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Early Man in East Africa

Recent excavations in Olduvai Gorge, Tanzania, have laid bare a new chapter in human evolution

Phillip V. Tobias

Olduvai Gorge in Northern Tanganyika (Republic of Tanzania) has in recent years thrown a flood of light on an early chapter in the evolution of man. Between 1955 and 1963, L. S. B. Leakey, M. D. Leakey, and their sons and helpers uncovered fossil bones representing no fewer than 14 individuals from various levels in the Olduvai strata (*1*). Although detailed descriptions are yet to be published (*2*), it is clear that earlier and lower mid-Pleistocene deposits of East Africa contain the remains of at least two different kinds of fossil hominids (that is, members of the Hominidae, the family of man). The first group of fossils fits comfortably into a well-defined category, the australopithecines, which have long been recognized as a partially hominized group, that is, a group possessing some characteristics like those of *Homo*. The second assemblage has proved most difficult to place in any existing category. After exploring every other possibility, we have been forced to attribute this second group of fossils to a new and lowly species of *Homo*, namely *Homo habilis*: this species represents a more markedly hominized lineage than the australopithecines and comprises a hitherto-unrecognized and even unsuspected transitional or intermediate form of early man (*3*).

In this article I consider the history and some of the characteristics of the new fossils, as well as their cultural and evolutionary position, and propose modifications to some existing schemes of hominid phylogeny in the light of these new discoveries.

The Olduvai Sequence

Before I review the new discoveries in detail, it may be useful to describe briefly the Olduvai stratigraphic succession (Fig. 1).

Olduvai Gorge has been cut by river action through a deep succession of old sediments, tuffs, and lavas. From the exposed strata, a remarkable series of fossils and implements has been recovered, ranging in age from Lower to Upper Pleistocene.

The strata exposed in the walls of Olduvai Gorge were divided by Hans Reck into five beds, numbered I to V, from the lowest upwards. This classification was adopted and the limits of the beds were more precisely defined by Leakey and, more recently, by Hay (*4*). It should be stressed, however, that these beds are not absolute stratigraphic units corresponding to sharp divisions in the Pleistocene sequence of events. Rather they are conveniently mappable units. Thus, as Hay has pointed out, two different marker beds have in various parts of the Gorge been regarded as the top of Bed I. Again, while Reck defined the base of Bed I as the basalt flows, Hay has preferred to include within Bed I the tuffs beneath the basalt. Hay thus regards the basalt flows as a constituent of Bed I in the eastern part of the Gorge.

Further, the newer analyses of fauna made by Leakey and his collaborators (*5*) tend to relate the fauna of the lower part of Bed II to that of Bed I and to interpret both as belonging to a final Villafranchian faunal stage. On the other hand, the fauna of the middle and upper part of Bed II is considered post-Villafranchian and so to be associated with that of Beds III and IV. The complex of Middle and Upper II, III, and IV comprises a mid-Pleistocene stratigraphic sequence.

In this presentation, the subdivision into five beds will be used to provide a background against which to consider the hominid remains.

Potassium-argon dates are available for several levels within Bed I. The span of time represented by these Beds is suggested by ages 1.75 and 1.65 million years for two levels in the lower half of Bed I. In a word, the chapters of human evolution which are dealt with here cover the period from about 2 million to about half a million years ago.

The author is professor and head of the Department of Anatomy at the University of the Witwatersrand, Johannesburg, Republic of South Africa.

The Australopithecine Chapter

Exactly 40 years have elapsed since R. A. Dart published a description of a new kind of higher primate which had been recovered from a limestone fissure at Taung in South Africa (*6*). This discovery was one of the most remarkable, perhaps the most important, in the history of paleoanthropology. Earlier discoveries of fossilized human ancestors had shown unequivocally human affinities: this is true of the Neanderthal group and even of the earlier and morphologically more primitive Java ape-man, *Homo erectus* (or *Pithecanthropus*, as he has been called until fairly recently). But the Taung specimen differed from the others in being so much smaller-brained, bigger-toothed, and in other respects morphologically more archaic, that its precise affinities remained a cause of dispute for decades. Initially, Dart claimed no more than that it was an ape with a number of features suggesting hominization, that is, an advance in a general human direction. He therefore called it *Australopithecus africanus*—simply the "southern ape of Africa."

With the wisdom of hindsight, we are today able to recognize in Dart's fossil the first real proof of the animal origins of man, the first concrete fossil evidence that Darwin's theory of the origin of species by small modifying steps and gradations from other pre-existing species is applicable to man. For here was an apelike creature which showed in its anatomical makeup a greater number of resemblances to hominids than are shown by any of the existing manlike apes of Africa or Asia.

It took time, as well as the discovery of many new specimens of *Australopithecus* (Table 1), the patient study of their anatomical features, and a closer look at the living great apes, to reach the now widely accepted conclusion that the australopithecines were an early branch of the Hominidae, the family of man, rather than of the Pongidae, the family of the apes. No fewer than eight sites in Africa have yielded australopithecine fossils (Fig. 2).

Most of the African australopithecines belong to deposits which have been classified, on comparative faunal evidence, as Lower Pleistocene. At least three sites have provided evidence that the australopithecines survived in Africa into the Middle Pleistocene—namely Swartkrans and Kromdraai in the Transvaal and Peninj (Natron) in Tanganyika.

Of all early hominid groups, the Australopithecinae are the best represented in our fossil storehouses. From the South African sites alone, no fewer than 315 australopithecine entries have been prepared for the forthcoming new edition of the *International Catalogue of Fossil Man*: some comprise a single isolated tooth, some an almost complete cranium. If we accept that all the isolated teeth from Swartkrans and Sterkfontein do indeed belong to australopithecines, the total number of australopithecine teeth now available is over 600 (Table 2). The figure for Olduvai includes only the 16 maxillary teeth of the type specimen of *A. boisei* (*7*), although others may need to be added to this total on further study. Juvenile and adult specimens are known, as well as male and female. Apart from age and sex variations, more than one kind of australopithecine is represented; the diversity is such that some would classify them as different genera, while others have lumped them into one genus (*Australopithecus*) with several subgenera; yet others would see them as simply different species of a single genus.

Whatever the proper classification, there is an abundance of evidence bearing on the anatomical structure and variation, the behavioral (or cultural) characteristics, and the ecological, geographical, and temporal background of the australopithecines. These lines of evidence concur in demonstrating that at least some of the known australopithecines, or of slightly earlier creatures of very similar aspect, fulfill the morphological requirements for a hypothetical human ancestor.

East African Australopithecines

Australopithecines have been found at three East African sites, Garusi (1939), Olduvai (1955, 1959, and ?1963), and Peninj (1964), all situated in northern Tanganyika.

The first specimen was found by Kohl-Larsen at Garusi in 1939. It comprises a fragment of upper jawbone containing both premolars. In 1943 Kohl-Larsen stated that his specimen resembled *Australopithecus* (*8*), but Weinert later reclassified it as an African species of *Meganthropus* (*9*). However, Robinson (*10*) has shown convincingly that the premolars fall within the range for the South African *Australopithecus* from Sterkfontein. This is the smaller-toothed *Australopithecus* which is usually classified today as *A. africanus*. As yet, the Garusi specimen is the only evidence we have suggesting the presence in East Africa of the gracile *africanus* species of australopithecine. The other East African australopithecines are of the larger-toothed *boisei* or *robustus* species.

The most important East African australopithecine is the specimen originally called by Leakey *Zinjanthropus boisei* (*11*) and now reclassified by Leakey, Tobias, and Napier as a species of the genus *Australopithecus*, namely *A. boisei* (*3*). For the time being the name *Zinjanthropus* is being retained to designate a subgenus within the genus *Australopithecus*. The specimen comprises a very complete cranium, including all 16 upper teeth; the wisdom teeth or third molars were still in process of erupting, suggesting that the individual was in his late teens at the time of death. A brief preliminary description has been given by Leaky (*1, 11*). Tobias (*12*) has placed on record the cranial capacity as 530 cubic centimeters; that is, the specimen's brain was no larger than that of the small-toothed *A. africanus* child from Taung. A detailed monograph on *A. boisei* will appear as part of a series of volumes on Olduvai Gorge by Leakey and his collaborators (*2*). It may be mentioned here that *A. boisei* is the biggest-toothed and most robust of all the australopithecines, exceeding in most dental dimensions even the largest-toothed of the crassident *A. robustus* group from Swartkrans in the Transvaal (Fig. 3).

It is probable that more large-toothed australopithecines are present in the Olduvai deposits. Three adult teeth, found at the site MNK II, in the lower middle part of Bed II, are for the most part of australopithecine form, shape, and dimensions (Fig. 1, hominid 15). According to Leakey (*5*), this part of Bed II is characterized by a post-Villafranchian fauna; it is early mid-Pleistocene. These teeth were referred to by Leakey and Leakey (*1*), but no attempt has yet been made to identify them specifically. Other australopithecine remains may well be present in Bed II, including the very large molar discovered in 1955, high in Bed II (*13*). Detailed studies of all these specimens are under way, and it will be some years before the complete series of full reports is published.

The third site in East Africa to yield an australopithecine is Peninj, on the west side of Lake Natron, about 80 kilometers northeast of Olduvai Gorge. Here, in January 1964, one of Leakey's assistants, Kamoya Kimeu, a member of the expedition led by Richard Leakey and Glynn Isaac, discovered a nearly complete and superbly preserved mandible of a large-toothed australopithecine (*1*). According to Leakey's provisional identification of the fauna from this new site, it is of early mid-Pleistocene age and thus much later than the original *A. boisei* from Olduvai. It would seem to be equivalent in age to the upper part of Bed II, or even to the overlying Beds III and IV, in the Olduvai sequence. Despite this age difference, it is of interest to note that the mandibular dental arcade fits that of the maxilla of the Olduvai *A. boisei* almost perfectly and may be provisionally identified as a mandible of *A. boisei* (Fig. 4). Although age comparisons between East and South Africa are fraught with difficulties, it would seem likely that the Peninj australopithecine is comparable in age with those of Swartkrans and Kromdraai. The three sites give evidence that the large-toothed australopithecines survived in Africa well into the Mid-Pleistocene (Table 3).

Table 1. Dates of discovery of australopithecine fossils.

1924	Taung (S. Afr.)
1936–1949	Sterkfontein Type Site (S. Afr.)
1938–1954	Kromdraai (S. Afr.)
1939	Garusi (E. Afr.)
1947–1961	Makapansgat (S. Afr.)
1948–1952	Swartkrans (S. Afr.)
1955–1959	Olduvai (E. Afr.)
1957–1958	Sterkfontein Extension Site (S. Afr.)
1964	Peninj, Lake Natron (E. Afr.)

Unlikely Claimants for Australopithecine Status

At least one other fossil from Africa has been claimed to be australopithecine, namely an incomplete cranium discovered in northern Chad and described by Coppens as an australopithecine (*14*). In 1963, we invited Coppens to visit South Africa and study the original australopithecine material. As a result of his study, Coppens has reached the same conclusion as Leakey and I reached independently, namely that the Chad fragment represented a more advanced hominid than *Australopithecus*. It may belong to the new species, *Homo habilis*, or even to the more advanced *Homo erectus*. The original diagnosis of the Chad fauna as very early Villafranchian is likewise being revised by Coppens; the site is apparently late Villafranchian. Unfortunately, the extremely weathered and distorted state of the Chad specimen may preclude exact comparison with other hominine remains, but it is possible that further hominid material and stone tools may yet be discovered in the area.

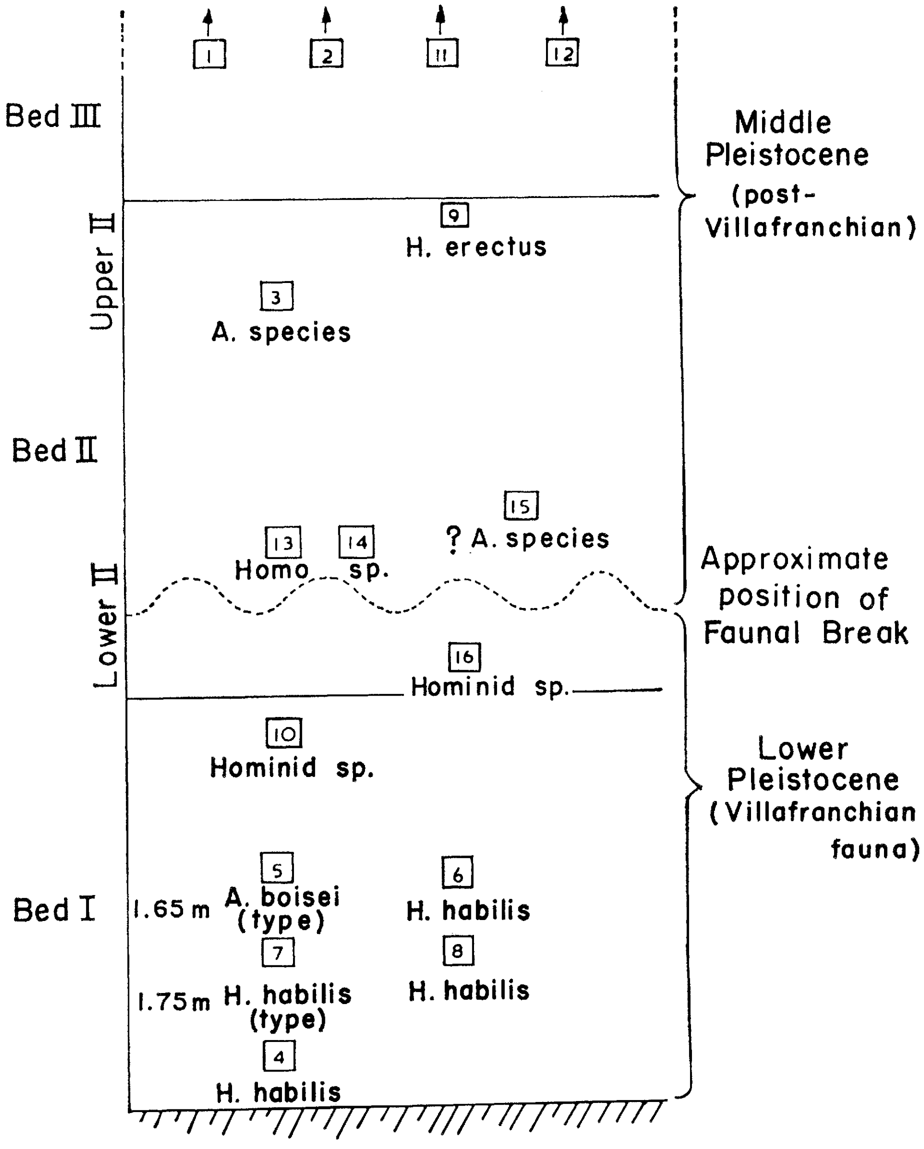

Fig. 1. Schematic representation of the lower half of the Olduvai sequence, showing the approximate vertical positions of hominid fossils (numerals enclosed in squares). The potassium-argon dates are indicated near the left margin (m = million years).

The possibility has been raised that the teeth and cranial fragments found outside Africa, at Ubeidiya on the Jordan River in Israel, may have belonged to an australopithecine (*15*). From a preliminary study of the scanty human remnants, generously placed at my disposal by M. Stekelis, these remains are highly likely to have belonged to *Homo* rather than to *Australopithecus*, although it may be impossible, without the discovery of further material, to attribute them to a particular species of *Homo*.

From Java has come another form of early hominid known as *Meganthropus palaeojavanicus*, of which three or possibly four mandibular fragments were found in the Djetis Beds dated to the beginning of the Middle Pleistocene (*16*). Robinson has suggested that this Javanese *Meganthropus* is simply an australopithecine (*10*). However, from a recent reexamination of the originals of *Meganthropus* I and II in comparison with original material from Africa, von Koenigswald and I concluded that, while *Meganthropus* *palaeojavanicus* has some strong resemblances to australopithecines, it shows several features in which it is somewhat advanced beyond the australopithecine grade (*17*). In this sense, it stands in the same relation to *Australopithecus* as does *Homo habilis* in Africa, except that *Homo habilis* has departed further from *Australopithecus* in some respects.

Another group of Asian fossils has been thought to possess australopithecine status, namely a group of isolated teeth from China attributed by von Koenigswald to *Hemanthropus peii* (*18*). Simons has suggested that these teeth are australopithecine (*19*). It is not impossible, however, that they may represent a more advanced hominid, such as *Homo habilis*; but it may be impossible to resolve the problem of their status until more specimens are recovered, including teeth in a mandible or cranium (*17*). The position of some claimants to australopithecine status is summarized in Table 4.

In sum, the case for the existence of an australopithecine stage in Asia remains unproven; the only convincing australopithecine sites remain the eight East and South African sites listed in Table 1.

The Gap between Australopithecus and Homo

Although *Australopithecus* fulfills the morphological requirements for an ancestor of man, there remains a substantial gap between the australopithecines and the most lowly representative of the hominines hitherto recognized (that is, *Homo erectus*, formerly called *Pithecanthropus, Sinanthropus, Atlanthropus*, and so on). The size of this morphological gap may best be illustrated by reference to three parameters which have shown most marked change during the process of hominization in the Pleistocene: brain size, tooth size, and tooth shape. Unfortunately, we cannot use the evidence of hand and foot bones, since we have insufficient evidence bearing on these features in *Australopithecus* and in *Homo erectus*. On the other hand, good samples of teeth and fair samples of braincases and endocranial casts exist for both of these groups.

From seven australopithecine crania it has been possible to make fair estimates of cranial capacity. One of these crania is the Olduvai type specimen of *A. boisei* and six are of small-toothed South African specimens. They include the child from Taung, whose estimated capacity is 500 to 520 cm^3; when allowance was made for probable changes with growth, his adult capacity was estimated by various workers (*12*) as 570, 600, and 624 cm^3, bigger, in fact, than any australopithecine capacity actually measured. Selecting the median value (600 cm^3), we obtain an australopithecine range of 435 to 600 cm^3 and a mean of 508 cm^3. The range for nine *Homo erectus* crania, including 1000 cm^3 for Olduvai hominid 9 (*20*), is 775 to 1225 cm^3 with a mean of 978 cm^3. The cranial capacity of the smallest-brained *H. erectus* was originally estimated by von Koenigswald as 750 cm^3; an earlier estimate by Weidenreich (*21*), subsequently disavowed by him, was 850 cm^3, while Boule and Vallois give 815 cm^3 (*22*). Most workers have accepted Weidenreich's final estimate of 775 cm^3. These variations, however, reinforce an impression I gained recently when, through the courtesy of D. Hooijer and G. H. R. von Koenigswald, I examined the original Javanese crania: there is a need for reassessment of the capacities of the several Javanese crania of *Homo erectus* (*23*).

Figure 5 represents the ranges and the gap between the presently accepted estimates of cranial capacity for *Australopithecus* and *H. erectus*. There is an interval of 175 cm^3 between the capacities of the largest-brained australopithecine and the smallest-brained *H. erectus*. However, this difference is rather meaningless unless we consider the estimated body size of the two forms. Jerison has analyzed brain size (to which cranial capacity is an approximation) into two independent components, one of which is determined by body size and the other of which is associated with improved adaptive capacities (*24*). Given certain assumptions, it has further been possible to estimate the number of cortical nerve cells in the brain as a whole, as well as in each of the two components. The number of "excess" nerve

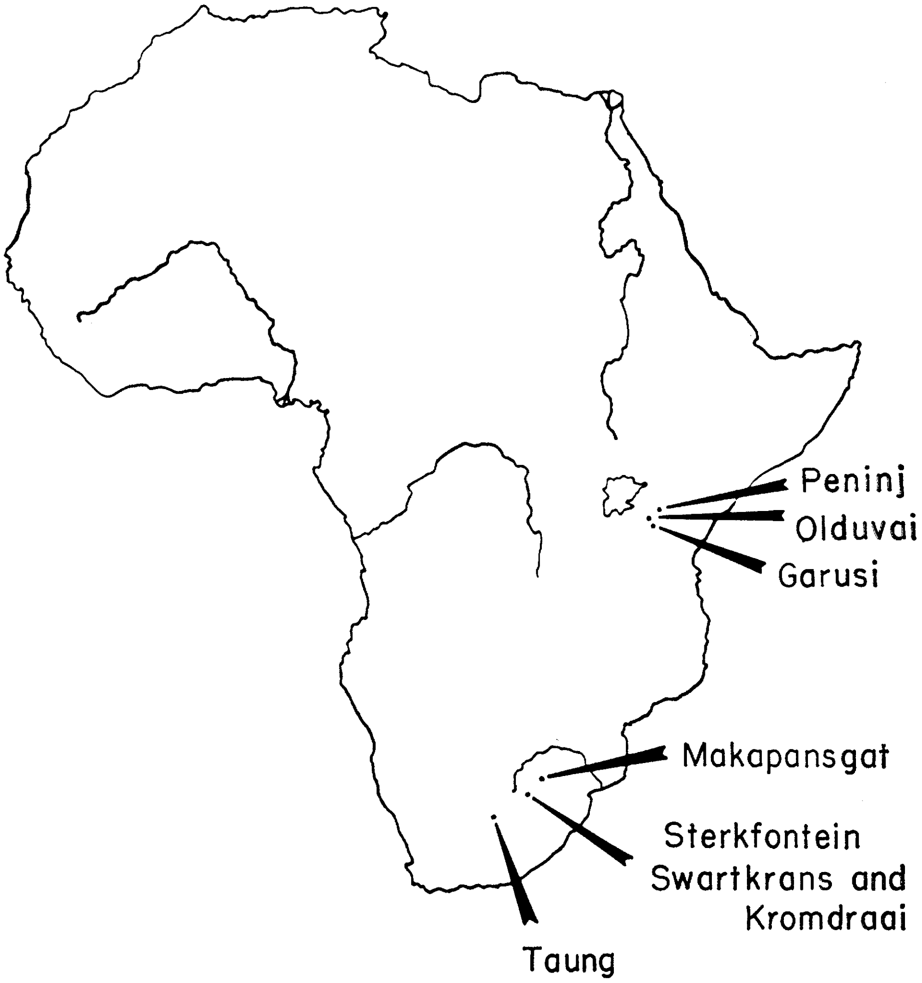

Fig. 2. The African sites which have yielded fossilized remains of *Australopithecus*, popularly known as ape-men, near-men, or half-men. The three northern sites are in the Republic of Tanzania; the five southern sites are in the Republic of South Africa.

Table 2. Number of australopithecine teeth from various sites available for study.

Taung	24
Sterkfontein	162
Kromdraai	39
Swartkrans (*35*)	311
Makapansgat	55
Garusi	2
Peninj (Natron)	16
Olduvai (*7*)	16
Total	621

cells—that is, of cells over and above those which can be accounted for by body size—may then be taken as a measure of the real advancement in brain volume, irrespective of body size.

The following are estimates of the numbers of excess nerve cells based partly on Jerison's estimates and partly on my own (*25*):

African great apes	3.4 to 3.6 billion
Australopithecines	4.0 to 5.0 billion
Homo erectus	5.8 to 8.4 billion
Homo sapiens	8.4 to 8.9 billion

If our estimates are correct, there is a bigger gap between *Australopithecus* and *H. erectus* than between the apes and the australopithecines or between *H. erectus* and *H. sapiens*. If, instead of comparing ranges, we compare the mid-values for the groups, we obtain values of 3.5, 4.5, 7.1, and 8.65 billion for the four groups, respectively. Clearly, there is a greater distance between *Australopithecus* and *H. erectus* than between any other two consecutive groups.

To compare dental features of the two groups, it is necessary to point out that on the basis of tooth size, the australopithecines fall into two more or less well-defined subgroups. The first—represented by the fossils from Taung, Sterkfontein, Makapansgat, and Garusi—has somewhat smaller cheek teeth (premolars and molars), but somewhat larger anterior teeth (incisors and canines); this group is called *Australopithecus africanus*. The second—represented by the australopithecine fossils from Swartkrans, Kromdraai, Olduvai, and Peninj (Natron)—has larger cheek teeth and smaller front teeth; this group comprises *A. robustus* and *A. boisei* in the most recent classifications.

Figure 6 demonstrates the ranges of tooth sizes for *A. africanus* and *H. erectus*. Once more the extent of the morphological distance between the Australopithecinae and *H. erectus* is apparent. The differences are more striking when *A. robustus* and *A. boisei* are compared with *H. erectus*.

Similarly, Fig. 7 reflects variations in the shape and size of the teeth of *A. africanus* and *Homo erectus*. In a word, australopithecine cheek teeth are broader buccolingually, while hominine cheek teeth are narrower (but more elongate) from front to back.

Table 3. Chronological and geographical distribution of australopithecines. The relative chronological positions of the East and South African sites are uncertain, as indicated by the question marks. Whereas potassium-argon dates are available for Olduvai, none is available for South African sites. Comparisons of fauna are valuable among the sites within each major geographical zone, as exemplified by forthcoming new analyses of fauna from South African sites by H. B. S. Cooke and from East African sites by L. S. B. Leakey. Since comparisons between fauna from the East and South African sites are somewhat vitiated by the large distance and ecological differences between the areas, this scheme must be regarded as highly provisional.

	South Africa	*East Africa*
Middle Pleistocene	Kromdraai	?Olduvai II (Upper)
		?Peninj (Natron)
	Swartkrans	?Olduvai II (Middle)
	?Sterkfontein Extension Site	?Olduvai II (Lower)
Lower Pleistocene		?Garusi
	Makapansgat	
	Sterkfontein Type Site	
	Taung	
		Olduvai I

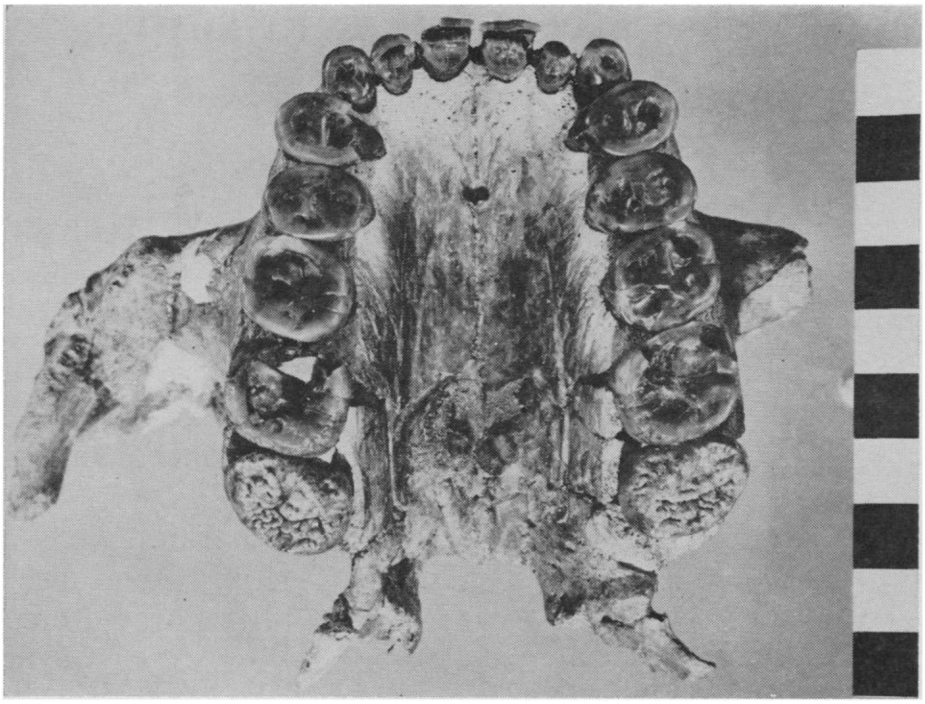

Fig. 3. The teeth and palate of the large-toothed hominid, *Australopithecus (Zinjanthropus) boisei*, from Bed I, Olduvai Gorge.

On the basis of these three parameters, there is a clear and sizable gap between known australopithecines and *Homo erectus*. Until recently, it has apparently been tacitly assumed that *Australopithecus* graded more or less insensibly into *Homo erectus* in the manner postulated in general terms by Charles Darwin. It is therefore of no small interest to note that so large a gap exists, not only with respect to one parameter, brain size, but, in the same creatures, with respect to dental traits.

It is this gap that has been filled by *Homo habilis*, the newly discovered hominid which, with respect to the three parameters used to characterize the gap, as well as with respect to other morphological markers, lies in a largely intermediate position.

Homo habilis: the Early Pleistocene Hominine

The family Hominidae may be divided into two subfamilies, the Australopithecinae and the Homininae. The term "hominine" is the common or colloquial name connoting a member of the subfamily Homininae.

From at least four levels in Bed I

and the lower (Villafranchian) and middle parts of Bed II in the Olduvai succession have come skeletal remains of another type of hominid (Fig. 1). This hominid differs widely from *A. boisei*, the large-toothed australopithecine found in the same beds. For instance, the teeth are appreciably smaller than those of *A. boisei.* While the sizes of the teeth of *A. boisei* in general fall *above* the top of the range for the South African australopithecines, the teeth of this second hominid, especially the premolars, fall at or below the lower end of the australopithecine range *(23)*. Such wide divergence between the two hominids from the same site is far in excess of what can be attributed to sexual dimorphism: in any event, it is accompanied by divergences in shape, proportions, and detailed morphology of the teeth, in cranial shape and curvature, and in cranial capacity. Clearly the second batch of fossils represents another type of hominid. In almost all the departures of the second hominid from the australopithecine morphological pattern, it approaches more closely to the hominine pattern. In other words, the total pattern is more markedly hominized than that of *Australopithecus.* To the Bed I form characterized by these more hominized features we have given the name *Homo habilis.*

The formal naming of the species was announced by Leakey, Tobias, and Napier on 4 April 1964 *(3)*. The generic name implies that this primitive hominid belonged to the genus *Homo*, while the specific name *habilis*, which was suggested by R. A. Dart, means "able, handy, mentally skillful, vigorous," from the inferred ability of the man to make stone tools.

In accordance with international convention in the naming of new species, one set of remains was selected as the "type specimen" of *Homo habilis.* These were the remains of a juvenile (No. 7 in Fig. 1) whose bones—comprising a lower jaw with teeth, an upper molar tooth, the incomplete parietal bones of the cranial vault, and a set of hand bones—were found scattered on a single floor at the site FLK NNI in the Olduvai Gorge (Fig. 8). In the 3 years that elapsed between his discovery and his naming, he was known as "pre-Zinjanthropus" because the living floor on which his bones were found lies some 35 cm *below* the living floor on which "Zinjanthropus" (or *A. boisei*) had been found. The youth of the individual represented was attested by the state of eruption of the teeth and by the signs of incomplete growth and ossification of the other bones, thus permitting the confident association of this group of bones as those of a single individual.

Apart from the type specimen, remains of four other individuals—three from Bed I (hominids 4, 6, and 8 in Fig. 1) and one from the middle part of Bed II (hominid 13)—were listed as "paratypes" of *Homo habilis.* Bones from two further individuals in the lower and middle parts of Bed II (hominids 14 and 16 in Fig. 1) were referred to the same species, but one of these only provisionally. All told, this batch of remains comprises some 40 teeth, two tolerably complete lower jawbones and a fragment of a third, parts of a pair of upper jawbones, varying portions of the brain-

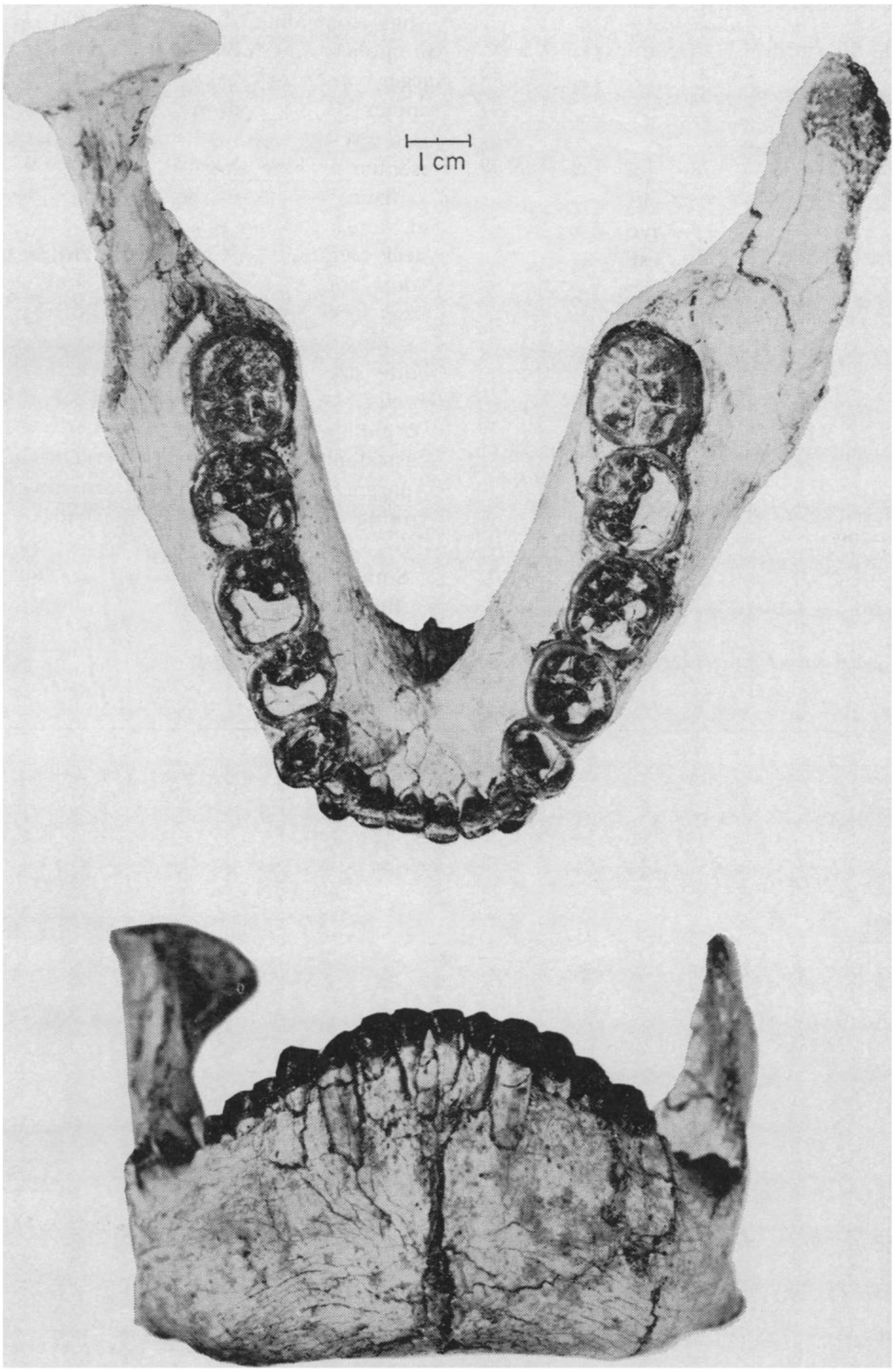

Fig. 4. Two views of the lower jawbone and teeth of a large-toothed australopithecine from Peninj, next to Lake Natron, some 80 km northeast of Olduvai Gorge. The very small front teeth (incisors and canines) and very large cheek teeth (premolars and molars) characteristic of the robust australopithecine are well shown. This mandible represents a Middle Pleistocene survivor of the African australopithecines, probably a late member of the Olduvai species, *A. boisei.*

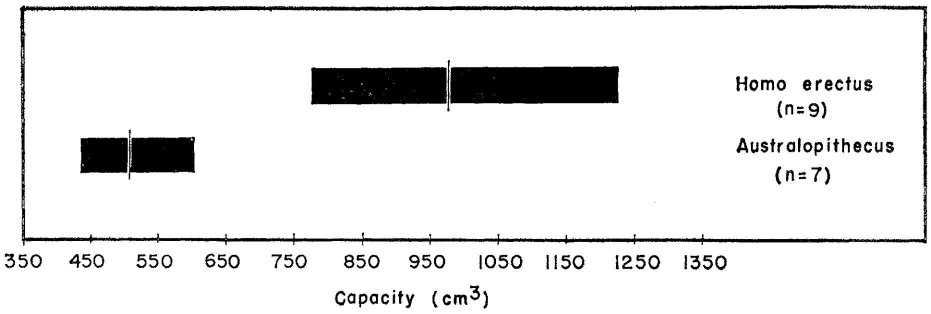

Fig. 5. The ranges and means of cranial capacity in two early hominids, *Australopithecus* (including both small- and large-toothed forms) and *Homo erectus* (formerly known as *Pithecanthropus*). The largest estimated australopithecine capacity is 600 cm^3 and the smallest of *Homo erectus* 775 cm^3.

Table 4. Some fossil hominids which have been claimed to be australopithecines.

Nature of specimen	Original designation	Revised attribution	Latest interpretation
		Swartkrans	
1 mandible, 1 mandibular fragment, and 1 radial fragment	*Telanthropus capensis*	Australopithecine (Dart, Le Gros Clark)	*Pithecanthropus* (Simonetta), *Homo erectus* (Robinson)
		Chad	
Craniofacial fragment	Australopithecine	*Homo* sp.	*Homo* sp. (unpublished)
		Ubeidiya	
2 teeth and 4 cranial fragments	Hominid	?Australopithecine	*Homo* sp. (unpublished)
		Sangiran (*Djetis Beds*)	
3 mandibular fragments	*Meganthropus palaeojavanicus*	Australopithecine (Robinson)	More advanced than African Australopithecine (*?Homo* sp.) (Tobias and von Koenigswald)
		China	
Isolated teeth	*Hemanthropus peii* (originally *Hemianthropus peii*)	Australopithecine (Simons)	Status not clear (*?Homo habilis*)

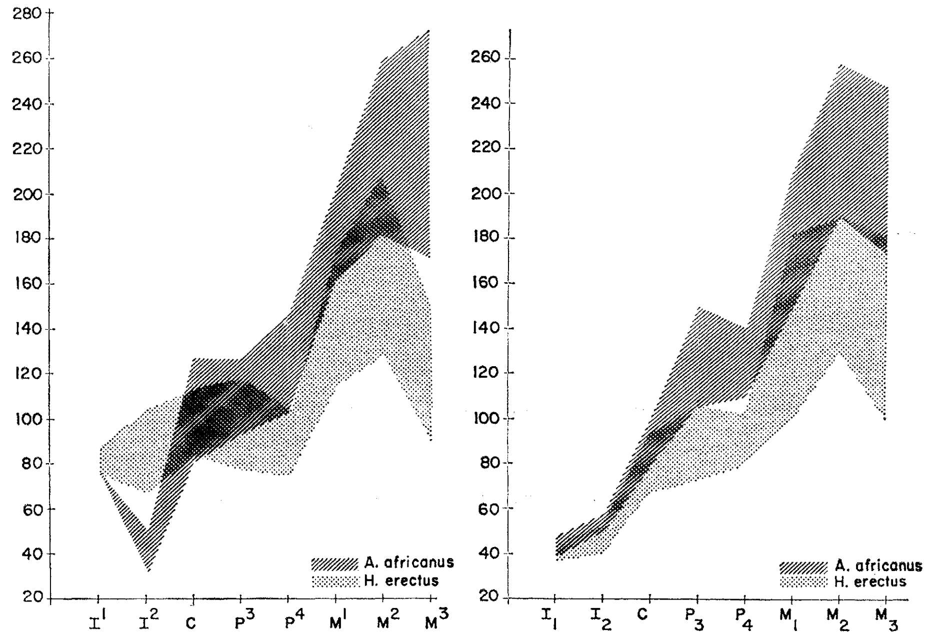

Fig. 6. Crown areas of the maxillary (*left*) and mandibular (*right*) teeth of *A. africanus* (the australopithecine from Taung, Sterkfontein, Makapansgat, and Garusi) compared with those of *H. erectus* from Africa, Asia, and Europe. Crown area is the product of the length and breadth of the crown of a tooth; values are in square millimeters.

cases of four skulls, the hand bones of at least two individuals, foot bones, and a collarbone. In addition, two leg bones (tibia and fibula) *may* belong to *H. habilis*, but we cannot rule out the possibility that they belonged to an australopithecine.

The features which distinguish *H. habilis* remains from those of australopithecines and relate them rather to the more advanced Homininae include the capacity of the braincase, both absolutely and in relation to estimated body size, the size, proportions, and shape of the teeth, the shape and size of the jaws, and the curvature of the cranial bones. In addition, the postcranial bones help us to obtain a picture of the very hominine morphological pattern of *Homo habilis*, but they do not assist in the taxonomic problem of deciding whether, for instance, the hand of *H. habilis* was closer to that of *Australopithecus* or to that of the Homininae. This is because we do not know enough about the structure of the hand in either the australopithecines or *H. erectus*.

In all those parts for which we do possess adequate comparative material for both australopithecines and early hominines, most of the bones of *H. habilis* fall at the extreme or beyond the range of variation for the australopithecines.

One important example of the greater degree of hominization shown by *H. habilis* is provided by his cranial capacity. Although the cranial vault of the type specimen is incomplete, it has been possible to estimate the capacity of the intact vault (*26*). The estimates range from 643 to 724 cm^3, with central values 674 and 681 cm^3. This is some 80 cm^3 more than the largest known capacity of *Australopithecus* and 95 cm^3 smaller than the smallest known capacity of *H. erectus*.

When Jerison's formulae (*24*) are applied to the estimate of 680 cm^3, the body size being estimated from the size of the foot bones, a value of 5.3 to 5.4 billion "excess nerve cells" is obtained. That is, the "intelligence" component of the brain of *H. habilis* has about 0.8 to 1.0 billion more neurons than that of the australopithecines, but about 1.7 to 1.8 billion fewer than that of *H. erectus* (*25*). Jerison's formulae thus provide striking confirmation of the evidence provided by absolute cranial capacity that *H. habilis* is a more advanced hominid than *Australopithecus* but not so advanced as *H. erectus*.

The parameter of tooth size has the same story to tell. Most of the teeth of *H. habilis* are smaller than those of most australopithecines. Thus, in 30 out of 38 comparisons, the absolute sizes of the *H. habilis* teeth lie at the extreme of the range for *Australopithecus* or outside the range.

Not only the size, but the shape of the teeth is distinctly different from that of *Australopithecus* (Fig. 9). Instead of possessing the great breadth characteristic of the teeth of the latter, the teeth of *H. habilis* are narrow and relatively elongated, this departure being found in 20 out of 30 comparisons with the australopithecine teeth. In this respect, the teeth of *H. habilis* resemble those of *H. erectus*.

In sum, *H. habilis* was a pygmy-sized hominid with a relatively large cranial capacity, reduced and narrow teeth, and a number of markedly hominine features in his limb bones. His total structural pattern was that of a creature appreciably more hominized than any of the large group of australopithecines of South and East Africa. The advanced features, moreover, were not those of an individual extreme variant, but characterized all the individuals represented over some considerable time. Clearly, this strain represents a distinct taxon intermediate between the most advanced *Australopithecus* and the most primitive *Homo*.

Since the original description was published in April 1964, a detailed comparison has been made between the original specimens from Tanganyika and those from Java. As a result, G. H. R. von Koenigswald and I have concluded that in the Bed II paratype of *H. habilis* (which lived some ¾ million years later than the type specimen), the hominizing trends have been carried still further; as a result, the jaws and teeth of the later specimen (Fig. 10) closely resemble those of *H. erectus* attributed to the early Middle Pleistocene Djetis Beds of Java (*17*). If these features represent sequential changes, we are virtually seeing here evolution in action, with subtle intergrades from one level of hominization to the next.

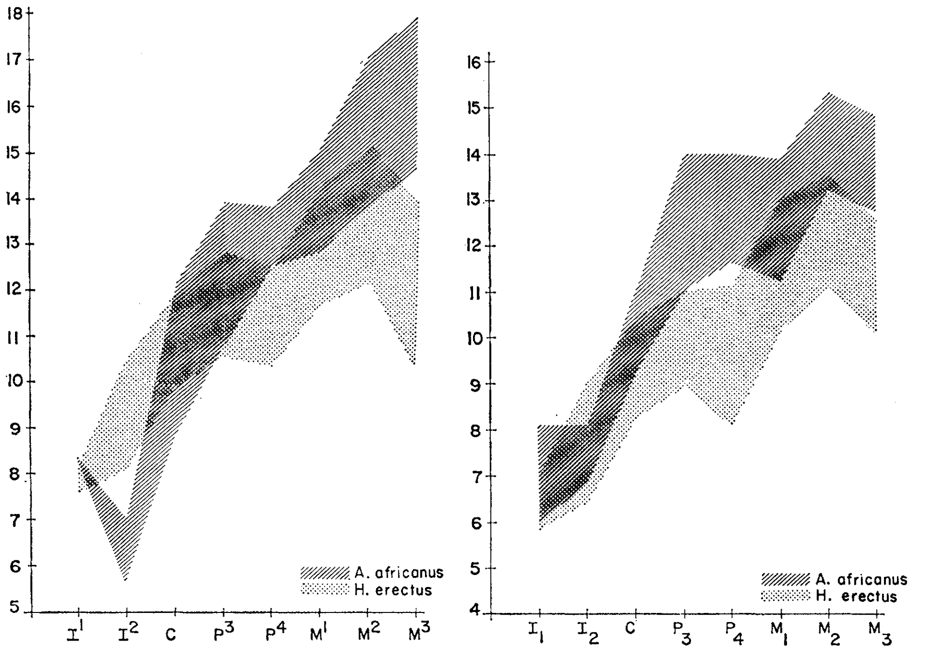

Fig. 7. Buccolingual breadths (in millimeters) of the maxiliary (left) and mandibular (right) teeth of *A. africanus* and *H. erectus*. The cheek teeth (from P3 to M3) of the australopithecines are characteristically broadened, as contrasted with those of the hominines, represented here by *Homo erectus*.

Cultural Status of Homo habilis

It is accepted that cultural or ethological evidence may be added to morphological evidence in assessing the taxonomic status of a group. We may ask the question: Did *H. habilis* behave like an *Australopithecus* or like a *Homo*?

At each of the levels in Bed I where remains of *Homo habilis* have been found, primitive stone implements have been recovered. These artifacts are commonly made from pebbles or irregular fragments, and the cultural phase represented by the succession of stone industries constitutes the Oldowan Culture, formerly known as the Oldowan phase of the pre-Chelles-Acheul Culture. For long, the identity of the makers of the Oldowan Culture

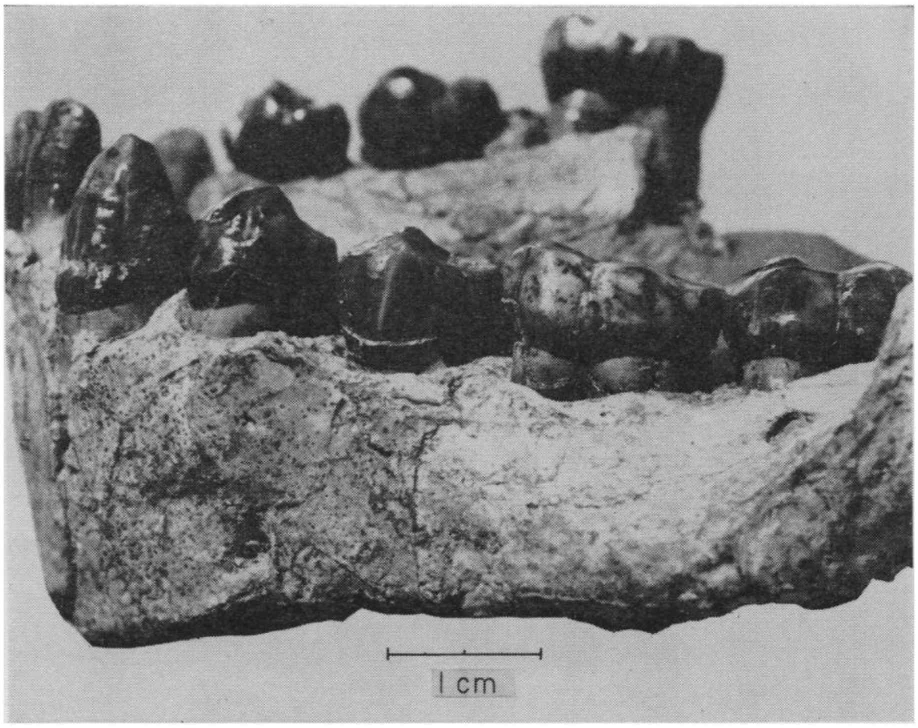

Fig. 8. Left lateral view of the dental arcade and body of the mandible of the type specimen of the new Olduvai hominine, *Homo habilis*. In this juvenile specimen, only the first two molars have erupted. The "enamel line" on each tooth is clearly defined; areas of hypoplastic enamel are well shown on the canine tooth.

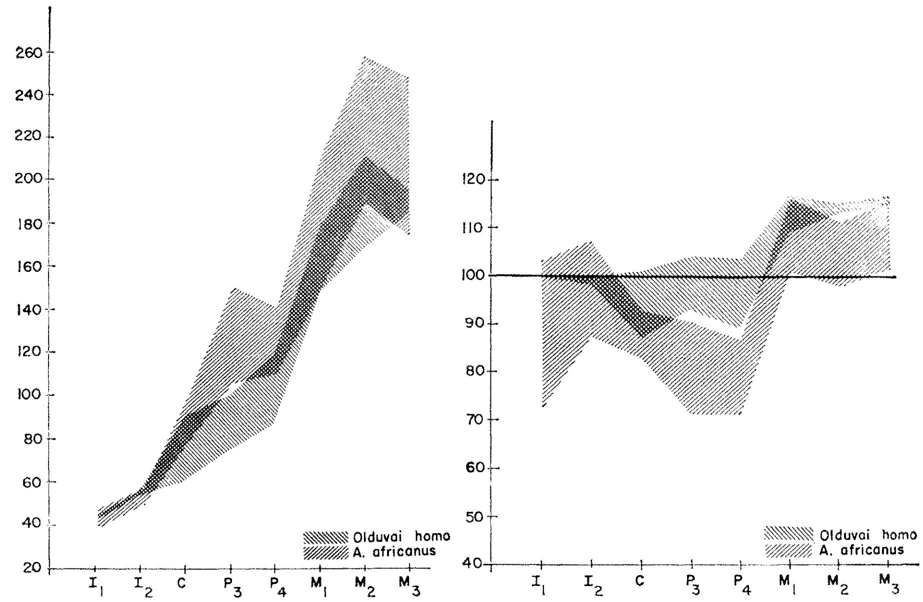

Fig. 9. Ranges of size and shape of mandibular teeth in the *H. habilis* from Bed I and the hominine from lower Bed II compared with those of *Australopithecus africanus*. *Left*, crown areas (mm^2). *Right*, the length of the tooth expressed as a percentage of the breadth. The cheek teeth (premolars and molars) of the hominines have higher indices because they are elongated and lack the characteristic australopithecine broadening of these teeth.

tools has been uncertain: some have maintained that the australopithecines were responsible, others have attributed the tools to early members of *Homo erectus*—but always on the basis of very indirect arguments. When in 1959 the cranium of the Olduvai australopithecine (*A. boisei*) was found on a living floor alongside Oldowan tools, at a time when no other adequate hominid remains were known to be associated with these tools, Leakey claimed that this australopithecine must have been the Oldowan toolmaker (*1*). This left a difficult problem: Why was the East African australopithecine associated with stone tools, whereas the Makapansgat australopithecine was associated with the bone, tooth, and horn tools described by Dart? Subsequently, however, remains of *H. habilis* were found on the same living floor as *A. boisei* and the tools. Furthermore, remains of *H. habilis* were found on the lower (earlier) living floors in Bed I, in each instance associated with Oldowan artifacts. While it is possible that both *A. boisei* and *H. habilis* made tools, it is probable that *H. habilis* was at least the more advanced toolmaker.

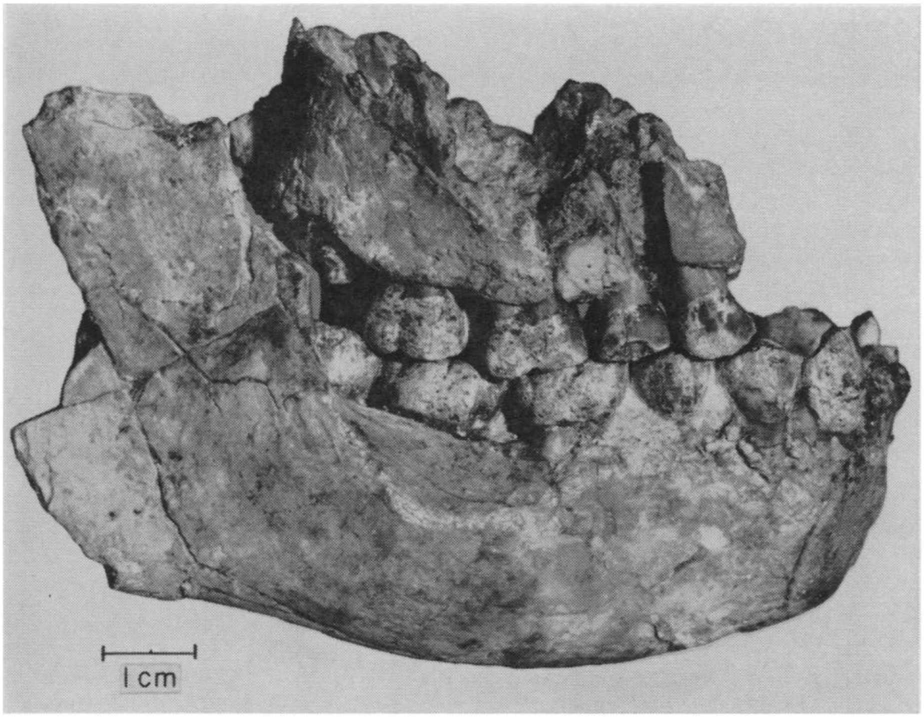

Fig. 10. Part of the right maxilla (upper jawbone) and the mandible of the hominine (no. 13) from the lower part of Bed II, Olduvai Gorge. These jaws and teeth bear close comparison with those assigned to the Djetis Beds of Java (the Sangiran IV cranium and the Sangiran B mandible).

Furthermore, if we make a survey of all the evidence from South and East Africa, we see that *Australopithecus* alone has not yet been found with stone objects which are undoubtedly tools, except where advanced hominid remains were present as well (*20, 25*). Six out of 12 deposits have yielded australopithecine remains with no stone tools (*27*); four sites which have australopithecines and stone tools contain, in addition, indications of a more advanced hominid. The remaining two deposits contain only the more advanced hominid and stone tools. At no site where australopithecine remains are the only hominid remains present are there any stone implements; conversely, at every site which has yielded stone implements and associated hominid remains, these hominid remains include those of a more advanced hominid, whether or not australopithecine remains are present in addition. Furthermore, at every site which has yielded the more advanced hominid, stone tools are present.

It has tentatively been concluded from these associations that no unequivocal evidence exists that *Australopithecus* made Oldowan stone tools to a set and regular pattern and according to a developing cultural trend. On the other hand, it seems very probable that *H. habilis* was the maker of the Oldowan stone tools, while *H. erectus* made the later (Chelles-Acheul) implements.

Dart (*28*) has demonstrated that the australopithecines were capable of a wide range of cultural activities. It may, however, be argued that all of these activities fall into the categories which Napier (*29*) has classified as *ad hoc* tool-using, purposeful tool-using, tool-modifying for an immediate or even for a future purpose, and possibly even *ad hoc* tool-making. But it may be questioned whether these australopithecine activities constitute cultural tool-making—that is, whether they exhibit a set and regular complex of patterns which, moreover, show developmental trends with the passage of time.

If this interpretation is correct, ethological or cultural evidence could be added to the anatomical evidence which tends to ally *H. habilis* with the hominines rather than with the australopithecines.

One further probable manifestation of the culture of the early Olduvai hominids is a rough circle of loosely piled stones discovered on a living floor at DK I in the lower part of Bed I (*3*). It suggests a crude shelter or windbreak and is on the same level as that on which the earliest remains of *H. habilis* were found (MK I). *H. habilis* may have been responsible for this rude structure.

Significance of Homo habilis

Both its structure and its place in time impart a unique significance to *Homo habilis*, while, culturally, it seems to provide us for the first time with a knowledge of the makers of the Oldowan Culture.

Structurally, *H. habilis* may be regarded as a most effective link between the Australopithecinae and the Homininae, between which, as has been mentioned, there is a larger gap than has hitherto been recognized. Its very intermediacy is underlined by the fact that some workers would regard the newly discovered form as the most advanced australopithecine and others as the most primitive hominine. Thus, even in the short time since the new fossils were discovered, various workers have believed that the habilines were simply another australopithecine (*30*), a new genus between *Australopithecus* and *Homo* (*31*), a new lowliest species of *Homo*, namely *H. habilis* (*3*), and even a new subspecies of *H. erectus*, namely *H. erectus habilis* (*32*). The position adopted by my colleagues and myself would seem to be a compromise between the extreme views on either side. Although argument on the exact taxonomic position may continue for some time, it seems that there is already fairly general agreement on this virtually uniquely linking position of *H. habilis*. Perhaps only *Meganthropus palaeojavanicus* of Sangiran, Java, lies in a similarly intermediate position between the Australopithecinae and the Homininae, albeit a little nearer to the australopithecines than is *H. habilis* (*17*).

Chronologically, the recognition of *H. habilis* means that a more hominized line of creatures was evolving alongside the somewhat less hominized australopithecines even in the Lower Pleistocene. Previously, the *H. erectus* remains of the Djetis Beds, agreed by most as belonging to the beginning of the Mid-Pleistocene, represented the earliest recognized hominine. It was still possible then to claim that, if indeed the Homininae stemmed off from an australopithecine ancestral group, this lineage of *Homo* need not have arisen any earlier than the end of the Lower Pleistocene. It now seems clear that, if the habilines are in fact members of the Homininae, then hominines were already present in Africa, and perhaps in Asia, during at least the second half of the Lower Pleistocene. The departure of the hominine line from its presumed australopithecine ancestor must then have occurred as early as at least the Upper Pliocene or the first part of the Lower Pleistocene.

The early hominines must have been contemporaries of several diversified australopithecines—a megadont line (*A. boisei*), a macrodont line (*A. robus-*

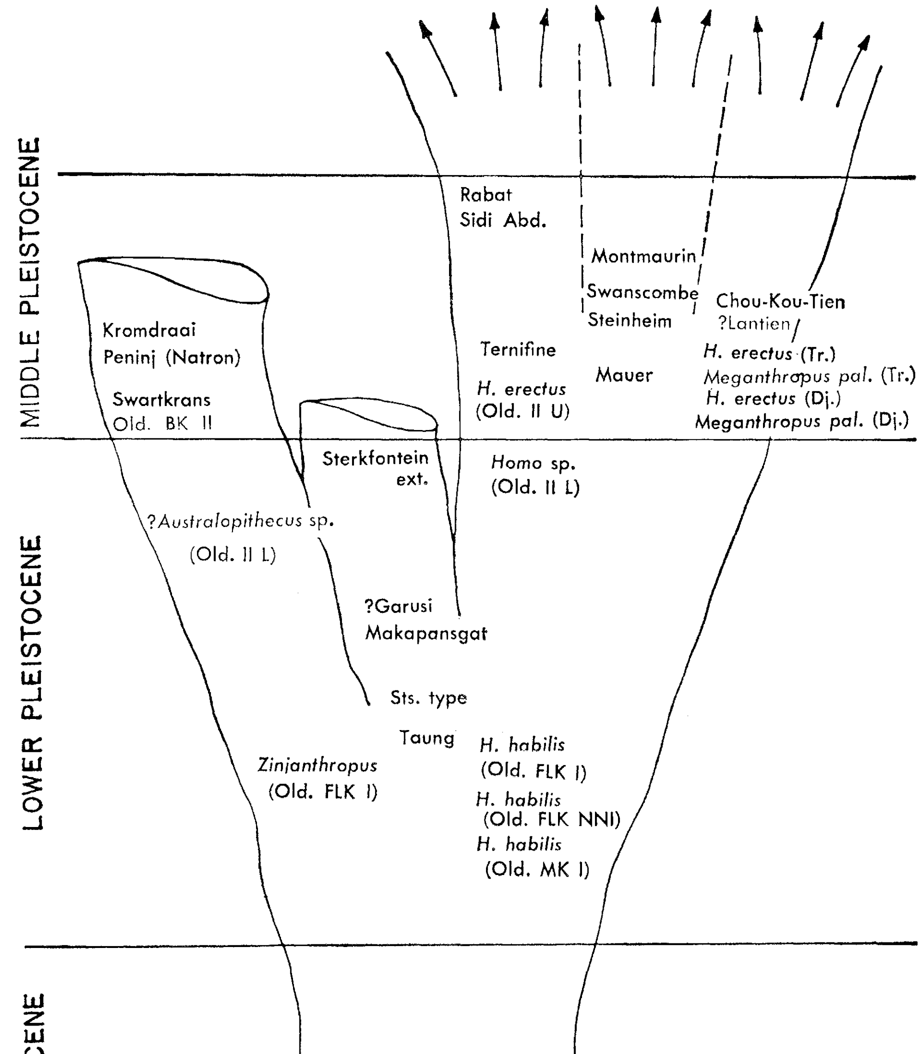

Fig. 11. Schema of Lower and Middle Pleistocene hominids, showing the position in time and space of the most important specimens discovered to date. The left trunk of the tree represents the large-toothed australopithecine line; the middle trunk the small-toothed australopithecine line; and the right trunk the hominine line leading to modern man. *Sts.*, Sterkfontein; *Sidi Abd.*, Sidi Abderrahman; *Old. II*, Olduvai Bed II; *U*, upper; *L*, lower; *Tr.*, Trinil beds; *Dj.*, Djetis beds.

tus), and a mesodont line (*A. africanus*). In fact, at least in East Africa, and probably, too, in South Africa, *H. habilis* and *Australopithecus* spp. were sympatric and synchronic. More precisely, Olduvai I provides us with early evidence of the sympatric coexistence of the largest-toothed australopithecine (*A. boisei*) and *H. habilis*, while Swartkrans gives us later evidence for the sympatric compresence of the large-toothed *A. robustus* and a more advanced hominine, *H. erectus* ("*Telanthropus*"). Doubtless, ecological differences permitted this situation to persist right through until the middle part of the mid-Pleistocene (Fig. 11).

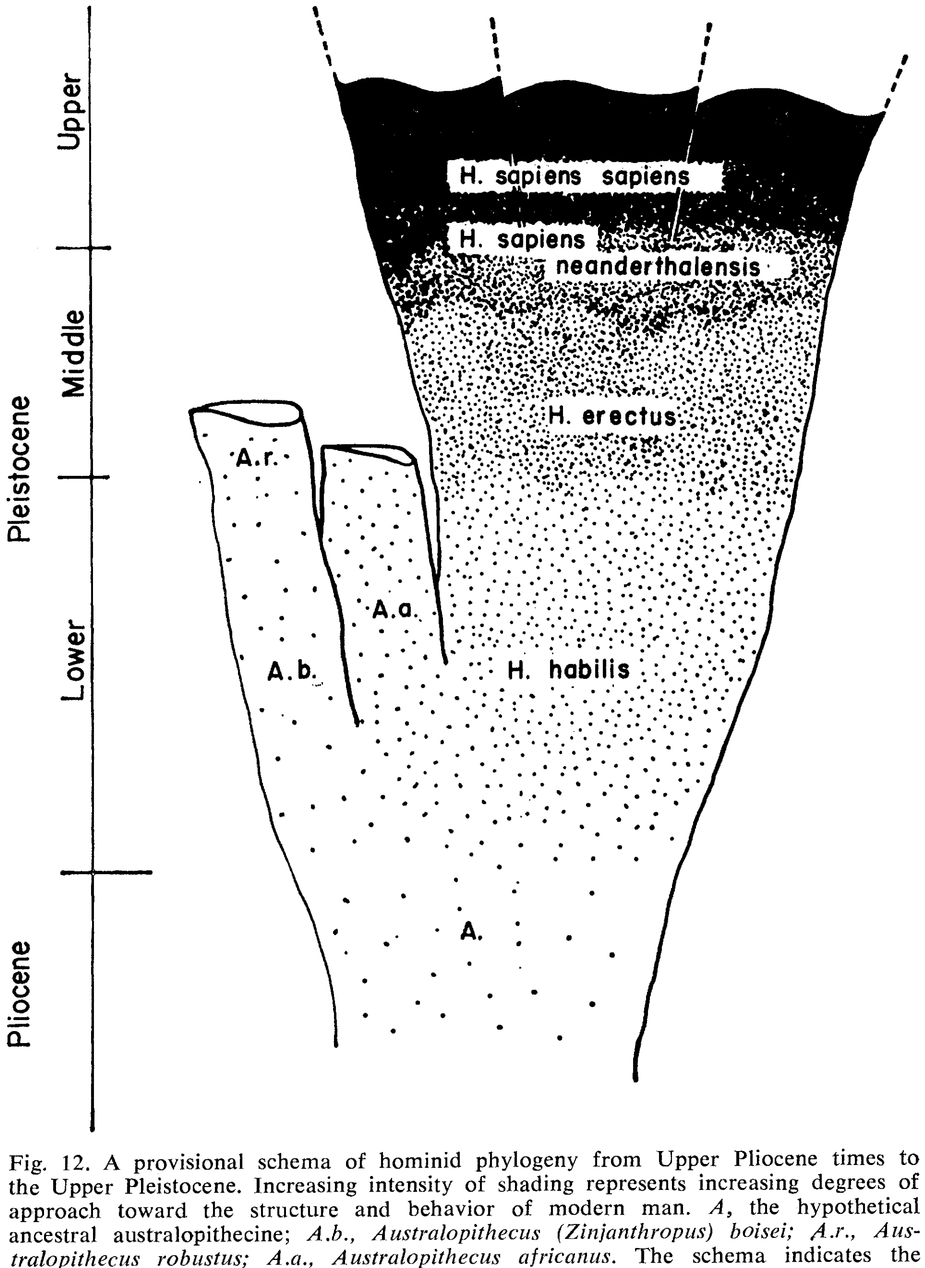

Fig. 12. A provisional schema of hominid phylogeny from Upper Pliocene times to the Upper Pleistocene. Increasing intensity of shading represents increasing degrees of approach toward the structure and behavior of modern man. *A*, the hypothetical ancestral australopithecine; *A.b.*, *Australopithecus (Zinjanthropus) boisei*; *A.r.*, *Australopithecus robustus*; *A.a.*, *Australopithecus africanus*. The schema indicates the synchronic coexistence of several different hominids in the Lower and Middle Pleistocene, the australopithecines surviving into the Middle Pleistocene alongside more advanced hominids of the genus *Homo*. This figure should be considered in conjunction with Fig. 11.

Bearings on Hominid Evolution

As a total morphological complex, *H. habilis* represents a more advanced grade of hominid organization than *Australopithecus*. Have the habilines arisen from the australopithecines? Since they are contemporary with *H. habilis*, the australopithecine populations represented by the actual fossils recovered to date are clearly too late —and possibly slightly too specialized —to have been on the actual human line, unless we are to postulate a polyphyletic origin of the Homininae at varying times from australopithecine stock. Morphologically, the gracile *A. africanus* is closest to *H. habilis* and seemingly least specialized. It would not be rash therefore to suggest that of the various australopithecines *A. africanus* has departed least from the common ancestor of *A. africanus* and *H. habilis*. On the other hand, the large-toothed, specialized *A. robustus* and *A. boisei* would seem to be far off the common *africanus-habilis* line. Two possible interpretations spring to mind:

1) The Pliocene ancestral australopithecine was large-toothed and perhaps adapted to a vegetarian diet (*33*); *A. boisei* and *A. robustus* would then represent a conservative line which maintained these qualities right through into the Middle Pleistocene, while *A. africanus* developed different ecological requirements which, perhaps through a more carnivorous or, at least, omnivorous diet, led to a relaxation of selective pressures maintaining large teeth. The gracile *H. habilis* stemmed off from this smaller-toothed line of australopithecines and became selected for increasingly hominine features.

2) The ancestral australopithecine was unspecialized, small-toothed, omnivorous. At some time in the Upper Pliocene, it diversified into macrodontic and megadontic lines (*A. robustus* and *A. boisei*), with specialized dentition, perhaps accompanying a specialized, essentially herbivorous diet. Another line remained little changed and unspecialized, eventually to dichotomize into a progressively more hominized line represented by *H. habilis* in Africa and perhaps *Meganthropus* in Asia and a more conservative residual line (*A. africanus*) which, because of ecological similarities to *H. habilis*, did not long outlast the emergence of this hominine.

Which of the two interpretations is correct, or whether other alternatives should be considered, only the direct evidence of Pliocene fossils will determine. Pending their discovery, I incline to favor the second view, on indirect lines of evidence to be presented elsewhere. That is, I tend to regard the large teeth and supporting structures of *A. robustus* and *A. boisei* as secondary specializations, rather than as primitive or ancestral features which J. T. Robinson seems to believe (*33*).

Irrespective of which interpretation we adopt, it seems reasonable to infer that late in the Pliocene, or thereabouts, some populations of ancestral *Australopithecus*-like hominids moved forward to a further grade of hominization, thus generating the Homininae.

We may tentatively conclude that *H. habilis* is on this direct hominine line. Such is the message of his morphology and his culture, while his position in space and time is compatible with this conclusion (*34*). As a Lower Pleistocene hominine, he bids fair to provide us with a population, one or more sections of which were ancestral to the mid-Pleistocene hominines (Fig. 12). Nothing in the structure or dating of the relevant fossils rules out the possibility that some populations of *H. habilis* underwent further hominizing changes by phyletic evolution late in the Lower Pleistocene, to attain the *H. erectus* grade of hominization.

Such a reconstruction permits us to recognize a series of grades of hominization, within which we may classify the available fossils. Despite wide variation within each grade—only a fraction of which is as yet known for most grades—we may recognize: (i) an australopithecine grade, represented convincingly only in South and East Africa; (ii) a habiline grade from Africa, perhaps corresponding to a meganthropine grade in Asia; (iii) an earlier *H. erectus* grade, represented in Africa possibly by remains from middle Bed II, Olduvai, and by "*Telanthropus*" from Swartkrans, and in Asia by the Djetis Beds hominines from Sangiran, Java; (iv) a later *H. erectus* grade, represented in Africa by "Chellean Man" from upper Bed II, Olduvai and by "*Atlanthropus*" of Northwest Africa; in Asia by the Trinil Beds and Chou-Kou-Tien hominines; and in Europe possibly by the remains of Mauer; (v) an earlier *H. sapiens* grade (Neanderthal) widely distributed in the Old World; and (vi) a later *H. sapiens* grade, ultimately worldwide in distribution. This sequence shows remarkable parallels between Africa and Asia from grade 2 onwards (*17*).

We see in conclusion that *H. habilis* has bridged the last remaining major gap in the Pleistocene part of the story of human evolution.

Summary. Recent discoveries of early Pleistocene hominids in East Africa have revealed a new stage in human evolution. The remains of *Homo habilis*, discovered by L. S. B. Leakey and his family, bridge the hiatus between the most advanced australopithecines and the most primitive hominines. The new species was bigger-brained and smaller-toothed than *Australopithecus*, the fossil apeman from South and East Africa. It is very probable that *Homo habilis* was, as his name implies, a "handyman," maker of the earliest stone culture, the Oldowan.

These primitive hominines were already in existence in the Lower Pleistocene, living alongside a variety of more conservative hominids, the australopithecines. The closeness of morphology between *H. habilis* and *Australopithecus africanus* points strongly to a common ancestry in the Upper Pliocene or the very beginning of the Pleistocene. The large-toothed *A. robustus* and *A. boisei* were already diverging by specialization from the postulated unspecialized ancestral australopithecine. The first hominines must thus have come into being by the beginning of the Pleistocene. Later, some populations of *H. habilis* seemingly underwent further hominizing changes to generate a new species, *Homo erectus*, bigger men with larger and more effective brains, smaller and more modern human teeth, probably more complete adjustment to upright stance and bipedal gait, a more precise manual grip, and an appreciably advanced material culture.

Homo habilis thus fills in the last remaining major gap in the Pleistocene story of human evolution.

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33. J. T. Robinson, in *Evolution und Hominisation*, G. Kurth, Ed. (G. Fischer, Stuttgart, 1962), p. 2 → J. T. Robinson, *S. African Archaeol. Bull.* **19**, 3 (1964).
34. P. V. Tobias, in *Britannica Book of the Year, 1964* (Encyclopaedia Britannica, Chicago, in press).
35. As a second type of hominid (*Homo erectus* or *Telanthropus*) is known to be present in the Swartkrans deposit, the possibility cannot be excluded that some of the large numbers of isolated teeth from this deposit may *not* belong to the australopithecine.

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