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The Emergence of Man in Africa and Beyond [and Discussion]

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The emergence of man in Africa and beyond

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Transformations of the nervous, masticatory, locomotor and manipulatory systems, with accompanying functional changes, marked the emergence of the Hominidae and of the genus *Homo*. Various systems evolved in a mosaic fashion. The manipulatory and locomotor systems hominized early, probably with the emergence of the hominid family. Major changes of brain form and size occurred later, with the emergence of *Homo*. The functional counterpart of brain change is often thought of as cultural behaviour (material and non-material). However, the evolution of a propensity for culture would not alone have ensured the perpetuation of culture. Only an advanced mechanism for social transmission could have handed on the culture itself: evolving speech was such an advanced mechanism. Direct and indirect evidence suggests that emergent *Homo* (though not *Australopithecus*) possessed at least the rudiments of a speech faculty about 2 Ma ago. Thereafter, biological and cultural evolution were in a positive reciprocal feedback relationship. In this autocatalytic system, speech was a crucial component: by making possible spoken teaching and learning, it enabled culture to evolve beyond what could be conveyed by grunts, snorts or nudges.

1. Definition of man

Without qualification, the term ‘man’ is vague. In one usage it may refer to the members of the family of man, in another to the genus of man and in yet another to the species of (recent) man. More precise terms for these three groupings are the hominids (or members of the Hominidae), the genus *Homo* and the species *Homo sapiens* respectively. Moreover, more than one usage is possible at each of these three levels.

For this discussion the broadest usage of the term ‘man’ seems most appropriate; accordingly, my contribution deals with a morphologically defined group of higher Primates, the hominids or members of the zoological family, the Hominidae.

2. Hominids in time and space

The recognition of the earliest hominids poses grave problems, both because of the paucity of available fossil remains dating from the period 4–10 Ma ago and owing to the fragmentary nature and hence morphological indeterminacy of the specimens that we do possess. Therefore, this discussion will confine itself to the fossil remains dating from 4 Ma B.P. to the present. Within this time span the primate fossil record is complete enough and sufficiently representative for the presence of the Hominidae to be recognizable. Thus, it is possible to claim with considerable assurance that the hominids were already in existence 3.77 Ma ago. The evidence from Laetoli testifies that they were an upright-walking group of creatures with canine teeth much smaller than those of the pongids (or anthropoid apes); both of these features are in evidence 3.0 Ma ago, in the fossils of that period from Makapansgat in the Transvaal and Hadar in Ethiopia. An additional line of evidence on the structure of these late Pliocene hominids is provided by remains from Makapansgat and Sterkfontein, namely that the brain size of these upright-walking hominids with moderate canine teeth was not enlarged, was in fact no bigger on average than that of the great apes.

(*a*) *Distribution*

By criteria such as dental size, shape and function, the size and form of the endocranial casts, the detailed anatomy of the cranial and postcranial remains, it has been possible to classify a considerable proportion of the hominid fossil record and to place it in time. After over 30 years of study of all the fossils concerned, the author's investigations, along with those of numerous students of fossil man, with due allowance for regional or geographical variation, have led to the view that all of the hominid fossils between 4 Ma ago and the most recent past may be accommodated in two genera, *Australopithecus* and *Homo*.

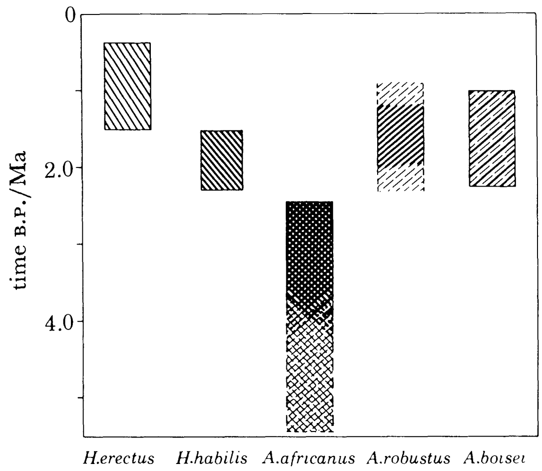

Figure 1. Schema of approximate distribution of five extinct hominid taxa in time (1979). The lighter shading on the *A. africanus* and *A. robustus* blocks indicates areas of uncertainty through incompleteness or indeterminacy of fossil record.

The temporal distribution of three species of *Australopithecus* and of two extinct species of *Homo* is shown in figure 1.

On presently available evidence, the geographical dispersal of these hominid taxa (or taxonomic groups) is at earlier stages restricted to Africa. Thus, the fossil record of early hominids before 2 Ma ago is confined to the Transvaal, Tanzania, Kenya and Ethiopia. Many hundreds of fossil hominid specimens are available from this end-Pliocene phase (4–2 Ma ago) and all are derived from the six sites in southern and eastern Africa. These sites lie between 10–11° N and 26° S and thus embrace equatorial and subtropical localities.

Between 2 and 1 Ma ago, the African fossil hominid record remains rich. In addition, the earliest traces of hominids start appearing in Asia and in Europe. From the last 1 Ma, not only do we find fossil human remains all over Africa, Asia and Europe, but ultimately man has penetrated into the last great hominid-free parts of the earth, America, Australia and, very recently, the Pacific islands, including Melanesia, Polynesia and New Zealand.

If we dismiss the possibility that the dating and geographical spread of the finds are accidents of discovery and the freakish consequences of an incomplete geological record, it is reasonable to hold that the late Pliocene hominids were a peculiarly African manifestation. It further seems valid to state that recent searches, in India, Pakistan, Burma and elsewhere, have not upset the inference that the hominids (as discussed here) arose in Africa, evolved and diversified in Africa and spread thence to Asia and Europe in the early part of the Pleistocene.

(*b*) *Variation*

The fossil hominids available from Pliocene Africa are spread over considerable distances. The continent itself comprises 27% of the land surface of the globe. Between the northernmost and southernmost australopithecine sites in Africa (Hadar and Taung) there lies a distance of a little less than 4800 km, while between the two virtually contemporaneous sites, Hadar in Ethiopia and Makapansgat in Transvaal, there is a span of close to 4000 km as the crow flies. Laetoli in Tanzania is removed by almost 1600 km from Hadar.

Over such vast distances, it is to be expected that early hominids would have been subject to geographical variation, even as other mammals are. In discussions on the systematics of the early hominids, it would seem that this factor has not received sufficient emphasis. As with other mammals, including baboons, monkeys and other primates, it is highly likely that the species of *Australopithecus* would have undergone geographical subspeciation. As an example, the species *A. africanus* is best known from the Transvaal, where it is called *A. africanus transvaalensis*. If this species occurred as well in east Africa, as is true of many other Plio-Pleistocene mammals, it is very likely that the Tanzanian form of *A. africanus* would have differed somewhat from its Transvaal conspecifics 2400–2700 km to the south; these differences might have been sufficiently detectable to connote a different subspecies of the same species. A commonly observed procedure for the naming of subspecies is to add a geographical appellation to complete the trinomial name; an appropriate name for the Tanzanian subspecies of *A. africanus* might thus be *A. africanus tanzaniensis*, the nomen matching *A. africanus transvaalensis* to the south.

Similarly, another geographical variant of *A. africanus* could have lived in Ethiopia, say, north of Lake Turkana (formerly Lake Rudolf) and in the Hadar of the northeastern part of the country. A most suitable name for such a subspecies would be *A. africanus aethiopicus*.

This principle of recognizing and appropriately naming geographical subspecies has been followed for the Pleistocene hominid, *H. erectus*; thus, we recognize *H. erectus erectus* from Indonesia, *H. erectus pekinensis* from China, *H. erectus mauritanicus* from NW Africa, the suggested *H. erectus olduvaiensis* (= '*H. erectus leakeyi*') from Olduvai, and *H. erectus heidelbergensis* from Germany.

When we take into account chronological differences within and among the fossil sites, the case for recognizing intraspecific variation becomes even stronger. Makapansgat member 3, for instance, has been dated palaeomagnetically to *ca.* 3 Ma. Sterkfontein member 4, found 320 km away, seems, on faunal grounds, to be somewhat younger, between 3.0 and 2.5 Ma old. These strata at both sites contain early hominid remains, and there are some morphological differences between the samples from the two sites. Once, when there was little appreciation of higher primate variability, these differences were thought to justify generic (Broom) or specific (Dart) distinction between the two hominid populations represented. In the fullness of time, the specimens from the two sites were deemed to have belonged not only to one species, but even to the same subspecies (*A. africanus transvaalensis*).

There are two lessons to be learnt from this case history. First, every site sample should be analysed separately, before decisions are taken on whether two site-samples may be pooled as representing a single population. Secondly, a moderate degree of variation is compatible with membership not only of the same species, but also of the same subspecies.

More specifically, on *a priori* grounds, one would have expected the east African representatives of *A. africanus* to have shown some differences from the Transvaal representatives and to have been classifiable possibly if not probably as distinct subspecies. Furthermore, between the northern and southern parts of east Africa (i.e. between Hadar and Laetoli), the same principle might have applied, with different subspecies in Ethiopia and Tanzania.

In sum, geographical and chronological variation within a species is a widespread phenomenon in the animal kingdom; it probably applied as well to early hominids; and insufficient note has been taken of this principle in some attempts to classify the early hominids.

3. Accommodating the Laetoli and Hadar fossils

Recently, an attempt, the latest of several, has been made to relegate *A. africanus* and, especially, its Transvaal subspecies, to a subordinate role in hominid phylogeny and, instead, to represent a succession of east African discoveries as the 'true' ancestral line of modern man. This attempt has been the claim of Johanson *et al.* (1978) and of Johanson & White (1979) that the 3.77–2.6 Ma old hominids of Laetoli in Tanzania and of Hadar in Ethiopia together represent a new species, '*A. afarensis*'. According to them, '*A. afarensis*' represents the common ancestral lineage of which *H. habilis* is the evolutionary continuation, while *A. africanus* affirms early stages in a specialized side branch leading to *A. robustus* (and *A. boisei*).

Unfortunately, some most unusual procedures have been employed by Johanson and his coworkers. First, the Hadar fossils have been 'pooled' with those of Laetoli before they (the Hadar specimens) have been described as a separate site sample, let alone as a succession of site samples, for the hominid-bearing deposits at Hadar span a time range 'from somewhat more than 3.1 Ma ago to somewhat less than 2.6 Ma ago' (Aronson *et al.* 1977). Thus, even within the Hadar deposits there may be a sequence of populations. Yet they have been treated as a single population and, for purposes of the creation of the species '*A. afarensis*', have been pooled with the Laetoli fossils, which are bracketed between 3.59 and 3.77 Ma B.P. (Leakey *et al.* 1976).

Secondly, in a most curious manner, a Laetoli mandible has been chosen as the type specimen of the supposed new species (apparently without the discoverer having given her consent), while the nomen '*A. afarensis*' is based on the Ethiopian site name, Afar. Thus, whatever subsequent revisions of classification these fossils undergo, we are left with the most unsatisfactory situation that an Ethiopian place name ('*afarensis*') is irrevocably attached to a Tanzanian jawbone and, by association and anatomical commonality, to all of Laetoli hominid fossils, unless, as the *International code of zoological nomenclature* allows, the nomen '*A. afarensis*' is suppressed.

Thirdly, in placing the Transvaal *A. africanus* fossils off the main hominid lineage and '*A. afarensis*' on it, Johanson & White (1979) have assigned too recent a date to the Transvaal *A. africanus*: they have shown the Transvaal sites as about 2.5–2.3 Ma, and, in one phylogenetic chart (Johanson 1978), as directly contemporaneous with *H. habilis*. The available evidence places the date of the *A. africanus*-bearing layers as 3.0 Ma B.P. at Makapansgat and 3.0–2.5 Ma B.P. at Sterkfontein. Moreover, they have erroneously assigned 'robust' elements to the Transvaal *A. africanus* populations, although such elements, used in a descriptive sense, have been reported in only a couple of Makapansgat specimens and not at all in the very large Sterkfontein site sample. Thus, the Transvaal *A. africanus* as a whole has been misdated and misrepresented as 'robust'.

A critical appraisal of the published diagnostic criteria of '*A. afarensis*' (Tobias 1979) has revealed that virtually every cited trait is to be found as well in the Transvaal samples of *A. africanus*. The supposed criteria, said to be diagnostic of '*A. afarensis*', do not distinguish the combined Hadar–Laetoli sample, at specific level, from *A. africanus* of the Transvaal.

Furthermore, it is by no means clear that the pooling, for statistical and comparative purposes, of the Hadar and Laetoli fossils is justified. Apart from the great distance separating the sites and the chronological distance of about 0.8 Ma between the midvalues of their time ranges, there appear, from the scanty anatomical data published on the Hadar fossils alone, to be indications of morphometric differences between them and the fossils of Laetoli, which have been well described by White (1977, 1980). For example there appear to be appreciable differences in tooth size, the teeth found at Hadar being smaller (like the smaller *A.* cf. *africanus* teeth from Omo reported by Howell & Coppens (1976)), whereas those of Laetoli are virtually indistinguishable in size from those of *A. africanus transvaalensis* (Tobias 1979).

Both procedurally, comparatively and morphometrically, it does not appear that a case has been established for the claims that the hominids of Laetoli and Hadar represent a single population and that that population has been sampled from a new species of early hominid.

It is recognized that, apart from Johanson's claimed criteria, some anatomical differences may exist between the *Australopithecus* of Sterkfontein–Makapansgat, of Laetoli and of Hadar, but it is indeed rather remarkable how slight those differences are, if we take into consideration the geographical and chronological distances involved. As an alternative hypothesis to explain those small variations among the three or four populations, it is proposed that the Laetoli and Hadar hominids belong to the same lineage as that represented by the hominids of Makapansgat members 3 and 4 and of Sterkfontein member 4. Moreover, it is hypothesized that the Laetoli and Hadar hominids cannot be separated morphologically, at the level of species, from *A. africanus* and that they represent two new subspecies of that species. Since the tying of the name '*A. afarensis*' to the Laetoli fossils is manifestly inappropriate and since it is considered that the case for '*A. afarensis*' has not been established, it is proposed formally that the name '*A. afarensis*' be suppressed. Instead, the author formally proposes the name *A. africanus tanzaniensis*, first proposed by him at the 41st Nobel Symposium (1978), on *Current argument on early man*, for the Laetoli hominids discovered by M. D. Leakey, and dated at 3.77–3.59 Ma B.P.

For the sequence of fossils from the Hadar deposits, the author proposes the name *A. africanus aethiopicus*; this subspecific nomen probably applies as well to the *A.* cf. *africanus* fossils from the older deposits at Omo, of which Howell & Coppens (1976) have spoken, as being somewhat smaller-toothed than *A. africanus transvaalensis*. Thus, from both Omo and Hadar, we have evidence for this somewhat smaller-toothed subspecies of *A. africanus*.

These newest east African discoveries afford confirmation of the hypothesis that *A. africanus* is the common ancestor of the two later hominid lineages, *A. robustus/boisei* and *Homo*.

4. Some anatomical trends

A voluminous and ever-growing literature on the morphology of the fossil hominids need not be reviewed here. However, three or four recent developments should be stressed.

(*a*) *Mosaic evolution*

It has become very plain that hominid evolution in the past four or more million years has been mosaic in character. If we consider the various complexes of characters that separate modern man and the apes, some of these complexes seem to have been early acquisitions and others late. There is now strong evidence, added to by the recent discoveries from Laetoli and Hadar, that the hominid locomotor system evolved before the majority of changes in the skull and teeth. Indeed, with Zihlman & Brunker (1979, p. 156), it seems fair to claim that, at least from an anatomical point of view, 'bipedalism initially defined the family Hominidae'. Figure 2 provides a schematic model of the suggested order of changes in the process of hominization: limbs changing early and teeth intermediately, while skulls and brains are the tardiest, in some respects, to attain modern form. The occurrence of development in this mosaic pattern adds to the difficulty in the identification of very early hominids, which might have begun to hominize structurally in a few respects but not in others. The case of *Ramapithecus* and the uncertainty about earlier claims for its hominid status may be illustrative of this point.

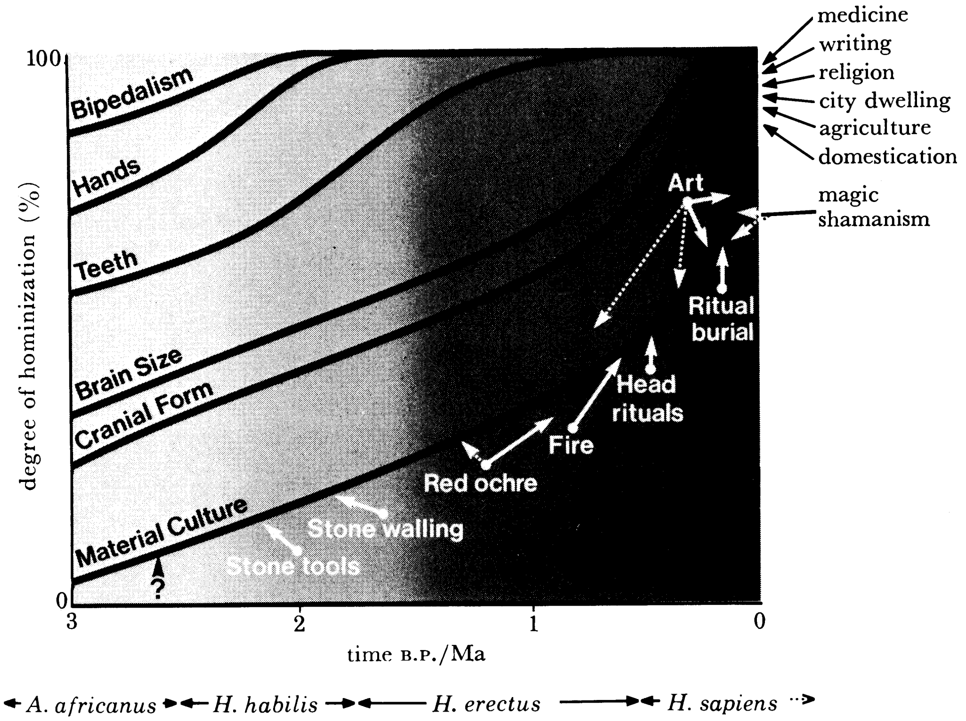

FIGURE 2. Schematic graphical representation of the degree and rate of hominization in respect of diverse structural and functional complexes and of cultural characters (100% hominization for modern man). The various complexes underwent hominization at different times and rates, as shown by the fossils and the archaeological record. The figure illustrates the mosaic character of hominid evolution.

(*b*) *Tooth material*

The 'tooth material' of the premolars and molars as a whole may be portrayed as the sum of the 'crown areas' (mesiodistal diameter multiplied by buccolingual diameter) of the two premolars and three molars of the upper half jaw and of the lower half jaw. This is a modification (Tobias 1967) of Howes's (1954) measure of tooth material. When the means or sums of means are used for samples of systematically identified fossil teeth, the data arrange themselves interestingly. If we leave out the Hadar teeth because of some doubts about the published measurements, we find that the oldest hominid tooth samples have intermediate values within the total range of hominid means. For the mandibular teeth, these values are: Laetoli 869 and *A. africanus transvaalensis* 861, which are nearly twice as great as the value (485) in modern *H. sapiens*. From these early values it seems that changes occurred in two directions. On the line of the robust hominids we find an increase in summed crown areas.

A. robustus robustus (Kromdraai)	882
A. robustus crassidens (Swartkrans	960
A. boisei (E Africa)	1312

On the line of *Homo* the following values are found, testifying to a progressive decrease in summed tooth areas.

H. habilis (E Africa)	787
H. erectus erectus (Indonesia)	695
H. erectus mauritanicus (NW Africa)	665
H. erectus pekinensis (China)	608
H. erectus heidelbergensis (Germany)	544
H. sapiens sapiens (worldwide)	485

The reduction of cheek-teeth occurs in the lineage of *Homo* in a definite sequence, at least in African material. Early *Homo* (*H. habilis*) shows a striking elongation of the premolars and first molar; on the other hand, M2 and M3 are mesiodistally abbreviated. The process of dental diminution seems to start at the posterior end of the dental arch. This posterior tooth reduction is part of a general reduction of the posterior part of the maxillary arch, which has been shown to produce profound functional effects on the pattern of tooth wear.

(*c*) *Tooth pattern and function in the Homo lineage*

In the early 1960s, while studying the Olduvai hominids assigned to *H. habilis*, the author noted changing occlusal slopes along the tooth row and a slightly helicoidal occlusal plane, although these features had not been noted in other early hominids. Subsequently, Wallace

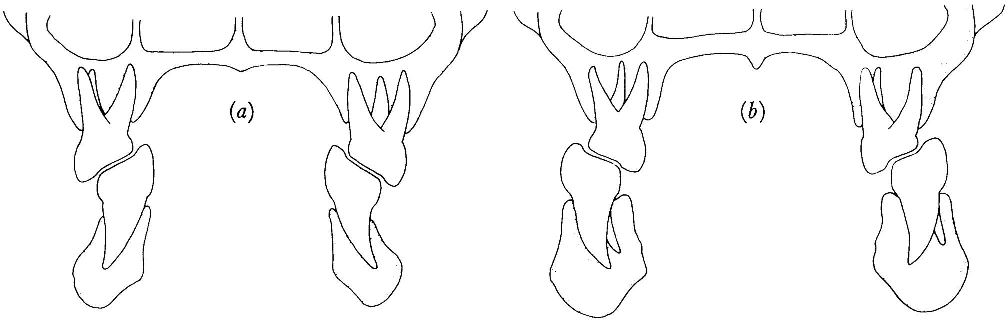

FIGURE 3. Relationship between upper and lower cheek teeth in (*a*) the more anterior and (*b*) the more posterior parts of the dental arcade. The changing relative widths of the maxillary and mandibular arcades, from front to back, leads to a change in the plane of the occlusal wear surface from mesial to distal; this changing plane is known as a helicoidal occlusal plane. It has been found in *Homo habilis*, in which there occurred reduction of the posterior part of the maxillary arch and of its contained teeth.

(1973) showed a total absence of the helicoid from the Transvaal australopithecines, and its presence in Swartkrans *Homo* (SK 45 and SK 80).

Recent studies on *H. habilis* confirm that all specimens studied, including Stw 53 from Sterkfontein member 5 (Hughes & Tobias 1977), show the helicoid. Hence this trait may help distinguish between *Australopithecus* and early *Homo*.

Of several hypotheses to explain the helicoidal occlusal plane, Campbell's (1925) proposal has gained widest acceptance, namely that the helicoid results from differences in upper and lower alveolar arch width. Measurements of maxillary arch widths of early hominids have shown that, whereas in *Australopithecus* arch widths increase to a maximum at M^3, in early *Homo* maxillary arch widths are greatest at M^2. The decline in posterior maxillary arch width is part of the general reduction of that region mentioned earlier.

It seems that the onset of posterior arch reduction, with the appearance of a helicoid, is a structural and functional concomitant of the transition from the presumed australopithecine ancestor to *H. habilis*.

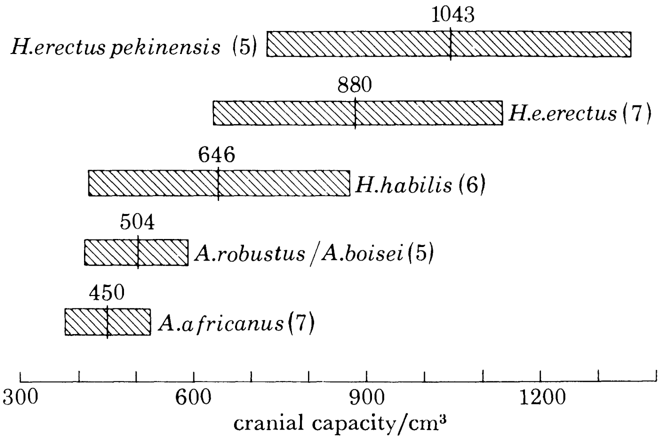

FIGURE 4. Means and 95 % population limits for the cranial capacities of five samples of hominid crania.

(*d*) *Brain size*

The newest data on the endocranial capacities of fossil hominids show slight differences from earlier published estimations. Figure 4 shows the means and the 95 % population limits in five taxa of early hominids for which data are available, while figure 5 shows the pattern of the changing trend in cranial capacity (and therefore in inferred brain size) from *A. africanus* to *H. sapiens*. Arbitrarily we may recognize four major stages in the increase of absolute capacity:

(i) the small-brained or *micrencephalic* hominids, the various species of *Australopithecus*;
(ii) the medium-brained or *mesoencephalic* hominids, *H. habilis*;
(iii) the large-brained or *macrencephalic* hominids, *H. erectus*; and
(iv) the *gigantencephalic* hominids, *H. sapiens*.

In round figures, the mean brain sizes of these four grades are respectively 1.0, 1.5, 2.0 and 3.0 times the sizes in the modern great apes.

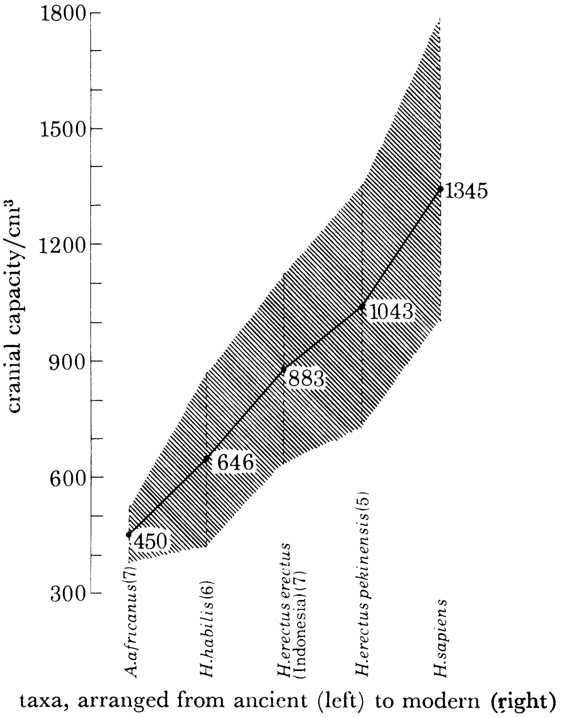

FIGURE 5. The pattern of the threefold cranial capacity increase over the past 2.5–3.0 Ma. For each of the five samples, the mean and 95 % population limits are indicated.

(*e*) *The pattern of brain enlargement*

Whatever the causal factors or selective advantages favouring brain enlargement, it is clear that even an autocatalytic or positive feedback system operating between brain size and culture could not have been successful if there were not available mutations favouring belated postnatal brain expansion. It is true that, as Mayr (1963), Bielicki (1964, 1969) and the author (Tobias 1971) have stressed, a positive feedback system of this nature could have led to a substantial increase in brain size. However, if the pattern of antenatal and postnatal brain growth had remained much the same as in apes, this might have had biologically disastrous consequences.

In apes at birth the cranial capacity is about 300 cm^3 or some 60–65 % of the adult cranial capacity (Keith 1931). In *Australopithecus*, with about the same mean adult capacity, the neonatal capacity could likewise have been 60–65 % of the adult capacity. However, if an *H. habilis* with an adult capacity of, say, 650 cm^3 had retained a neonatal brain ratio of 60 %, its cranial capacity at birth would have been about 390 cm^3. On the same basis, *H. erectus* of Java would have had a neonatal cranial capacity of 530 cm^3 and *H. erectus pekinensis* one of 625 cm^3, while modern *H. sapiens* would have been faced with the daunting prospect of giving birth to a swollen-headed baby with a cranial capacity of 810 cm^3. It is obvious that, had brain enlargement been achieved in this irresponsible manner, an increasing number of individuals would have had difficulty in giving birth to their large-headed babies. On the one hand, the feedback system could have proceeded wantonly to increase brain size, because of its great cultural advantages, while, on the other hand, such a pattern of increasing brain size would have been decidedly detrimental to survival. The deviation-amplifying system would have been powerless to overcome the high incidence of obstructed labours, and foetal and neonatal deaths. The system would have become not only counter-productive, but counter-reproductive.

Fortunately, we may infer that it did not happen like this. The bland agency of natural selection operated on the whole feedback system and allowed the brain size increase to be effected without such a menace to survival. Instead, it favoured the evolution of a new pattern of brain growth, whereby absolute brain size at birth seems not to have altered appreciably, the neonatal capacity of modern man being about 350 cm^3, only slightly more than the value for modern apes.

If we accept 300 cm^3, in round figures, as the neonatal capacity, a newborn *H. habilis* would have attained only 46% of its adult capacity (instead of 60% as in apes and as postulated for *Australopithecus*). In Java man, that percentage would have dropped to 35%, in Peking man to 29%, and in modern man to about 22%. At a neonatal capacity of 350 cm^3 in modern man, the figure would be about 26%.

Natural selection clearly favoured variants showing belated brain expansion. Thus, there was a progressive drop in the percentage of adult brain size attained by birth, along successive stages in the human lineage. In this way, the biological equipment was brought into line with the demands of the positive feedback system. A corollary of this change is that the brain at birth became progressively more immature. Neonatal dependence on the mother accordingly became ever greater.

(*f*) *Brain form*

When the structure of the australopithecine endocast is compared with the structure of the endocast of the apes, it is seen that the hominid endocast shows some evidence of transformation, though its size is approximately the same. Of especial interest are the marked prominence of the inferior frontal convolution and a tendency towards expansion of the pairietal lobe. Though the position of the lunate sulcus remains, in this author's opinion, indeterminate, it does seem that the parietal enlargement affects both the superior and inferior portions more or less equally. There is no evidence of especial enlargement of that very basic secondary association cortex, the inferior parietal lobule. In fact, in several australopithecine endocasts, this region is rather flat, being overshadowed rather by the upper part of the parietal lobule.

However, in the endocasts of *H. habilis*, as the author first pointed out in 1973 (see Tobias 1975), there is a clearly developed rounded fullness of the inferior parietal lobule. This indicates a relatively strong development of part of the brain, comprising the angular and supramarginal gyri and containing one of the developmentally youngest parts of the brain. It includes part of Wernicke's area, known to be a part of the central mechanisms concerned with the control of speech. Unfortunately, the relatively poor endocranial marking of the lateral or Sylvian fissure has thus far prevented our detecting any signs of asymmetry of the length of that fissure or of the height of its posterior terminus, the Sylvian point.

Nevertheless, the striking development of the inferior parietal lobule in Olduvai hominid 24 and in KNM-ER-1470, together with the strong development of the posterior part of the inferior frontal convolution (Broca's area), strongly suggests that the structural and functional bases of articulate speech were present in *H. habilis*. In *Australopithecus* only a hint of an enlarged Broca's area, but not of Wernicke's area, could be detected.

Thus, just at the stage where the first allometric enlargement of the brain becomes apparent, in *H. habilis*, structural speech centres make their appearance. A further coincident phenomenon is that cultural manifestations appear in the record at the same time. What is the relationship among these phenomena?

5. Anatomy, function, speech and culture: a new proposal for an autocatalytic feedback system

Many adaptive advantages have been hypothesized as flowing from man's bigger and reorganized brain (see Gabow (1977) and Tobias (1980) for recent summaries). Some of these explanations could have applied if brain enlargement were a non-recurring event. However, encephalization was not a unique event; it was sustained for 2 Ma or more and it carried the lineage across a generic boundary into *Homo* and continued in the three consecutive chronospecies, *H. habilis*, *H. erectus* and *H. sapiens*. The brain changes transcended systematic categories, geographical dispersion, cultural diversification, ecological radiation and ethological variegation. Whatever selective and other causal agencies were operating, they must have continued influencing the hominid brain throughout the assumption of a bewildering array of new life styles and circumstances.

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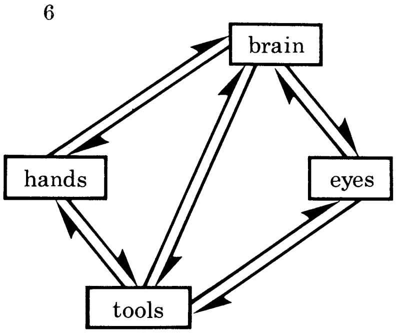

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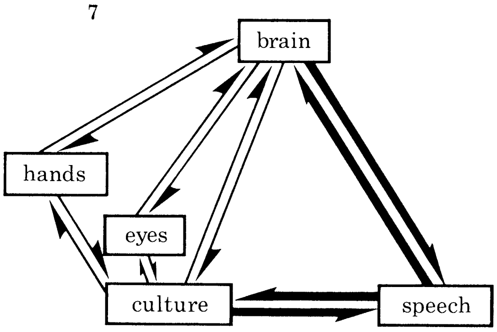

Figure 6. Positive feedback system featuring three biological components and a cultural component. This earlier version is now held to operate within a generation, but not necessarily across the generations, in respect of cultural progress.

Figure 7. Modified, trans-generational feedback system incorporating speech, the biologically determined faculty that enables cultural beliefs and practices of survival value to be transmitted to future generations. In this autocatalytic system, speech is believed to play a predominant role.

One pattern of causal factors that could stand up to this difficulty is the positive feedback system, for such an autocatalytic system, once established, could continue operating more or less under its own momentum, despite behavioural and ecological diversity, Mayr (1963) proposed that brain size and the duration of parental care were so related to each other. The author earlier stressed such a feedback relationship between culture and its genetic bases, between physical and cultural evolution (Tobias 1971). Bielicki (1964, 1969) suggested the interplay of two-way causal links or feedbacks between cultural and non-cultural components of hominization. However, as indicated above, this system does not operate in a vacuum and must be considered as still subject to the operation of natural selection.

It is proposed that the enlargement and reorganization of the brain in hominid phylogeny was in a positive feedback relationship with the rise and increase in complexity of culture. This is a deviation-amplifying system: a small shift or initial kick on one side of the feedback equation would have stimulated or favoured a shift on the other side, and so on. Certain material aspects of cultural evolution, very obvious in the archaeological record, required visual and motor skills as participants in this autocatalytic system: centrally, this involved specific parts of the brain; peripherally, it brought in the eye and the hand.

These were the components and the limits of the feedback system that the author earlier proposed. The whole autocatalytic system was under the influence of natural selection. At that stage the stress was on material culture, the implemental life, and on a generalized brain enlargement, together with efficient eyes and hands, as the three biological components. This feedback system was proposed to explain the persistence of brain enlargement and reconstruction, so that the advantages that applied about $2\frac{1}{2}$ Ma ago were still valid 1 and even $\frac{1}{2}$ Ma ago. The earlier formulation could be summarized thus: better brains made for better culture; better culture increased chances of survival; challenges to survival placed a premium on still better brains. The unstated assumption implicit in this formulation is that if the next generation had better brains, the culture would automatically persist. As this assumption is unacceptable a new hypothesis has been made.

The system now proposed has several new features.

(1) On the cultural side are included the whole panoply of non-material as well as material aspects of man's social heritage, for the concepts and social structure might have been as crucial to survival as material innovations and improvements.

(2) On the biological side, stress is laid on the special development of certain areas of the cortex, rather than on a generalized enlargement. The evolutionary benefits lay in having enlarged parietal lobes (and especially the inferior parietal lobule on the left), inferior frontal lobes and superior temporal convolutions. The ape's brain already has much localization of functions; therefore, it is suggested, in the hominid lineage the whole brain enlarged for the sake of highly desirable enlargement of certain areas. The very areas that have shown the most striking enlargement are those that provide the clue to the third new feature.

(3) The main new proposal is that speech be brought into the feedback system as a fifth and predominant component.

Enlargement of certain areas of the brain went hand-in-hand with the development of an increasingly complex culture, as a revolutionary new survival kit. So intricate a culture did man develop that only articulate speech could have transmitted it from generation to generation. It is suggested that the main natural selective advantage flowing from brain enlargement and especially of the lower frontal, lower parietal and upper temporal regions was the evolution of mechanisms for the transmission of culture, and that means primarily cognitive abilities and articulate speech. By making possible a new kind of inheritance, cultural or social inheritance, articulate speech facilitated the learning of the new techniques by children of the next generation and so helped ensure their survival.

This system of culture and cultural transmission was, in effect, a new kind of inheritance, cultural or social inheritance. It took the universal mammalian capacity for learned behaviour, refined it into a powerful mechanism for ensuring the survival, not merely of one current generation, but of future generations. The survival of future generations is precisely what evolution is all about.

The feedback system operated for approximately 120000 generations of hominids. It continued until it produced a situation in which articulate speech was the ineluctable destiny of every normally developing individual, and even of most abnormal and defective subjects. It operated until, as Washburn & Benedict (1979) have put it, it is extremely difficult to stop people speaking. It operated until a kind of threshold quantity of relevant brain tissue to permit the acquisition of spoken speech was reached at younger and younger ages, as Krantz (1961) suggested. This meant that one's brain and one's speech mechanisms permitted active learning and participation in the cultural process from young childhood.

When these advanced stages were reached, the whole process slowed down. Beyond a certain point of cultural evolution, it was no longer an advantage to have bigger and better brains. Cultural sharing and the benevolence of social life had taken the place of nimble wits of the individual, as an insurance against extinction. Encephalization was no longer at a premium. One could manage and be as educable with 1250 g of brain as with 2250 g.

The transgenerational aspect of culture impels us to see in speech the cardinal factor in the evolution of the human brain and intellect. Differential enlargement of the brain enabled man to become not only culture-bound but speech-dependent: in a word, it made over a speechless animal into a speaking man.

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Discussion

B. Campbell (*Sedgeford Hall*, *Hunstanton PE*36 5*LT*, *Norfolk*, *U.K.*). I should like to comment on a number of points in Professor Tobias's lecture.

In making comparison between two samples, such as those of Hadar and Makapan, it is always necessary to review the total morphological pattern. A series of individual measurements, such as are listed as diagnostic criteria of *A. afarensis*, compared one by one can be of value, but do not give us all the information that we need to make an assessment of morphological difference or distance. At the same time, measurements of breadth and length of teeth are notoriously difficult to standardize and those taken by different workers are often not accurately comparable. They constitute a coarse means of morphological comparison. Multivariate analysis is the appropriate tool to make statistical comparisons of the total morphological pattern of populations.

The schematic model (figure 2), which indicates successive phases of evolution of distinct functional complexes, followed by the evolution of 'material culture', summarizes in a striking fashion the mosaic sequence of hominid evolution. We do need to remember, however, that the progress of material culture is only a weak reflection of cultural behaviour in its broadest sense. In practice it seems clear that behavioural adaptation and modification preceded anatomical change: behaviour led the way into hominization, and was presumably the motive force applying selection pressures leading to morphological changes. Material culture itself was surely a late development in the evolution of hominid culture.

Regarding the evolution of the hominid brain, it is important to realize that brain size and cranial capacity are correlated with body size and should be scaled accordingly if they are to be given the kind of meaning that is attributed to them in this Discussion. For example, the earliest *Australopithecus* hominids were small creatures, probably not much more than 3 ft (*ca.* 0.9 m) in stature. Although their brains were roughly the same size as those of African apes, being relatively smaller animals they were already significantly more highly encephalized. Similarly, the 'threefold cranial capacity increase' shown in figure 5 is partly due to increase in body size.

The form of the curve in figure 5 can be determined only by plotting every individual skull datum point without regard to taxonomic grouping. Such grouping gives a false impression of stepped cranial evolution. In particular, it completely hides the levelling out of the trend of increasing cranial capacity during the last 100 ka.

Regarding early brain growth, Professor Tobias states that during hominization natural selection favoured the evolution of 'a new brain growth' to achieve a relatively low neonatal cranial capacity. It is surely more accurate to state that the period of gestation was relatively shortened during hominization, with the result that the human baby is born with an immature brain only *ca.* 26 % of its final size.