the other crania than for *Homo erectus*. The upper part of the occipital bone is expanded relative to the nuchal area below. A bar-like articular tubercle marks the anterior margin of the glenoid cavity, and the tympanic plate is thin. Cranial bases appear to be shortened, and the basioccipital proportions of Broken Hill, for example, are comparable to those of recent people (24). Brain volume is larger than expected for *Homo erectus*. Evidence concerning the mandible is limited, but a chin eminence is present in at least one of the Arago individuals.

Some of these characters are synapomorphies linking the Middle Pleistocene group to modern humans, while others are indicative of trends common to both taxa. The African and European specimens display few if any derived traits that are not shared with *Homo sapiens*. As a consequence, it will be difficult to distinguish between these populations except by reference to the primitive features retained by *Homo heidelbergensis*. This is a problem that may become tractable only as the Middle Pleistocene record is pieced together in greater detail. Fossils from the Far East will surely be informative, when more complete descriptions are available. The cranium from Dali in China, for example, shows some primitive characters but has been called (early) *Homo sapiens*. Such discoveries will help to document the extent of variation present in later Middle Pleistocene populations, and systematic study of all the fossils will make it clearer whether the view of *Homo heidelbergensis* advanced here is accurate. Without more work, it will be hard to trace

evolutionary branching events that may have occurred late in the history of the *homo* clade.

The Question of Continuity in Asia

The record of human evolution in the Far East, like that of Europe, raises important questions. *Homo erectus* seems to have persisted in this region for a long time, and archaic populations were resident at sites such as Zhoukoudian until late in the Middle Pleistocene. As is well known, Weidenreich (52) believed that these hominids were part of a lineage evolving toward modern Asians. In support of this view, he cited a number of cranial, mandibular, dental, and even postcranial features characteristic of the Zhoukoudian people that occur in the skeletons of living Chinese. Links between *Homo erectus* of Java, the Ngandong assemblage, and present-day Australians were also claimed by Weidenreich (53), who pointed to the Wajak skulls as providing further confirmation of continuity in this region. This hypothesis has since been elaborated by Coon (11). Coon notes that the Ngandong crania are primitive in many respects, and for him these Solo people are still *Homo erectus*. In contrast, the Wajak individuals are unmistakably modern anatomically. Differences between the Solo and Wajak populations are substantial. At the same time, parallels between Wajak and recent Australians are not particularly clear (22, 56).

These difficulties with the Javanese record have prompted supporters of Weidenreich and Coon to turn increasingly to Australia itself. Thorne & Wolpoff (48) emphasize the burials from Kow Swamp and Cohuna in their discussion of Australasian human evolution. The Kow Swamp skeletons are of latest Upper Pleistocene age, and all can be characterized as *Homo sapiens* of fully modern aspect. These individuals are compared to Indonesian *Homo erectus*, as represented by the large (male?) cranium of Sangiran 17. Points of similarity are said to be apparent in both the vault and face, but traits of the facial skeleton are held to be most important in demonstrating the existence of a local "clade." Features suggesting continuity include eversion of the lower border of the cheek bone, rounding of the orbital margin, and overall reduction of the face and posterior dentition.

In a later report, these authors expand on the same themes (56). Treatment again centers on the Kow Swamp collection, which is compared to the Ngandong series rather than to Sangiran *Homo erectus*. Several "unique points of resemblance" are recognized. In one Kow Swamp cranium, for example, the most lateral part of the brow forms a triangular eminence. In another, there is hollowing on each side of the frontal bone, and this extends posteriorly as a depression paralleling the temporal line. These conditions, along with other "unusual" aspects of anatomy, are mirrored by the Solo population. Wolpoff et al (56) do concede that there is variation within these

assemblages, and they note that no single specimen closely resembling the Ngandong group has been recovered in Australia. However, they insist that similarities among the fossils from southeast Asia should be interpreted as evidence for gradual local change.

That there has been continuity of Asian populations throughout the Middle and the Upper Pleistocene is one interpretation of the fossil record. Versions of Weidenreich's view have been accepted by a number of paleoanthropologists, but this issue is not regarded as settled in all quarters. For the southeast Asian region, it must be questioned whether links between Javanese *Homo erectus* and later Australians are clear enough to make the hypothesis of local change compelling. One concern is that at least some of the characters identified by Thorne & Wolpoff (48) in Indonesian *Homo erectus* and in the Kow Swamp skeletons occur also in populations outside of Australia. Rounding of the inferior orbital margin is common in many crania of archaic *Homo*. Sangiran 17 and later Pleistocene Australians, described as showing overall reduction of the face and posterior dentition in the 1981 paper, are said instead to exhibit "facial massiveness" coupled with "dental megadonty" by Wolpoff et al (56). In any case, these traits are so general as to imply no special relationships among populations. The fact that facial heights and tooth dimensions for one Sangiran individual are similar to the Kow Swamp (male) means need not be read to indicate evolutionary continuity over several hundred thousand years.

The Ngandong assemblage is claimed to be "morphologically intermediate" between the Sangiran hominids and modern Australians, but this also can be questioned. Thorne & Wolpoff argue that the Ngandong crania differ from Sangiran 17 in many features, including form of the brow ridge and morphology of the occipital torus. I agree that some differences are present. The Solo brows do tend to be less thickened centrally, and the frontal lacks extreme postorbital narrowing. The most medial part of the occipital torus is projecting. At the same time, the Ngandong crania are very much like those of *Homo erectus*. Similarities extend not only to overall size and proportions of the braincase but also to many anatomical details. That all of the Indonesian hominids possess a common set of features was acknowledged earlier by Weidenreich and Coon, and this has been stressed again by Santa Luca (42). Certainly there is variation, but the Solo series does not seem clearly to be intermediate between archaic and modern populations.

Given this interpretation of the fossils, it would be reasonable to emphasize traits that occur consistently in Indonesian *Homo erectus* in any search for continuity with later Pleistocene Australians. Characters such as facial massiveness and megadonty are not appropriate. These terms are so broadly descriptive as to define complexes that can be found in all archaic populations. The use of certain more specific features by Wolpoff et al (56) may

also be challenged. Some of the traits said to link the Ngandong and Kow Swamp groups are either poorly expressed in the Sangiran fossils or differ explicitly from states described by Thorne & Wolpoff for Sangiran 17. Evidently these aspects of morphology exhibit a good deal of variability, and their importance as "clade features" is doubtful.

Solid evidence for evolutionary continuity is in fact not readily compiled. Indonesian *Homo erectus* displays many archaic features, whereas the Kow Swamp and Cohuna people are fully modern anatomically. This much is agreed by all workers, even if there is suspicion that several of the Kow Swamp crania have been deformed (7). The Kow Swamp postcranial bones also conform to the condition seen in recent humans (23). In my view, it is difficult to identify any special similarities of Middle Pleistocene *Homo erectus* to these later Upper Pleistocene Australians. The Ngandong assemblage from eastern Java does not fill the intervening gap. These specimens, still poorly dated, share many features with Sangiran *Homo erectus* and are best referred to the same taxon.

Here I do not wish to imply that there are no ties between *Homo erectus* and later humans. If continuity in southeast Asia cannot be established, then hominid history in this region may not have been as straightforward as Weidenreich proposed. It may be easier, when the newer fossils from China have been studied fully, to support a case for local change further to the North. Or we may have to look elsewhere, perhaps toward Europe, for evidence linking *Homo erectus* to later species.

SUMMARY

The first discoveries of *Homo erectus* were made in Asia, late in the last century. For more than 50 years, this extinct form of human was known only from the Far East. Other skulls and postcranial bones resembling the Asian fossils have since come to light in Africa. Assemblages from Olduvai Gorge and the Turkana basin provide much information about the morphology and behavior of populations inhabiting East Africa more than 1.6 million years ago. These people are similar to *Homo erectus* from China and Indonesia, and all of the fossils can be grouped in one species. *Homo erectus* differs in a number of respects from other hominids. This taxon can be distinguished easily from more modern humans, and traits such as heavy brows, a flexed occiput, certain cranial crests and ridges, and thickened vault bones set *Homo erectus* apart from earlier *Homo* and *Australopithecus*. It is my contention that *Homo erectus* can be defined as a real paleospecies rather than an arbitrary grade or stage in the evolution of our own lineage. Acknowledging this discrete nature of extinct taxa is important to the process of working out relationships. Until all valid species are recognized and described, it will not be possible to reconstruct the phylogeny of the hominids.

To date, most anthropologists have assumed that species of *Homo* succeeded one another in an unbroken linear sequence, ending with the appearance of modern *Homo sapiens*. This scenario invoking gradual change and continuity of populations in different geographic regions is open to serious challenge. Some of the oldest fossils unearthed in Europe are distinct in important ways from *Homo erectus*, and at the same time they do not closely resemble the Neanderthals or more recent Europeans. These crania and jaws from Petralona and Arago Cave are most similar to later Middle Pleistocene specimens from Broken Hill, Lake Ndutu, and Elandsfontein in Africa. While they have usually been regarded as representing an archaic grade of *Homo sapiens*, Petralona and Broken Hill may better be placed in a separate species. Whether fossils from sites such as Dali in China should also be referred to this taxon cannot be established until the Chinese material is more thoroughly described.

The question of continuity in Asia is addressed, with particular attention to Indonesia and Australia. Supporters of Weidenreich have insisted that this record is one of gradual change, illustrating the slow transformation of *Homo erectus* via the Solo population into modern forms. However, the Solo people may be characterized as *Homo erectus* rather than as "intermediate" in their morphology. There are no clear links in Southeast Asia between *Homo erectus* and recent humans. Perhaps the story of human evolution in this part of the world is more complex than pictured by Weidenreich, and we shall have to look toward Europe or Africa to find the ties of *Homo erectus* to later species.

ACKNOWLEDGMENTS

My work on earlier *Homo* has been carried out with the assistance of many individuals and institutions. I am grateful for access to the fossils and for all the help offered by my colleagues. The governments of Indonesia, Kenya, and Tanzania have kindly given me clearance to conduct research in these countries, and the National Science Foundation has provided funding. F. C. Howell, R. G. Klein and C. B. Stringer commented on a draft of the manuscript.

Literature Cited

1. Andrews, P. 1984. An alternative interpretation of characters used to define *Homo erectus*. *Cour. Forsch. Inst. Senckenberg* 69:167-75
2. Arambourg, C., Hoffstetter, R. 1963. Le gisement de Ternifine. *Arch. Inst. Paléontol. Hum.* 32:1-190
3. Bilsborough, A., Wood, B. A. 1986. The nature, origin and fate of *Homo erectus*. In *Major Topics in Primate and Human Evolution*, ed. B. Wood, L. Martin, P. Andrews, pp. 295-316. Cambridge: Cambridge Univ. Press
4. Brown, F. H., Feibel, C. S. 1985. Stratigraphical notes on the Okote Tuff Complex at Koobi Fora, Kenya. *Nature* 316:794-97
5. Brown, F. H., Harris, J., Leakey, R., Walker, A. 1985. Early *Homo erectus* skeleton from West Lake Turkana, Kenya. *Nature* 316:788-92
6. Brown, F. H., McDougall, I., Davies,

- T., Maier, R. 1985. An integrated Plio-Pleistocene chronology for the Turkana basin. In *Ancestors: The Hard Evidence*, ed. E. Delson, pp. 82–90. New York: Liss
7. Brown, P. 1981. Artificial cranial deformation: a component in the variation in Pleistocene Australian aboriginal crania. *Arch. Phys. Anthropol. Oceania* 16:156–67
 8. Cerling, T. E., Brown, F. H. 1982. Tuffaceous marker horizons in the Koobi Fora region and the lower Omo Valley. *Nature* 299:216–21
 9. Clarke, R. J. 1976. New cranium of *Homo erectus* from Lake Ndutu, Tanzania. *Nature* 262:485–87
 10. Cook, J., Stringer, C. B., Curren, A. P., Schwarcz, H. P., Wintle, A. G. 1982. A review of the chronology of the European Middle Pleistocene hominid record. *Yearb. Phys. Anthropol.* 25:19–65
 11. Coon, C. S. 1962. *The Origin of Races*. New York: Knopf
 12. Delson, E., Eldredge, N., Tattersall, I. 1977. Reconstruction of hominid phylogeny: a testable framework based on cladistic analysis. *J. Hum. Evol.* 6:263–78
 13. de Vos, J., Sartono, S., Hardja-Sasmita, S., Sondaar, P. Y. 1982. The fauna from Trinil, type locality of *Homo erectus*: a reinterpretation. *Geol. Mijnbouw* 61:207–11
 14. Geraads, D. 1981. Bovidae et Giraffidae (Artiodactyla, Mammalia) du Pléistocène de Ternifine (Algérie). *Bull. Mus. Nat. Hist. Nat. C* 3:47–86
 15. Geraads, D., Hublin, J. J., Jaeger, J. J., Tong, H., Sen, S., et al. 1986. The Pleistocene hominid site of Ternifine, Algeria: new results on the environment, age and human industries. *Quat. Res.* 25:380–86
 16. Grine, F. 1984. Comparison of the deciduous dentitions of African and Asian hominids. *Cour. Forsch. Inst. Senckenberg* 69:69–82
 17. Hay, R. L. 1976. *Geology of the Olduvai Gorge. A Study of Sedimentation in a Semi-arid Basin*. Berkeley: Univ. Calif. Press
 18. Holloway, R. L. 1975. Early hominid endocasts: volumes, morphology and significance for hominid evolution. In *Primate Functional Morphology and Evolution*, ed. R. H. Tuttle, pp. 393–415. The Hague: Mouton
 19. Howell, F. C. 1978. Hominidae. In *Evolution of African Mammals*, ed. V. J. Maglio, H. B. S. Cooke, pp. 154–248. Cambridge, Mass: Harvard Univ. Press
 20. Hublin, J. J. 1986. Some comments on the diagnostic features of *Homo erectus*. *Anthropos (Brno)* 23:175–85
 21. Jacob, T. 1975. Morphology and paleoecology of early man in Java. In *Paleoanthropology, Morphology and Paleoecology*, ed. R. H. Tuttle, pp. 311–25. The Hague: Mouton
 22. Jelinek, J. 1982. The East and Southeast Asian way of regional evolution. *Anthropos (Brno)* 21:195–212
 23. Kennedy, G. 1984. Are the Kow Swamp hominids “archaic?” *Am. J. Phys. Anthropol.* 65:163–68
 24. Laitman, J. T., Heimbuch, R. C., Crellin, E. S. 1979. The basicranium of fossil hominids as an indicator of their upper respiratory systems. *Am. J. Phys. Anthropol.* 51:15–34
 25. Leakey, M. D., Hay, R. L. 1982. The chronological position of the fossil hominids of Tanzania. In *L’Homo erectus et la Place de l’Homme de Tautavel Parmi les Hominidés Fossiles*, ed. M. A. de Lumley, pp. 753–65. Nice: CNRS
 26. Leakey, R. E., Walker, A. C. 1985. Further hominids from the Plio-Pleistocene of Koobi Fora, Kenya. *Am. J. Phys. Anthropol.* 67:135–63
 27. Le Gros Clark, W. E. 1964. *The Fossil Evidence for Human Evolution*. Chicago: Univ. Chicago Press
 28. Leinders, J. J. M., Aziz, F., Sondaar, P. Y., de Vos, J. 1985. The age of the hominid-bearing deposits of Java: state of the art. *Geol. Mijnbouw* 64:167–73
 29. Liu, Z. 1985. Sequence of sediments at Locality 1 in Zhoukoudian and correlation with loess stratigraphy in northern China and with the chronology of deep-sea cores. *Quat. Res.* 23:139–53
 30. Macintosh, N. W. G., Larnach, S. L. 1972. The persistence of *Homo erectus* traits in Australian aboriginal crania. *Oceania* 7:17
 31. Matsu’ura, S. 1982. A chronological framing for the Sangiran hominids. *Bull. Nat. Sci. Mus. (Tokyo)* 8:1–53
 32. McDougall, I. 1985. K-Ar and ⁴⁰Ar/³⁹Ar dating of the hominid-bearing Pliocene-Pleistocene sequence at Koobi Fora, Lake Turkana, northern Kenya. *Geol. Soc. Am. Bull.* 96:159–75
 33. Pope, G. 1983. Evidence on the age of the Asian Hominidae. *Proc. Natl. Acad. Sci. USA* 80:4988–92
 34. Rightmire, G. P. 1976. Relationships of Middle and Upper Pleistocene hominids from sub-Saharan Africa. *Nature* 260:238–40
 35. Rightmire, G. P. 1979. Cranial remains of *Homo erectus* from Beds II and IV,

- Olduvai Gorge, Tanzania. *Am. J. Phys. Anthropol.* 51:99-115
36. Rightmire, G. P. 1981. Patterns in the evolution of *Homo erectus*. *Paleobiology* 7:241-46
 37. Rightmire, G. P. 1983. The Lake Ndutu cranium and early *Homo sapiens* in Africa. *Am. J. Phys. Anthropol.* 61:245-54
 38. Rightmire, G. P. 1984. Comparisons of *Homo erectus* from Africa and Southeast Asia. *Cour. Forsch. Inst. Senckenberg* 69:83-98
 39. Rightmire, G. P. 1985. The tempo of change in the evolution of mid-Pleistocene *Homo*. In *Ancestors: The Hard Evidence*, ed. E. Delson, pp. 255-64. New York: Liss
 40. Rightmire, G. P. 1986. Species recognition and *Homo erectus*. *J. Hum. Evol.* 15:823-26
 41. Rightmire, G. P. 1986. Stasis in *Homo erectus* defended. *Paleobiology* 12:324-25
 42. Santa Luca, A. P. 1980. *The Ngandong Fossil Hominids: A Comparative Study of a Far Eastern Homo erectus Group*. New Haven: Yale Univ., Dept. Anthropol.
 43. Stringer, C. B. 1983. Some further notes on the morphology and dating of the Petralona hominid. *J. Hum. Evol.* 12:731-42
 44. Stringer, C. B. 1984. The definition of *Homo erectus* and the existence of the species in Africa and Europe. *Cour. Forsch. Inst. Senckenberg* 69:131-43
 45. Stringer, C. B. 1985. Middle Pleistocene hominid variability and the origin of late Pleistocene humans. In *Ancestors: the Hard Evidence*, ed. E. Delson, pp. 289-95. New York: Liss
 46. Stringer, C. B., Howell, F. C., Melentis, J. K. 1979. The significance of the fossil hominid skull from Petralona, Greece. *J. Archaeol. Sci.* 6:235-53
 47. Tattersall, I. 1986. Species recognition in human paleontology. *J. Hum. Evol.* 15:165-76
 48. Thorne, A., Wolpoff, M. H. 1981. Regional continuity in Australasian Pleistocene hominid evolution. *Am. J. Phys. Anthropol.* 55:337-49
 49. Weidenreich, F. 1936. The mandibles of *Sinanthropus pekinensis*: a comparative study. *Palaeontol. Sin. (Ser. D)* 7:1-162
 50. Weidenreich, F. 1937. The dentition of *Sinanthropus pekinensis*: a comparative odontology of the hominids. *Palaeontol. Sin. (New Ser. D)* 1:1-180
 51. Weidenreich, F. 1941. The extremity bones of *Sinanthropus pekinensis*. *Palaeontol. Sin. (New Ser. D)* 5:1-150
 52. Weidenreich, F. 1943. The skull of *Sinanthropus pekinensis*: a comparative study of a primitive hominid skull. *Palaeontol. Sin. (New Ser. D)* 10:1-484
 53. Weidenreich, F. 1945. Giant early man from Java and South China. *Anthropol. Pap. Am. Mus. Nat. Hist.* 40:1-134
 54. Wolpoff, M. H. 1980. Cranial remains of Middle Pleistocene European hominids. *J. Hum. Evol.* 9:339-58
 55. Wolpoff, M. H. 1984. Evolution in *Homo erectus*: the question of stasis. *Paleobiology* 10:389-406
 56. Wolpoff, M. H., Wu, X., Thorne, A. 1984. Modern *Homo sapiens* origins: a general theory of hominid evolution involving the fossil evidence from East Asia. In *The Origins of Modern Humans*, ed. F. H. Smith, F. Spencer, pp. 411-83. New York: Liss
 57. Woo, J. K. 1964. Mandible of *Sinanthropus lantianensis*. *Curr. Anthropol.* 5:98-101
 58. Woo, J. K. 1966. The skull of Lantian man. *Curr. Anthropol.* 7:83-86
 59. Wood, B. A. 1984. The origin of *Homo erectus*. *Cour. Forsch. Inst. Senckenberg* 69:99-111
 60. Wu, R. 1985. New Chinese *Homo erectus* and recent work at Zhoukoudian. In *Ancestors: the Hard Evidence*, ed. E. Delson, pp. 245-48. New York: Liss
 61. Wu, R., Dong, X. 1982. Preliminary study of *Homo erectus* remains from Hexian, Anhui. *Acta Anthropol. Sin.* 1:2-13
 62. Wu, R., Lin, S. 1983. Peking man. *Sci. Am.* 248:86-94