

THE EARLY *AUSTRALOPITHECUS* AND *HOMO* FROM TANZANIA*

PHILLIP V. TOBIAS (JOHANNESBURG)

Earlier- and lower Mid-Pleistocene deposits of East Africa have yielded remains of at least two different kinds of fossil hominid. The first group of fossils belongs to the australopithecines, a partially hominized group. The second has been attributed to a new and lowly species of the genus *Homo*, namely *Homo habilis*, and represents a more markedly hominized lineage. It is the purpose of this paper to give a brief review of the main features of the two kinds of hominid and to discuss the cultural, taxonomic and phylogenetic implications of these discoveries.

THE EAST AFRICAN AUSTRALOPITHECINES

Australopithecines have been found at three East African sites, Garusi (1939), Olduvai (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 maxilla containing both upper premolars. In his two-volume work, *Auf den Spuren des Vormenschen*, published at Stuttgart in 1943, Kohl-Larsen stated that his specimen resembled *Australopithecus*, but Weinert later re-classified it as an African species of *Meganthropus* (1950, 1951). However, Robinson (1953, 1955) has shown convincingly that the premolars fall within the range for the South African *Australopithecus* from Sterkfontein. This is a smaller-toothed *Australopithecus* which is usually classified to-day as *A. africanus* (Campbell, 1963). As yet, the Garusi specimen is the only evidence we have of the presence in East Africa of the gracile *africanus* species.

The most important East African australopithecine is the specimen originally called by Leakey *Zinjanthropus boisei* (1959) and now re-classified by Leakey, Tobias and Napier (1964) as a species of *Australopithecus*, namely *A. boisei*. It is represented by a very complete cranium, including all 16 maxillary teeth. A brief preliminary description has been given by Leakey (1959, 1960), while Tobias (1963) has placed on record the cranial capacity as 530 ccs. i.e. no bigger than

that of the small-toothed *Australopithecus* child skull from Taung. A detailed monograph on *A. boisei* has been prepared by the present author and will appear as part of a new series of volumes on Olduvai Gorge to be published by the Cambridge University Press. It may be mentioned here that *A. boisei* is the biggest-toothed and robustest of all the australopithecines, exceeding in most dental dimensions even the biggest of the large-toothed *A. robustus* group from Swartkrans and Kromdraai in the Transvaal.

It is probable that further large-toothed australopithecines are present in the Olduvai deposits. Three adult teeth, found in M. N. K. II, in the lower part of Bed II, are for the most part of australopithecine form, shape and dimensions: according to Leakey (1965) this part of Bed II, like Bed I, is characterized by a Villafranchian fauna: it is still Earlier-Pleistocene. These teeth were referred to by Leakey and Leakey (1964), but no attempt was made to identify them specifically.

Yet another group of remains which are seemingly of australopithecine affinities are those referred to as Olduvai Hominid 16 (Leakey and Leakey 1964) and which were recovered as scattered surface finds in Maiko Gully, F. L. K. II. At first, they were provisionally referred to *Homo habilis* (Leakey, Tobias and Napier, 1964), but further study suggests dental and gnathic affinities with *Australopithecus* (Tobias, 1965a). They may represent a later, evolved form of *A. boisei*, possibly a female; but it is not proposed at this stage to attempt to identify them specifically.

Suffice it to say that, within the stratified Olduvai deposit, big-toothed australopithecines are represented.

The third site in East Africa to yield an australopithecine is Peninj, on the west side of Lake Natron, about 50 miles north-east of Olduvai Gorge. Here, in January 1964, one of Doctor Leakey's assistants, Mr Kamoya Kimeu, discovered a nearly complete and superbly preserved mandible of a large-toothed australopithecine. According to Leakey's provisional identification of the fauna from this new site, it is of Mid-Pleistocene age and thus much later than the original *A. boisei* from Olduvai (Leakey and Leakey, 1964). It would 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 mandible fits the maxilla of the Olduvai *A. boisei* almost perfectly

* To make the discussion complete, we also include the lecture of Prof. P. V. Tobias delivered in the Palaeo-anthropology and Anthropogenesis section of the same Congress, since the lecture's text is fully related to the discussed questions and interpretations of Prof. Tobias. Into the text the editors have included also the respective documentation according to the publications of Prof. Tobias (Ed.).

and it may be provisionally identified as a mandible of *A. boisei*.

The mandibular teeth of Natron differ in some respects from those of the large-toothed South African australopithecine, *A. robustus*.* Only certain

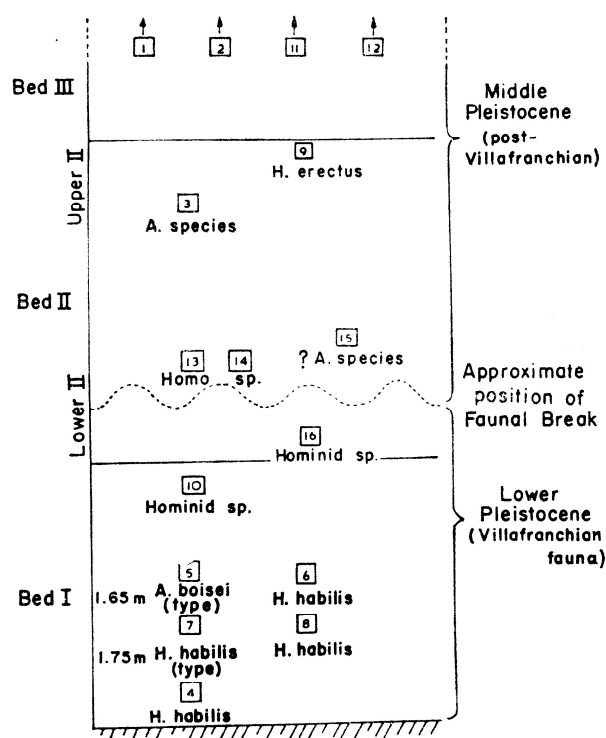


FIG. 1.

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).

metrical differences will be referred to here (Table 1). The lateral incisor is even smaller than those of *A. robustus*, especially in the buccolingual breadth. On the other hand, the cheek-teeth — the premolars and molars — are larger than those of *A. robustus*; for instance the Crown Areas of the P_4 and M_1 fall beyond the maximum for samples of 14 and 20 *robustus* homologues respectively, while the Crown Areas of the P_3 , M_2 and M_3 lie at or close to the upper limit of the *robustus* range for 12, 14 and 13 homologues respectively. This size excess is due more to a buccolingual than to a mesiodistal expansion: so markedly is the P_3 expanded transversely that its length/breadth index falls below the lower limit of the range for 12 *robustus* homologues. Conversely, the P_4 shows a marked degree of molarization, the mesiodistal elongation of the tooth placing its L/B index near the top of, or even beyond, the *robustus* range for

* For the dental comparisons, a comparative series has been based upon the invaluable data of Robinson (1956), supplemented by additional measurements on Makapansgat australopithecine teeth made by Dart (1962) and by myself (unpublished data).

TABLE 1
Dimensions and Indices of Peninj
(Natron) Mandibular Teeth

		Mesio- distal Length	Bucco- lingual Breadth	Module	Crown Area	Shape Index Length/ Breadth
I_1	(L)	5.5	6.1	5.80	33.55	90.2
	(R)	5.6	6.1	5.85	34.16	91.8
I_2	(L)	5.9	6.4	6.15	37.76	92.2
	(R)	6.2	6.5	6.35	40.30	95.4
\bar{C}	(L)	7.3	8.1	7.70	59.13	90.1
	(R)	7.4	8.3	7.85	61.42	89.2
P_3	(L)	9.2	13.5	11.35	124.30	68.1
	(R)	9.9	13.5	11.70	133.65	73.3
P_4	(L)	14.5	15.2	14.85	220.40	95.4
	(R)	12.7*	14.8	13.75*	187.96*	85.8*
M_1	(L)	16.4	15.3	15.85	250.92	107.2
	(R)	16.1	15.5	15.80	249.55	103.9
M_2	(L)	17.4	16.2	16.80	281.88	107.4
	(R)	17.2	16.1	16.65	276.92	106.8
M_3	(L)	18.8	16.3	17.55	306.44	115.3
	(R)	18.7	15.7	17.20	293.59	119.1

* Marked compression and interproximal attrition

the right and left teeth respectively. Apart from the premolars, the shape indices of the other mandibular teeth all fall within the range of variation of the *robustus* sample from South Africa. In this respect, the maxillary teeth of *A. boisei* from Olduvai agree with the mandibular teeth of Natron in having premolars and molars which tend to be bigger than those of the South African *A. robustus* group, and a third premolar which tends to be shorter and broader than its *A. robustus* counterpart, i.e. to have a lower L/B index. In other respects, the Olduvai and Natron australopithecines do not agree with each other in fine details: for instance, while the front teeth tend to be smaller in Natron, they tend to be somewhat bigger in Olduvai *A. boisei*, as compared with the *A. robustus* homologues. Larger series of teeth from East Africa will need to be analysed before we can determine to what extent these metrical departures from the South African australopithecine teeth represent a consistent trend. Clearly, however, the East African australopithecines are more closely related to the bigger-toothed South African form, *A. robustus*, than to *A. africanus* — save that the Garusi specimen seems to fit within the range for the smaller-toothed South African form, *A. africanus*, rather than that of *A. robustus*.

THE EAST AFRICAN HOMININES OF THE EARLIER- PLEISTOCENE

From at least four levels in Bed I and the lower (Villafranchian) part of Bed II, in the Olduvai succession, have come skeletal remains representing a second type of hominid. They differ widely from *A. boisei*, the megadont australopithecine found in the same Beds. While the *A. boisei* teeth in general

fall above the top of the range for the South African australopithecines, the teeth of this second hominid fall below the lower end of the australopithecine range (Tobias, 1965a). Such wide divergence is far in excess of what can be attributed to sexual dimorphism; in any event, it is accompanied by other divergences — in the shape, proportions and detailed morphology of the teeth, in cranial shape and curvature, in cranial capacity. In almost all the departures of the second hominid from the australopithecine morphological pattern, it approaches more closely to the hominine pattern. The total pattern is more markedly hominized than is that of *Australopithecus*. We have called this creature *Homo habilis*.

One important example of the greater degree of hominization shown by *H. habilis* is provided by his cranial capacity, which in turn is related to brain size. Although the cranial vault of the type specimen is incomplete, it has been possible to estimate the capacity of the intact vault. The method has been described elsewhere (Tobias, 1964). The estimates range from 643 ccs to 724 ccs, with the central values being 674 and 681. The cranial capacity determined on *A. boisei* from Olduvai Gorge is 530 ccs while 6 South African australopithecines have capacities ranging from 435 to 600* ccs (Tobias, 1963). On the other hand, the range for a sample of 7 crania of *Homo erectus* (formerly known as *Pithecanthropus*) is from 775 to 1225 ccs. In other words the value of 680 ccs for *H. habilis* is some 80 ccs more than the largest known capacity of *Australopithecus* and 95 ccs smaller than the smallest known capacity of *H. erectus*. This intermediate position in absolute cranial capacity parallels almost exactly the intermediate position occupied by the dentition of *Homo habilis*.

From an estimate of the body size of *H. habilis*, it is possible to take the analysis of the cranial capacity value further. Jerison (1963) has demonstrated that it is possible to analyze brain size into two apparently independent components, one of which is determined by body size and the other of which is associated with improved adaptive capacities. Given certain assumptions, it is further possible to estimate the number of cortical neurones in the total brain size as well as in each of the two components. He has developed a series of equations for the calculation of these neuronal values, given the size of the brain and the size of the body. By applying these formulae, he has been able to compute the number of "extra" neurones that may be associated with the evolution and adaptation of brain: behaviour mechanisms in response to the challenge of the environment. It is instructive to apply his approach to the results for *H. habilis* and to consider them in relation to *Australopithecus*, on the one hand, and to *H. erectus* on the other.

Table 2 conveys the results obtained for a series of primates (Jerison, 1963); the values for

TABLE 2

Estimates of "Extra Neurones" in Hominoids
(modified and added to after Jerison 1963)

	Measured Brain Size (in gms. or ccs.)	Estimated Body Size (in gms. or ccs.)	Estimates of Total Neurones (in thousands of millions)	Estimates of "Extra" Neurones (in thousands of millions)
Chimpanzee	400	45,000	4.3	3.4
Gorilla I	540	200,000	5.3	3.5
Gorilla	600	250,000	5.7	3.6
<i>A. boisei</i> ("Zinjanthropus")	530	50,000	5.2	4.2*
<i>A. africanus</i>	500	25,000	5.0	4.3*
<i>H. habilis</i>	680	40,000	6.2	5.3
<i>H. erectus</i>	900	50,000	7.4	6.4
<i>H. erectus</i>	1,000	50,000	8.0	7.0
<i>H. sapiens</i>	1,300	60,000	9.5	8.5

* Re-computed for different brain or body size
+ Own data

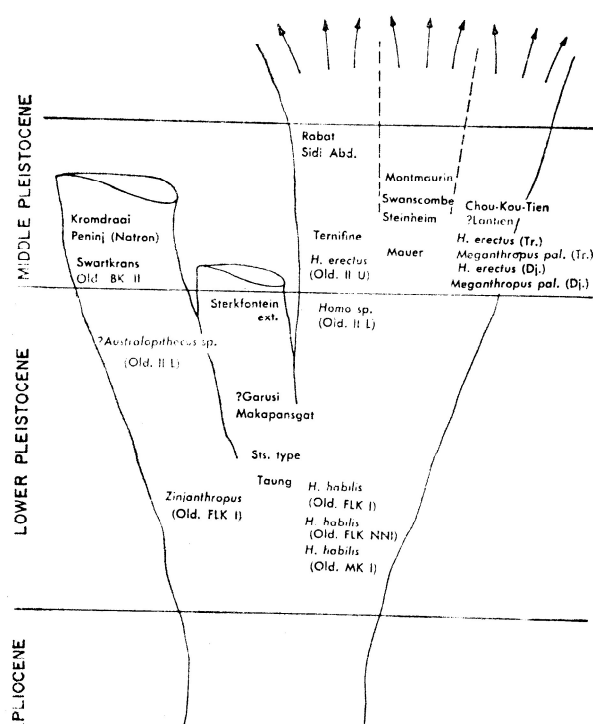


FIG. 2.

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.

* Later re-computed as 435–562 ccs.

A. africanus and for *A. (Zinjanthropus) boisei* have been re-computed by me on the basis of later data than those upon which Jerison based his original estimate. Thus, for *A. africanus*, he based his estimate on a brain size of 500 grams and a body size of 20,000 grams: it seems to me that 20 Kilo. is somewhat too small an estimate for the body size of the small-toothed australopithecine and, accordingly, I have re-calculated this value for a body size of 25,000. The effect on the estimate of "excess neurones" is, however, not marked: it is altered from 4.4 to 4.3 billion neurones. Again, Jerison used a guess of 600 for the brain size of *A. boisei*: it has been possible to obtain a fairly exact value of 530 (Tobias, 1963) and I have accordingly re-calculated the "excess neurones" for the Olduvai australopithecine. The value altered from 4.7 to 4.2. Thus, two australopithecine values, one for a big-toothed and one for a small-toothed form, have 4.2–4.3 billion "excess" neurones. This is higher than the values for anthropoid apes (chimpanzee and gorilla), which work out at 3.4 to 3.6. *H. erectus*, on the other hand, yields values of 6.4–7.0. The body weight of *H. habilis*, to judge by the size of his post-cranial bones, was probably about that of a present-day pygmy: accordingly, using the central value of 680 for the brain size and an estimate of 40,000 for body weight, I have computed the "excess neurones", according to the equations of Jerison, as 5.3. Thus, not only the absolute brain-size, but also the estimated value of that part of the brain not immediately related to body size, lie approximately midway between the australopithecine and *H. erectus* values. Even if the body weight of *H. habilis* were estimated at 45 Kilos. (although he was undoubtedly a smaller individual than *H. erectus*), this still does not lower the number of "excess neurones" below 5.3 billions in round figures. On the other hand, if his body size were not much bigger than that of the small *Australopithecus*, i.e. 25 Kilos. the value for "excess neurones" would be increased to 5.5. Similarly, if we took the extreme values for the range of estimates of total brain-size for *H. habilis* (643–724), these would yield a similar range of estimates of "excess neurones", namely from 5.1 (for a cranial capacity of 643) to 5.6 (for a capacity of 724). Even if we use the combination of opposite extremes of brain and body size, we obtain values of 5.1 for a brain of 643 in a body of 45,000 and 5.8 for a brain of 724 in a body of 25,000! Jerison's formulae thus provide striking confirmation of the evidence provided by absolute cranial capacity and by the dentition, that *H. habilis* is a more advanced hominid than *Australopithecus* but not so advanced as *H. erectus*.

Not only is the total morphological pattern of *habilis* more hominid, but the same hominizing features seem to be maintained over a lengthy period of time — as reflected in fossil hominids from the lowest part of Bed I through to the more intensely hominized fossils in the lower half of Bed II. If the Potassium 40-Argon 40 dates are to be trusted, this represents a lapse of time of some

750,000 years. Clearly *habilis* represents not a single freakish and aberrant creature, perhaps the extreme of the range of australopithecines, but a definite lineage extended in time for a lengthy period. We therefore feel justified in regarding it as a definite taxon, a new species, of character intermediate between the most advanced *Australopithecus* and the most primitive *Homo*. But morphology alone seems unable to help us decide whether the new species should fall within the genus *Australopithecus* or within *Homo*.

THE CULTURAL BEHAVIOUR OF THE NEW SPECIES

It is only when we supplement morphological data by ethological data that the status of the new species becomes clear. In other words, we need to ask the question: did he behave like an *Australopithecus* or like a *Homo*?

TABLE 3
Associations of Early Hominid Fossils
and of Early caps/Stone Implements

Site/Deposit	Presence of australopithecine fossils	Presence of more advanced hominids	Presence of stone tools
Sterkfontein Type Site	Yes	—	—
Sterkfontein Extension Site (Middle Breccia)	Yes	Yes	Yes
Taung	Yes	—	—
Makapansgat	Yes	—	—
Swartkrans	Yes	Yes	Yes
Kromdraai	Yes	—	—
Garusi	Yes	—	—
Peninj (Natron)	Yes	—	—
Olduvai Bed I MKI	—	Yes	Yes
FLKNNI	—	Yes	Yes
FLKI	Yes	Yes	Yes
Olduvai Bed II MNKII	? Yes	Yes	Yes

An important part of the answer is derived from a study of the associations of the fossils. In Table 3, a series of sites or living-floors relevant to our theme is tabulated, with a statement of the associated remains found on each. It is seen that 6 out of 12 listed deposits have yielded australopithecine remains alone: while probably 4 out of 12 which have australopithecine remains and stone implements have, in addition, indications of a more advanced hominid. At the remaining two deposits, only the more advanced hominid is present along with stone implements. In short, 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 the more advanced hominid, whether or not australopithecine remains are present *in addition*. Furthermore, at every site which has yielded the more advanced hominid.

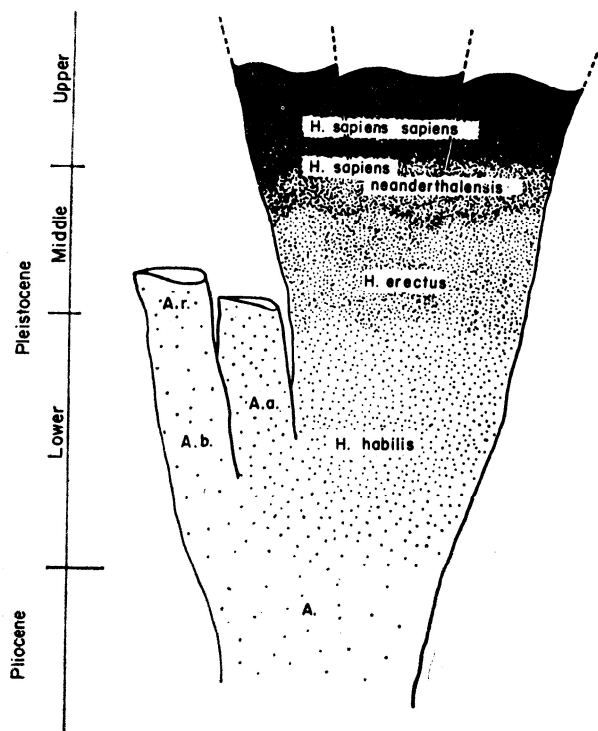


FIG. 3.

A provisional schema of hominid phylogeny from Upper Pliocene times to the Upper Pleistocene.

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. 2.

stone tools are present. The most reasonable hypothesis to explain these data is that *Australopithecus* was not the maker of the stone implements (as indeed Robinson and Mason, 1957, have claimed for Sterkfontein), but that the more advanced hominid almost certainly was.

A more advanced hominid is now well known from the Olduvai succession, where we have seen reason to regard it as a new hominid species. It is not so well represented in the South African deposits, being known from Swartkrans only by one nearly complete mandible, a second mandibular fragment, a maxilla, some teeth and, possibly, a radial fragment, and from Sterkfontein Extension Site only by two or three teeth. This is insufficient evidence on which to decide whether more than one kind of more advanced hominid is present: Robinson (1961) has claimed that the one from Swartkrans is *Homo erectus*, and preliminary study by the present author indicates that it is very similar to the Olduvai advanced hominid from

Bed II. From the resemblance of the Bed II hominine to the Javanese fossils, "*Pithecanthropus IV*" and Sangiran B, it seems likely that the Olduvai Bed II hominine has crossed the next taxonomic boundary and is a member of *Homo erectus* (Tobias and von Koenigswald, 1964).

The point is that there now seems to be little doubt that the earliest and most primitive stone implements found in Africa — belonging to the Oldowan Culture — were made by the *habilis*-type of creature. He was a maker of stone implements to a set and regular pattern, which, moreover, is progressive over a long period of time. Such behaviour characterizes the other species of *Homo*, namely *erectus* and *sapiens*: it is not characteristic of *Australopithecus*. True, Dart (1957) has demonstrated that the australopithecines were capable of a wide range of cultural activities, but these are all of the type which has been well classified by Napier (1963) 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 is not regarded as *cultural tool-making*, in the sense of a set and regular complex of patterns which, moreover, shows developmental trends with the passage of time.

Ethologically, therefore, *habilis* shows the critical behaviour pattern of *Homo*, not that of *Australopithecus*. We have therefore classed the new species *habilis* within the genus *Homo*.

THE IMPORTANCE OF *HOMO HABILIS*

The new primitive species of *Homo* provides us, for the first time, with a knowledge of the makers of the Oldowan Culture. For a long time, it has been uncertain whether or not an australopithecine was responsible. When "*Zinjanthropus*" was first found in Bed I at Olduvai, he was not unnaturally claimed as the probable author of the Oldowan tools found alongside him on the same living-floor. 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 (1957)? Subsequently, however, the discovery of the more advanced hominid satisfactorily cleared up this problem. The australopithecine level of hominid organisation, we have seen, was *not* associated with the making of the Oldowan or other stone tools; the *Homo habilis* level was.

Secondly, the finding of a *Homo* alongside an *Australopithecus* in the Earlier-Pleistocene brings in its wake certain consequences for hominid phylogeny. If both lines stemmed from a common ancestry, and there is scarcely room for doubt that they did, then the division into two or more lineages must have occurred earlier than had been imagined. Previously, *Australopithecus* was known as a Lower and Middle Pleistocene hominid, while the earliest known *Homo* was *erectus* from the earliest part of the Middle Pleistocene. It was still

possible then to claim that the lineage of *Homo* stemmed off from an australopithecine lineage within the Pleistocene. Now, we have to push these hominine origins at least back into the later Pliocene, or the very beginning of the Pleistocene.

Thirdly, there previously remained a large morphological gap between *Australopithecus* and *Homo erectus*, and in many respects ranges of variation of the two groups did not overlap even slightly, despite fairly large samples. *Homo habilis* has now provided us with a morphological intermediate, of which the range of variation for the various morphological traits undoubtedly overlaps with those of both *Australopithecus* and *Homo erectus*. From every point of view, its position in space and time, its morphology and inferred ethology, *Homo habilis* thus bridges the last remaining major gap in the Pleistocene part of the story of hominid phylogeny.

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Fig. 1, 2, 3.

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DISKUSSIONSBEITRAG

Nach den Vorstellungen der Synthetischen Theorie der Evolution benötigt jede sich neu herausdifferenzierende Art zunächst einen regionalen Isolationsbereich, bevor sie sich von diesem aus durch Radiation weiter verbreiten kann. Dabei sind die Anfangsphasen zunächst noch eine Unterart der bisherigen, bis der Speziationsprozeß im Rahmen der Phylogenese eine Entscheidung darüber zuläßt, ob er systematisch als Dauererscheinung taxonomisch abgetrennt werden kann. Deshalb ist die Annahme, daß innerhalb eines Zeithorizontes auf der Erde immer nur eine Art unserer Gattung Homo gelebt haben könne, nicht mehr vertretbar, sobald wir dabei Prozeßabläufe innerhalb des Pleistozäns betrachten. Denn die lange Generationsdauer der Homininen wie ihre nach allen paläodemographischen Befunden nur gering anzusetzende Zuwachsrates lassen für das Ersetzen einer weltweit verbreiteten Art durch eine neue nur ganz erhebliche Zeitspannen als wahrscheinlich annehmen. Dabei ist auch noch zu berücksichtigen, daß jede Ausbreitung in neue ökologische Räume und deren endgültige Erschließung entsprechende Anpassungszeiten voraussetzt.

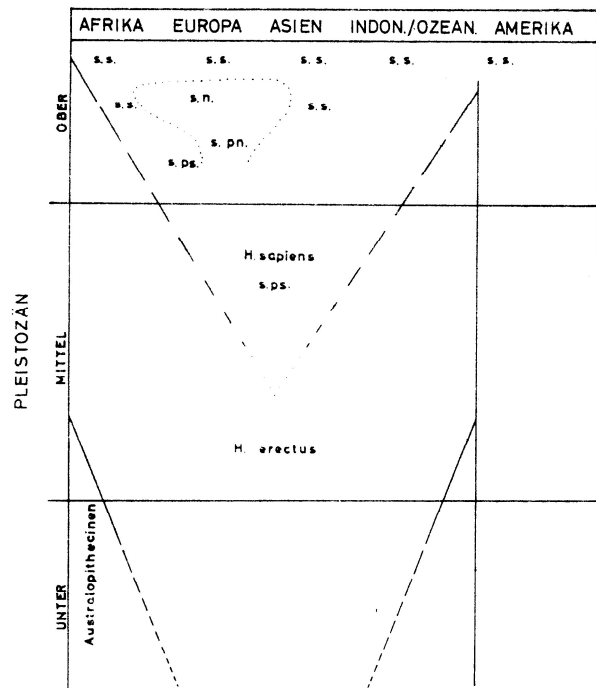
Bei der sehr wahrscheinlich nur geringen Besiedlungsdichte und großen regionalen Revieren der einzelnen Kleinpopulationen/Zeugungsgemeinschaften müssen wir auch als Folgen relativer Engzucht faßbare morphologische Unterschiede erwarten, die nicht in gleichem Maße systematisch ausgewertet werden sollten. Denn unsere humane Leistungsfähigkeit hat im kulturellen Bereich zusätzliche Kontakt- und Austauschmöglichkeiten erschlossen, die das Entstehen physiologisch wirksamer Zeugungsbarrieren zumindest verlangsamt haben dürften.

Die geringe Zahl unserer Fossilbelege und ihre große zeitliche wie räumliche Streuung raten so wieso zur Zurückhaltung in der Fixierung ihres systematischen Ortes innerhalb des durch sie angezeigten phylogenetischen Prozesses. Immerhin können wir aber schon heute eindeutig sagen, daß ganz erhebliche zeitliche Überschneidungen zwischen (Eu)Homininen und frühen humanen Hominiden — Australopithecinen — für Ostafrika bis ins Mittelpleistozän hinein beweisbar sind und für Indonesien vermutet werden können. Gleiches ist innerhalb der (Eu)Homininen zu erwarten. Deren früh-mittelpleistozäne Belege für Ostafrika, Europa, Ostasien und Indonesien setzen bei dieser weltweiten

Verbreitung voraus, daß ihre Radiation bereits tief im Unterpleistozän begonnen haben muß. Das beigegebene Schema soll dies ganz vereinfacht darstellen, wobei die zunehmende Verdichtung der Linien den ablaufenden Speziationsprozeß andeuten soll, ohne daß wir nach dem gegenwärtigen Kenntnisstand bereits in der Lage sind, Aussagen über den jeweils tatsächlich erreichten Raum, Grad oder Abschluß zu machen.

Für Mittel- und Oberpleistozän sind dabei nur noch die Arten *Homo erectus* und *Homo sapiens* angenommen, für letztere die vier Unterarten *s. praesapiens* — *s. ps.* —, *s. praeneanderthalensis* — *s. pn.* —, *s. neanderthalensis* — *s. n.* — und *s. sapiens* — *s. s.* — in grober Darstellung eingetragen. Für den Neanderthalerkreis wurde durch die Punktlinie überbetont zum Ausdruck gebracht, daß für ihn keine eigene Art, sondern nur noch ein räumlich wie zeitlich begrenzter Differenzierungsprozeß wahrscheinlich zu machen ist.

Eine sichere Stufenfolge im alten Sinne ist so wieso nicht mehr vertretbar, da die weltweite Gleichzeitigkeit eines Stufenhorizontes unter populationsgenetischen Gesichtspunkten für größere Zeitabschnitte unhaltbar geworden sein dürfte.



Schematische Darstellung der zeitlichen wie räumlichen Überschneidung von Speziationsprozessen der (Eu)homininen in Mittel- und Oberpleistozän.