THE COMMUNICATION OF THE DEAD

EARLIEST VESTIGES OF THE ORIGIN OF ARTICULATE LANGUAGE

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Gerrit heinrich kroon (1868-1945) Myriads of people claim to be able to communicate with the dead. They are spiritualists, mediums, and channellers. Sir Arthur Conan Doyle, the creator of Sherlock Holmes, was a devotee. Great numbers of people still seek the help of these mediums, often after a death, to help them get into touch with the departed one. Ancestor worship which is widespread is predicated upon the belief that the spirits of one's forbears concern themselves with the day-to-day affairs of the society and make their presence felt by deeds or by words. I suppose you could apply the term "Communication of the Dead" to such activities. If anyone reads this under the mistaken impression that it is a discourse on such matters, it would perhaps be best to discontinue now.

My subject is a search for the signs left in stones and bones from which we are able to read, or infer, indications of the earliest beginnings of spoken language. It will follow not Conan Doyle, but Sherlock Holmes, in reading the clues, not of recent crimes, but of ancient happenings where time is measured in hundreds of thousands and even millions of years. It will follow St. Bernard when he wrote 850 years ago, "You will find something more in woods than in books. Trees and stones will teach you that which you can never learn from masters". We shall pursue the faint echoes of those words in William Shakespeare's *As you Like It:*

"And this our life, exempt from public haunt, Finds tongues in trees, books in the running brooks, Sermons in stones, and good in everything."

To look for clues to the emergence of language, one needs above all to study brains. The brain qualifies as one of Charles Darwin's "organs of extreme perfection and complication". He admitted that it was most difficult to explain, on 'his' theory, how such organs of astonishing complexity could have evolved gradually and by natural selection. One such structure was the eye of higher animals. The human language capacity is another evolutionary achievement of extraordinary perfection and complexity. Like other human skilled activities, it involves both central (neural) and peripheral (vocal and respiratory) complexes. It is staggeringly difficult to reduce these to simpler building-stones to which evolutionary principles may be applied. It is a far more formidable task to reconstruct the evolution of the brain than, say, that of the bones and the teeth.

Brains do not fossilise. Where then do we find the evidence from which we may infer how brains have evolved? One source of information is the comparative anatomy of the brains of living species. For one thing, modern human brains are, in absolute size, about three times as large as those of living great apes. Human brains permit us to use spoken language and to read and write, whereas so far as is known the brains of no other living animals contain the neurological bases of these functions. Comparative neuro-anatomy has taught us a great deal about the brains of living mammals and, especially, the primates. From such comparative data, it is possible to discern which areas of the brains of humans differ from the corresponding parts of ape brains. In turn, we may infer that, if we and the great apes have in the past had common ancestors, the features which are peculiar to the human brain must have emerged and developed after the lineage leading to Homo sapiens diverged from the lines of descent leading to chimpanzees and gorillas. We are able to supplement such information on brain structure by studies on brain function and on behaviour in living primates including humans. Very advanced new techniques enable us to locate functions in the brain in living subjects. For example, we are able to insert an inert substance, radio-xenon, into a living person; this material is localised to any part of the brain which is active. The subject is given a specific task, while images of the brain are taken. If a particular task always leads to a special region of the brain lighting up, we may conclude that the neurological basis

of that function is localised to that part of the brain. This technique is called PET-scanning (positron emission tomography).

The fossil record enables us to confirm these inferences from studies on living creatures about the brains of ancient members of the human lineage. Yet, as I said earlier, brains do not fossilise. The key to this brain-teaser is to be found in the curious and unique relationship between the brain and the brain-case or calvaria.

BRAINS AND BRAIN-CASES

The anatomist reads and interprets the markings and impressions of ligamentous and muscular attachments to bones, as well as the grooves, notches, foramina and smoothings owing to the impingement on bones of other structures such as arteries, veins, nerves, ligaments, and tendons in transit. In the same way, much information on functionally important soft tissue anatomy may be garnered from the careful study of even the most ancient fossilised bones.

Of no structure has this proved more valid than the brain, because it is the only organ that is totally enclosed in a hollow bony box, the calvaria, which in life is faithfully moulded upon the contents. These contents are the brain, its coverings (the meninges), blood-vessels and blood, cerebrospinal fluid and the stumps of emerging cranial nerves. The brain makes up the bulk of the contents, varying between 66% and 95% of the capacity. There is a fine reciprocal relationship between brain and braincase during the development of an individual. Under conditions of normal development, a larger brain dictates the growth of a larger calvaria and a smaller brain is housed in a smaller calvaria. A broad brain is accommodated in a broad brain-box. A subject with a relatively small cerebellum has a proportionately small posterior cranial fossa. If the superior sagittal venous sinus passes to the left, instead of to the right as is more common, the imprint of the corresponding groove likewise passes to the left. If a particular gyrus or convolution on the surface of the cerebrum is well developed and protrudes, there is a matching hollow on the endocranial surface (Figures 1 & 2).

All such features of the soft tissue contents of the calvaria may readily be confirmed in modern cadavera. Hence, from the inner surface of a calvaria, one may draw conclusions about the brain and blood-vessels that once occupied that braincase. We may facilitate the study by filling an empty brain-case with a plaster or plastic medium and making an artificial endocranial cast or endocast (Figure 3). In size and form, such an endocast faithfully reproduces the size and form of the endocranial cavity. Hence, from the surface of an endocast one may read the sulcal, gyral and vascular impressions directly.

Sometimes a natural endocast forms during fossilisation. This is especially likely to happen if the cranium comes to rest in a protected site such as a cave, and particularly when the cranium lies upside down – since the cave earth gains access to the calvaria mainly through the foramen magnum, the large opening on the base through which, in life, the brain joins the spinal cord. If a cementing agent such as lime is present in the surrounding rocks, the sandy filling of the brain-case becomes calcified.

There results a natural endocast. An example is the beautifully developed endocast of the Taung skull that Raymond Dart (1925) revealed to the world seventy years ago (Figure 4). Details of brain and vessels may be read from a natural endocast, as from an artificial endocast. Thus, endocranial surfaces and endocasts provide raw data for palaeoneurobiological research.

THE MESSAGE OF THE AUSTRALOPITHECINE ENDOCASTS

The most obvious results of endocast studies are the endocranial capacities. We have mean values for three specimens of *A. afarensis* from Hadar, Ethiopia, six of *A. africanus* from Taung, Sterkfontein and Makapansgat, South Africa, and seven of *A. boisei*² from Omo in Ethiopia, Koobi Fora in Kenya and Olduvai in Tanzania. The three mean values are c413.5cm³ for *A. afarensis*, 440.3cm³ for *A. africanus*, and 463.3cm³ for *A. boisei*. These values are close to those of the extant apes. If we express the means for the apemen as percentage ratios of the means for four ape species, we find the following ratios:-

A. afarensis, of which there is a poor and inadequate sample: 120% of Pan paniscus; ?108% of Pan troglodytes; ?82% of Gorilla gorilla; and ?102% of Pongo pygmaeus. A. africanus, respectively, 128%, 115%, 87% and 109%.

A. boisei, respectively, 135%, 121%, 92% and 114%.

In round figures, the mean values in species of the genus Australopithecus range from ?82% to 135% of the values in apes. That is they are of approximately the same order of magnitude as in the apes, but they are only about 33% of the mean values in modern humans. All of the means cited are for combined sex samples. Only in relation to the gorilla mean values do the australopithecine data show shortfalls, the respective decrements being ?18, 13 and 8 per cent. In relation to the other three species of modern apes, the australopithecine values show small but definite advances in absolute brain size, the increments ranging from ?20 to 35 in comparison with the bonobo, ?8 to 21 in comparison with Pan troglodytes, and 2 to 14 when compared with the orang-utan. In contrast with these small increments, the percentage ratios by which modern humans exceed these apes are 293, 252, 168 and 233 per cent respectively. It is clear that, in absolute terms, the australopithecines show only a small

increase in mean endocranial capacity over the chimpanzee (which molecular data assign as most closely related to modern humans).

Estimates of the body size of the apemen are used to provide measures of relative brain size or indices of encephalisation. These confirm that the various australopithecine species were somewhat more encephalised than the chimpanzee. For example, Hemmer's Coefficient of Cephalisation shows that the value in *A. africanus* is 18.2% (Tobias, 1987) or "approximately 20%" (Hemmer, 1985) greater than in the modern chimpanzee. It is only when we consider the mean endocranial capacity in *Homo habilis* that we find a marked increase, in both absolute and relative terms, over the brain-size of the chimpanzee and other apes (see below).

Apart from gross size, there are few differences in the morphology of the australopithecine endocasts as compared with those of the apes. These may be summarised as follows:-

A. afarensis: The earliest available hominid endocasts, dated to about 3 million years ago (mya), reveal only that the cranial venous sinus drainage was of the unusual occipital-marginal pattern in 6 out of 6 Hadar crania, but of the transverse-sigmoid pattern in one Laetoli cranium for which the relevant part is available. On this trait, the Hadar specimens group themselves with the robust (A. robustus) and hyper-robust (A. boisei) australopithecines, rather than with A. africanus and H. babilis (Tobias, 1991a; Tobias and Symons, 1992). Apart from this curious venous sinus drainage, to whose presence in some early hominids I first drew attention in 1967 (Tobias, 1967, 1968), Holloway (1983, 1988) has referred to the putative position of the lunate sulcus in one Hadar specimen (A.L. 162-28) in support of his claim that A. afarensis showed reorganisation of its cerebral cortex in a human direction. A careful examination of the evidence adduced in support of Holloway's claim leaves room for doubt. I remain unconvinced that there is any plausible evidence that these early hominids showed any differences of brain form – or, for that matter, size – from the apes. We may draw the provisional conclusion that, for 2 to 5 my after hominids came into being, there were few or no externally manifest changes in the brain, either of size, form, or sulcal or gyral patterns. Further discoveries of hominid calvariae and endocasts older than 3.0 mya may lead us to alter this interpretation.

A. africanus:³ Between 2.5 and 3.0 mya, we have a number of natural endocasts from South Africa (Figure 5). We have seen that the members of this taxon show a small but definite advance over the chimpanzee in absolute and relative brain size. The following features of these endocasts appear to distinguish them from those of extant apes:-

I. In gross pattern, the impression of the australopithecine foramen magnum, which is regarded as reflecting the position of the brainstem, reveals a somewhat more anteriorly implanted brainstem than in the brains of extant apes, toward the position that pertains in later humans. In modern humans, we have found an appreciable discrepancy between the small diameters of the brainstem and the large diameters of the foramen magnum. In the plane of the foramen, the medulla occupies, on average, 28% of the anteroposterior diameter (basion to opisthion), and 38% of the transverse diameter of the foramen. Even if we allow for possible shrinkage in the embalmed specimens studied, the mean values remain close to 30% and 40% respectively. We found no detectable difference in the percentages between infant and adult specimens (Tobias and Symons, 1992). Hence, in the assessment of the brainstem's position in early hominids, it is important to allow for this loose fit of the brainstem as it traverses foramen magnum.

2. The parietal lobe of the cerebrum is well developed (Holloway 1988) (Figure 6).

3. The cerebellar hemispheres are underslung (Tobias 1967), so that the occipital poles of the cerebrum generally form the most posterior part of the endocast.⁴

4. Most of the australopithecine endocasts show the combination of right fronto-petalia and left occipito-petalia. This combination Galaburda (1984) describes as the most common in modern humans, while Holloway (1988 p. 98) states that it is not found in the apes, 'even the highly asymmetrical endocasts of *Gorilla*'.⁵

Two further features have been claimed by various investigators, as human-like aspects of the A. africanus endocast. They are the supposed position of the lunate sulcus and the presence of a Broca's cap.

Some investigators, most notably Dart (1925), Schepers (1946) and, more recently Holloway (1970, 1974, 1975, 1985, 1988), have urged a fifth criterion, namely the putative position of the lunate sulcus. Holloway, following Dart and Schepers, interprets this in early hominid endocasts as in a human-like posterior position, rather than in an ape-like anterior position. Others, chiefly Falk (1989) and Falk *et al.* (1989), see only ape-like sulcal patterns in the australopithecine endocasts. As far as the lunate sulcus is concerned, I agree with Clark (1964) that it is really not possible to identify the lunate sulcus with certainty from the impressions on the early hominid endocasts.

As regards the Broca's area impression (Brodmann's field 44a), Schepers (1946, 1950), in his original study of the South African australopithecine endocasts, claimed to be able to identify this anterior motor speech cortex. Tobias (1987) has identified Schepers' well-developed cortical bulbosity in the homologous area, while Falk (1983) believes that the sulcal arrangement in that area is totally ape-like and unlike that in *Homo habilis* (see below) and in *H. sapiens*; Holloway (1983, 1985), however, contests Falk's view. Whilst the last word on this matter has clearly not yet been written, it remains true that a cortical protrusion in the position of Broca's area is detectable in the few *A. africanus* endocasts in which that region is preserved. Schepers (1946) recognises also that the primary auditory associative area (field 21) has "undergone an expansion [in the apemen] comparable to that seen in the human brain" (op. cit., p. 253). Other investigators have not been able to confirm this. Nor has Schepers' claim that fields 39 and 40 are large in the fossils been corroborated. The question whether *A. africanus* possessed the propensity for spoken language is referred to later.

Apart from these two contested claims, the above four numbered items remain the only clear-cut and widely accepted features of the *A. africanus* brain cast which appear to distinguish it from those of extant apes. The incompleteness of the Hadar endocasts assigned to *A. afarensis* leads one to the interim conclusion that there are at present no features known to distinguish between the endocasts of *A. afarensis* and *A. africanus*, save that, on a tiny and partly contested sample of capacity estimates of *A. afarensis*, the mean capacity for *A. afarensis*. We do not know if the Broca cap recognised in *A. africanus* was present also in the Hadar hominids.

THE MESSAGE OF THE HOMO HABILIS ENDOCASTS

Homo babilis lived in Africa from c2.3 to c1.6 mya. Estimates of its average endocranial capacity vary somewhat according to which crania are included in the sample. Four crania from Olduvai Gorge, Tanzania, are accepted by me (Tobias, 1987, 1991a, 1994) and by Wood (1991) as belonging to this species, but we differ in our interpretation of two or three specimens from Koobi Fora in northern Kenya. Moreover, for three Olduvai crania, Wood uses earlier estimates by Holloway (1983), whereas Tobias employs newer estimates of their endocranial capacities. Wood's series yields a mean of 609.5cm³ with a coefficient of variation (C V.) of 10.25%. Tobias's corresponding figures are 640.2cm³, and 12.9%. Although some investigators believe that this C.V. is too big for members of a single species, the value 12.9% is of the same order of magnitude as those of *A. boisei* (12.0%), the Beijing crania of *H. erectus* (12.7%), and a sample of 22 Asian and African *H. erectus* (13.2%), while it falls well below the estimated C.V. for *A. afarensis* (?20.2%) (Miller, 1991; Tobias, 1995a).

The latest estimates of the mean capacity of *H. habilis* show that this species had a brain size bigger by half than the average values in *Australopithecus*. Thus, it was with *H. habilis* that the human trend toward great cerebral expansion began. For *H. eractus* the mean value of 937.2cm³ is 46.4% greater than the sample mean for *H. habilis* (Tobias, 1992a, 1994), whilst the estimated capacity in modern *H. sapiens*, irrespective of sex and race, namely 1350cm³ exceeds the *H. erectus* sample mean by some 44.0%

When we turn to relative brain size, we note that much attention has been devoted recently to 'scaling', that is, the structural and functional consequences of differences in size (or scale) among organisms of more or less similar design (Jungers, 1984, 1985). Some studies stress the problem of the systematic level at which comparisons of brain scaling are most meaningful (Harvey and Mace, 1982; Holloway and Post, 1982). Others underline the metabolic constraints in brain enlargement (Martin, 1980, 1981, 1982; Armstrong, 1981, 1983, 1984; Hofman, 1982). In a study on the quantitative genetic aspects of the problem of brain size/body size, Lande (1985) observes that "genetic uncoupling" of brain and body sizes in primates would have facilitated encephalisation in primates, because natural selection for larger brain size would then not necessarily have carried along an uneconomical, correlated increase in body size: "...if the genetic correlation between brain and body size within populations in the human lineage was ... low as suggested by the data on primates, hominids would have been enabled to rapidly increase brain size in response to selection for more complex behavior without the cost of antagonistic selection to prevent the evolution of gigantism" (Lande, 1985: p. 30).

Estimates of relative brain size show that *H. habilis* was clearly more encephalised than any of the australopithecine series and represented a major step, indeed the first such, in the expansion of the hominid brain. Its values reveal that it had attained some 50% of the *H. sapiens* degree of encephalisation (Tobias, 1987). More marked encephalisation followed from *H. habilis* to *H. erectus*, the latter species reaching some 70% to 80% of the degree of encephalisation of *H. sapiens*.

H. habilis is thus more encephalised than *A. afarensis* and *A. africanus*. Since the estimated body size is built into the encephalisation formulae, the values in *H. habilis* represent a real advance in encephalisation over the small-brained australopithecines.

The data on relative brain size show that, while the australopithecines were encephalised slightly more than the chimpanzee, *H. babilis* had unequivocally begun the remarkably "uncoupled" or disproportionate enlargement of the brain that is a critical hallmark of humankind.

The increase of brain size, whether absolute or relative to body size, is the most dramatic change to have occurred in hominid evolution in the last three million years. In that period, spanning some 200,000 generations, brain-size trebled along the human lineage. The advantages of the larger size have been much speculated upon and over a dozen hypotheses have been advanced to explain the sustained tendency in our lineage towards increased encephalisation (see reviews of Gabow. 1977 and Tobias, 1981a).

An encephalising trend connotes not only that a bigger percentage of one's bodily bulk is occupied by brain tissue. For size change is only a gross, external indicator of encephalisation. In modern animal groups, when comparisons are made between smaller-brained and larger brained species, it is found that, with larger brain-size, more neurones, more dendrification and connectivity of the nerve-cells, and a higher glia-neurone ratio occur – and, with the latter, a decreased packing density of the neurones. It is reasonable to infer that changes in these features must have occurred during hominid encephalisation. In addition, direct observations on fossil endocasts tell us what reorganisation of the surface of the brain, mainly of the cerebrum, has occurred during encephalisation.

The endocasts of H. *habilis* show morphological features that point to major restructuring of the brain in a modern human direction:-

r. The increase in the *H. babilis* brain involves a definite broadening (mainly of the frontal and parietal lobes of the cerebrum), and a moderate heightening, but scarcely any lengthening of the cerebral hemispheres.

2. The sulcal pattern of the frontal lobes is similar to that of modern H. sapiens and quite different from that of extant apes.

3. The gyral impressions on the frontal lobe include a wellmarked prominence in the posterior part of the inferior frontal convolution, in the position of Broca's area.

4. There is a right fronto-petalia in the few *H. habilis* endocasts in which left and right frontal poles are preserved. The posterior or caudal projection of the occipital pole is more variable: in a presumptive male of *H. habilis*, left occipito-petalia is present and, in two putative females, we find right occipito-petalia. In a modern human series reversal of the modal pattern of right fronto- and left occipito-petalia occurs more commonly in women, while the blend of right fronto-petalia with right occipito-petalia (as in one female *H. babilis* specimen) occurs in association with non-right-handedness (Bear et al. 1986).

5. The superior parietal lobule is well developed and, in several endocasts of *H. habilis*, is asymmetrical with left predominance (Figure 7). The anterior part of the superior parietal lobule corresponds to Brodmann field 7 (Mountcastle et al., 1975, 1984; Roland, 1985; Eccles 1989). In Roland's PET-scanning studies, he finds slight asymmetry of reaction in the posterior parts of the lobule. It would be useful to pursue the observation of a new structural asymmetry, that of the superior parietal lobule in *H. habilis*, to see whether it is present in larger series of early hominids and in modern humans. If the anatomical asymmetry is confirmed, it may provide a structural basis for functional asymmetry in visuospatial discrimination and judgment.

6. The parietal lobe in *H. habilis* is well expanded transversely and the inferior parietal lobule is strongly developed – in contrast with the arrangement in australopithecines and apes. The impressions of the supramarginal (area 40) and angular (area 39) gyri, comprising the inferior parietal lobule, are present for the first time in the hominid lineages. This area forms part of the larger Wernicke's area or posterior speech cortex.

7. One *H. habilis* endocast (Olduvai hominid 7) shows evidence of asymmetry of the lateral sulcus (Sylvian fissure) (Figure 8). The left-right difference tallies with that in modern humans (Cunningham, 1892; LeMay and Culebras, 1972; LeMay, 1976, 1977).

8. The anterosuperior part of the occipital lobe is expanded, as is the adjacent posterosuperior part of the parietal lobe. This parieto-occipital transverse expansion is more marked than the frontal transverse expansion and gives the endocast an ovoid contour when viewed from above.

9. The pattern of the middle meningeal blood vessels is more beset with branches and anastomoses than are the patterns in the

australopithecines (Saban 1983; Tobias 1967, 1987).

10. Unlike the Hadar hominids and the "robust" and "hyperrobust" australopithecines, *H. habilis* endocasts show the transverse-sigmoid pattern of venous sinus drainage as in *A. africanus* and *H. sapiens*. In two out of three specimens in which the area is preserved, the superior sagittal sinus groove drains to the right, whereas in one it drains to the left.

The most important morphological traits of the *H. habilis* brain are the presence of the two main cerebral areas that in modern humans are the seat of spoken language, Broca's and Wernicke's areas. *H. habilis* was the earliest hominid to show both of these well developed.

We have therefore the revealing and provocative concurrence of several phenomena: the parts of the brain that govern spoken language and a human sulcal pattern became manifest at that stage when appreciable brain enlargement and marked encephalisation first obtruded. These major alterations in the structure of the brain became apparent at approximately the same time as deliberately fashioned stone tools first appeared in the fossil record.

THE DAWNING OF SPOKEN LANGUAGE

The human language capacity is an evolutionary achievement of "extreme perfection and complication", to borrow Charles Darwin's phrase. What evidence do we have for the appearance, on brains and endocasts of living and fossil higher primates, of Broca's area and of the parieto-occipito-temporal complex (POT), including Wernicke's area?

First, in non-hominid primates, Geschwind, following the earlier work of Elliot Smith (1907) and of Critchley (1953), states, "The situation in man is not simply a slightly more complex version of the situation present in the higher primates but depends on the introduction of a new anatomical structure, the human inferior parietal lobule, which includes the angular and supramarginal gyri..."

(Geschwind, 1965, p. 73)

No trace of this inferior lobule is detectable in the macaque. However, it is present, though only in rudimentary form, in apes (Critchley, 1953; Geschwind, 1965; Bailey, von Bonin and McCulloch, 1950; c.f. Connolly, 1950). Hence Geschwind (1965, p. 276) acknowledges that "the exact degree of the uniqueness of the inferior parietal region in man remains to be determined".

Eccles (1989, p. 89) points out that "No area corresponding to the anterior speech area of Broca has been recognised in apes...Even more remarkable are the larger inferior parietal area, the angular [Brodmann's area 39] and supramarginal gyri [area 40], which, at most, are just detectable in the orang brain and the gibbon brain and doubtfully present as a small area of the chimpanzee brain." This means that there would have been scarcely any trace of impressions over the language-relevant cyto-architectonic areas in archaic apes before the appearance of the earliest hominids. Hence, it is not in the ancestral apes but in the earliest hominids that we might expect Broca's area and POT, or their immediate forerunners, to have emerged.

When we seek more direct evidence, we are faced with the imperfection of the geological record. We have no good endocranial casts older than about 3 mya: in other words, the hominid brain is (thus far) mute for the first half of the time of humans on earth! *Australopithecus africanus* endocasts of the 3-2.5 mya period are small (scarcely larger, absolutely or relatively, than those of extant apes), have an essentially ape-like sulcal pattern (and the author agrees in this regard with Falk, 1983, 1989) and show slight development of a Broca's cap (Schepers, 1946) but no trace of inferior parietal lobe development.

Wilkins and Wakefield (1995) postulate that these areas were initially evolved to fulfil a function other than linguistic and they suggest that skilled manipulative activities constituted these non-linguistic functions. They suggest that these areas were subsequently redeployed – by what they call *evolutionary reappropriation* – for linguistic purposes (see below).

From their analytical standpoint, they have arrived at the same conclusion reached 21 years ago, namely that *Homo habilis* (and not modern *Homo sapiens!*) was the first hominid to possess the neural basis for language (Tobias, 1975, 1980, 1981a,b, 1983a,b).

THE DISCOVERY OF THE SPEECH AREAS IN HOMO HABILIS

I have been steeped in the study of *H. habilis* since the first Olduvai specimen of this species was found in 1959 (L.S.B. Leakey, 1960, 1961). In 1964, Louis Leakey, John Napier and I launched the new species (Leakey et al., 1964). In 1973, at the IXth International Congress of Anthropological and Ethnological Sciences held in Chicago, U.S.A., I first reported that, on the endocranial cast of Olduvai hominid 24, identified as a female *H. babilis*, I had recognised certain impressions underlying the parietal bone, namely three parts of the parietal lobe of the cerebrum.

These were the superior and inferior parietal lobules, and the arcus parieto-occipitalis, as well as possibly the parieto-occipital sulcus and the intraparietal sulcus. I drew attention also to the greatly expanded breadth of the endocast, which is most strikingly apparent in the posterior two-thirds of the endocast over the parietal and occipital lobes, but it was also impressive in the region of the frontal lobes.

In the discussion that followed my paper and others on the evolution of the brain in that Chicago symposium, nobody raised the implications of the appearance of a clearly-defined inferior parietal lobule in the *H. habilis* brain. This area is virtually featureless in the endocasts of *Australopithecus*; yet it was there, well developed, in an endocast of *H. habilis*. That area of the parietal lobe forms a part of the posterior speech cortex known, after Karl Wernicke's work in 1874, as Wernicke's area.⁶

The inferior parietal lobule is a most distinctive region of the human brain. It comprises in the main the supramarginal gyrus about the upturned end of the lateral or Sylvian fissure, and the angular gyrus about the upturned posterior end of the superior temporal sulcus.

The arrangement of the gyri is highly variable. The area is late to myelinate (it is one of Flechsig's 'terminal zones'). Its dendrites appear very late and the cellular maturation of the lobule is delayed and may occur only in late childhood. It receives few afferent fibres from the thalamus. Phylogenetically it is a new region of the cortex. It is not concentric about one of the primary projection areas for vision, hearing or tactual sensibility. Instead it lies at the point of junction of the primary projection areas for these three modalities. Above and below it is flanked by attenuated or squeezed-out areas of cortex that Elliot Smith (1907) called the visuo-sensory band and the visuo-auditory band respectively. It appears to function as an *association area of association areas*, or a *secondary association area* in more classical parlance (Geschwind, 1965, pp. 273-275).

Sited between the areas of three great sensory modes - seeing, hearing and feeling - the inferior parietal lobule is probably

involved in cross-modal associations. For this and further reasons, Geschwind and others believe that the region is involved in the development of speech, since cross-modal associations are a prerequisite to the ability to acquire speech. Indeed the second major 'speech centre' of the human brain, Wernicke's area, includes the inferior parietal lobule, as well as the superior temporal gyrus and the planum temporale on the upper surface of the temporal lobe.

This region in the fossil endocasts is not well-preserved, for the Sylvian fissure is notoriously 'silent' in declaring its presence by markings on the endocranial surface. Hence it is usually not possible to detect whether asymmetry of the length and of the posterior termination of the Sylvian fissure was present in an endocast. What can be detected, however, is the rounded fullness of the region in the endocasts of later hominids including modern man. When we explore this region on the ancient hominid endocasts, however, we find that in the australopithcines the area which one would expect to be occupied by the inferior parietal lobule is not well-rounded, indeed it is commonly flattened or even depressed, in comparison with the well-rounded contour of the superior parietal lobule above. On the other hand, the endocast of *Homo habilis* shows a full elevation in this region of the inferior parietal lobule.

The evidence suggests that only part of the cerebral basis for speech was present in *Australopithecus* (Broca's area), whereas in the larger endocasts of *H. babilis* there is evidence of both Broca's and Wernicke's areas.⁷

The endocasts thus provide evidence that the neurological basis of speech, as far as it can be detected on an endocast, was present in part only in *Australopithecus*, whereas both Broca's and Wernicke's areas seem to have been well developed in the brain of *H. habilis*.

Complex as are the functions ascribed today to Wernicke's area, it was astonishing to realise that there was a well-developed part of the Wernicke field in the brain-cast of a hominid that had lived some 1.8 million years ago. Probably it was the very unlikelihood of the discovery that led those present at the Chicago Symposium to overlook its implications. With hindsight, I too, was rather shocked and did not at first make the outright claim that *Homo habilis* used the identified speech areas – to speak! Indeed, although the impressions of Broca's and Wernicke's areas in *H. habilis* were thus known from 1973, for the next five years no claim was made that *H. habilis* could speak. In other words, I initially distinguished between the presence of the neurological basis for language and its use for linguistic purposes, an aspect to which I shall return later.

As late as February 1979, in an opening address to an L.S.B. Leakey Memorial Symposium in San Francisco, I attributed the earliest spoken language, not to H. habilis, but to H. erectus (Tobias, 1979). In the ensuing six months, there was a change of mind and I came to realise that H. habilis was a speaking hominid. With the judgment of hindsight, it seems to me that two key factors triggered this change of mind. One was the evidence and inferences from the archaeological record (especially by Isaac, 1978, and Parker and Gibson, 1979). This was a cardinal factor in tipping the scales and leading me to claim, in the latter part of 1979, that H. habilis did in fact utilise its capability for spoken language – to speak. The second factor was the contemporaneity between the first known appearance of the modern human sulcal pattern, the parts of the brain that govern spoken language, and the first appreciable relative enlargement of the hominid brain and marked encephalisation. As if that remarkable synchronism were not enough, these major alterations in the structure of the brain became apparent at approximately the same time as deliberately fashioned stone tools first appeared in the archaeological record. The earliest fossil bones and teeth

which have been attributed to *H. habilis* are dated to about 2.2-2.3 mya, whilst the earliest stone tools are dated to some 2.5 mya. If we bear in mind the imperfections of the geological and archaeological records, these dates lie within a narrow range of time (Figure 9).

In September 1979, I posted to La Recherche in Paris the manuscript of my Broca centenary paper, "L'evolution du cerveau humain". A month later, in October 1979, I flew to Adelaide, South Australia, to deliver the First Andrew Abbie Memorial Lecture: it was devoted to 'The evolution of the human brain. intellect and spirit' (Tobias, 1981a) and I restated the case that H. habilis had been the first speaking hominid. When the French paper appeared in March 1980, it was the first published version of my claim that H. habilis had a mastery of spoken language (Tobias, 1980). In the same month, March 1980, at a symposium on 'The Emergence of Man' organised jointly by the Royal Society and the British Academy in London, I reiterated the claim (Tobias, 1981b) and I developed it further in my contribution to the Eleventh International Congress of Anatomy at Mexico City in August 1980 (Tobias, 1981c). Additional reiterations were offered at Jerusalem in 1981 (Tobias, 1982), the Pontifical Academy of Sciences, Vatican City in May 1982 (Tobias, 1983a), and Edmonton, Alberta, Canada in October, 1982 (Tobias, 1983b). Thus, by 1983, the claim had appeared in print seven times, but it was not until that year that any support for my claim was forthcoming. Before we consider the reception that the claim has received in the 15 years that have elapsed, let us examine the reasoning on which the claim was based.

EVIDENCE OF THE ENDOCASTS

The presence of well-developed areas of Broca and Wernicke on the endocasts of Olduvai *H. habilis* has been mentioned. Up to date accounts are given by Tobias (1987, 1991a). It is especially OH 24 that reveals these markings, though signs of asymmetry of the lateral or Sylvian fissure are present in OH 7 (Figure 8). In Dean Falk's study of the endocast of KNM-ER 1470, which is considered to be a Kenyan representative of *H. habilis* from Koobi Fora, she refers to "the human condition" of the sulcal pattern of the frontal lobe of this specimen. Moreover, she states, "If Fig. I {of the left frontal lobe of KNM-ER 1470] illustrated an endocast of an extant human skull rather than that from KNM-ER 1470, one would conclude that the external gross morphology near and partially in Broca's area appeared normal and that the human in question had probably been capable of speech, as suggested by Tobias..." (Falk, 1983. p. 1073).

Thus, on both the sulcal pattern and the Broca and Wernicke protrusions, the brain represented by the endocasts of H. *habilis* closely resembles that of modern humans.

EVIDENCE OF THE CULTURAL RECORD

The American anatomist, George Washington Corner, jocularly expressed a profound truth on the relationship between speech, brain and culture, when he declared that the only reason an ape does not speak is that it has nothing to speak about! The point of this *bon mot* is that emphasis is thrown on the mind of the ape, not on its vocal organs. For it is surely true that we speak with our brains, rather than with our tongues. To turn the epigram about, what did *H. habilis* have to speak about?

There is now little doubt that *H. habilis* possessed a stone toolmaking ability and was responsible for the Oldowan cultural assemblages (M.D. Leakey, 1971). This lithic cultural phase was characterised by a predominance of tools known as choppers, while other forms recognised are proto-bifaces, polyhedrons, discoids, spheroids and sub-spheroids, heavy-duty and light-duty scrapers, burins and sundry other tools. Of the choppers, five

types have been described: side, end, two-edged, pointed and chisel-edged (op. cit., p. 264). To this variegated suite of tooltypes must be added the evidence that H. habilis was capable of constructing some form of shelter in the form at least of stone walling. The implemental and constructional activities bespeak a complex culture. Inferences from the fossil and archaeological record have led to the claim that the culture of H. habilis included the aimed throwing of missiles, the butchery of large animal carcasses with stone tools, the transport of meat and other foods to a home base, delayed consumption, the sharing of food, and the distribution of the meat to adult and juvenile members of the group (M.D. Leakey, 1971; Isaac, 1978). Glyn Isaac's claims, published in 1978, about home-bases, food-sharing, division of labour, pair-bonding etc., played a major role in convincing me that the cultural and cognitive life of H. habilis was probably more complex than any of us had dared conceive previously. These inferred activities imply that H. habilis possessed various human-like propensities and abilities. The cultural achievements, both those observed and those inferred, imply a high degree of intelligent activity and I believe it is unlikely that such a culture could have been transmitted down the generations without some form of speech (Figure 10).

As a theoretical proposition, it may reasonably be supposed that there is a limit or threshold to the degree of complexity of behaviour and of the cognitive components of cultural life which may be transmitted without speech. Those behavioural traits and propensities of which apes are capable – especially tool using by chimpanzees (Goodall, 1963) – are transmitted to the young by observational learning, imitation and gestural activities. In these respects the apes, and especially the chimpanzee, have carried the mammalian potential for learned behaviour to a high degree of development. Indeed, it would seem that among the mammals, the living great apes – and perhaps, by inference, *Australopithecus* – have carried non-verbalised, learned behaviour to its highest pinnacle (unless the giant marine mammals have gone as far or further). More complex procedures, which necessarily invoke a greater cognitive element, abstract notions, a sense of the past and of futurity, require more than grunts, nudges, observation and imitation to transmit them to the next generation. When evidence of such complicated cultural and cognitive mechanisms appears in, or may be inferred from, the palaeontological and archaeological record, it becomes necessary to postulate the presence of a more efficient mechanism than example and imitation: one form of such a more efficient teaching mechanism is speech.

The complexity which archaeologists have shown in, or inferred from, the life-style of *H. habilis* seems to me to mark the point at which adequate and efficient transmission of cultural practices and innovations to the offspring required at least rudimentary speech.

Several attemps have been made to evaluate the intelligence of H. habilis in terms of a Piagetian genetic epistemology. Piaget, it will be recalled, recognised major stages in the ontogeny of intelligence: the first was that of sensorimotor intelligence, the second that of pre-operational intelligence, and the third that of operational intelligence. The third stage in Piaget's sequence marked the adult stage in modern human development. Parker and Gibson (1979) have been responsible for a rather daring breakthrough in the analysis of the level of intelligence of early hominids. They attempt to apply Piaget's ontogenetic sequence to the hominid phylogenetic stages, in a recapitulative manner. In effect, they reason that if ontogeny recapitulates phylogeny in structural and functional complexes, might it not do so also in respect of behavioural attributes? If so, might one not use such an approach as a basis for the inference of habiline intelligence? They use as holistic a picture of the life-style of H. habilis as archaeological evidence and inferences (including those of Isaac,

1978) would permit. They infer that *H. habilis* has surpassed the first Piagetian stage (of sensorimotor intelligence) and exploited the full gamut of pre-operational intelligence, right up to the threshold of the third phase, that of operational intelligence. This appraisal of the intelligence of *H. habilis* sets the habiline people clearly ahead of the apes, whose range of activities spans all the stages of sensorimotor intelligence. This analysis by Parker and Gibson, coming hard on the heels of that by Isaac, was another factor that led to my change of mind about the speech proclivities of *H. habilis* during the course of 1979.

Wynn (1981) has made a more limited study of the Piagetian stage attained by *H. habilis*. Using a narrow range of attributes, namely the geometrical features of the choppers, polyhedrons and scrapers from Olduvai, and the minimum necessary spatial concepts underlying them, he infers that the manufacture of these Oldowan artefacts requires only pre-operational intelligence (the second Piagetian stage), that is, his conclusions about the intelligence of *H. habilis* stop short of the stage inferred by Parker and Gibson. It should be stressed that Wynn's analysis does not embrace the full range of cultural operations, tool types and technologies in the Oldowan; nor does it take within its purview the evidence of constructional activity, nor the patterns of behaviour that may be inferred from the living floors excavated by Mary Leakey and other archaeological records.

It could well be questioned whether Haeckelian recapitulation may validly be applied to the behavioural analysis of ancient hominids in the way attempted by both Parker and Gibson (1979) and Wynn (1981). The work of the former investigators has been criticized on this basis by Brainerd (1979), Dingwall (1979), Snowdon and French (1979), though supported by Gould (1979). However, at least we have here some systematic attempts to analyse the evolution of human cognitive attainment. Later, Wynn takes his analysis of H. habilis artefacts further and argues that its culture was very apelike, much more so than that of H. erectus (Wynn and McGrew, 1989; Wynn, 1993a). "Although the Oldowan lithic culture differs from anything known for free-ranging apes...all of the capacities needed to make it are manifested in the non-lithic tools of chimpanzees... The challenge is to find anything uniquely hominid in the capacities needed to make these artefacts." (McGrew, 1993, p. 165). If this is true, Wynn adds, "... then Homo erectus represented the first truly 'non-ape' hominid" (Wynn, 1993a). Yet even H. erectus, according to Wynn (1993b), did not possess the reflective abilities of H. sapiens, so that the culture of H. erectus was based on "non-reflective cognition". Moreover, whilst acknowledging that "Palaeo-anthropologists are entitled to feel frustrated by the data still missing from primatologists" (McGrew, 1993, p. 164), McGrew berates palaeo-anthropologists who seek to make inferences about human evolution for "inexplicably ignoring other primates" (op. cit., p. 165). He points out that "Wild chimpanzees live in environments virtually indistinguishable from what Olduvai was like in Plio-Pleistocene times ...; they prey regularly on mammals...; they scavenge carcasses from other predators...; they use tools to process bones ...; they leave lithic work-sites with characteristically altered tools. Everything attributed to hominids at the level of Oldowan culture at Olduvai or Koobi Fora could have been made by pongids." (op. cit., p. 166). Turning to language, McGrew claims that 'Vocal communication shows no necessary adaptive connection to tool-use ... In reconstructing the phylogeny of spoken language during hominisation, there is no reason to link it with tool-use" (op. cit. pp. 166-167).

Several investigators stress the relationship between tool-using activities and imitational skills. As one passes from monkeys to apes and, especially, from apes to humans, there are great increases in tool-using activities and in imitational skills (Meltzoff and Moore, 1983; Meltzoff, 1988). Innovative behaviours, it is suggested, could have been disseminated by imitation in ancestral hominids, whereas in apes, this would have been true only in circumscribed situations (Visalberghi, 1993).

McGrew's, Wynn's and Visalberghi's views represent one pole in a spectrum of thoughts on these questions, at a time when this field of studies is progressing rapidly.

Other investigators have argued that language and tool-use *were* linked by common mental constructive capacities (e.g. Gibson, 1983, 1993, 1993, 1994; Reynolds, 1983: Lock, 1993; Kempler, 1993) and an historical review of the subject has been presented by Hewes (1993).

In contradistinction to Wynn and McGrew, Potts (1988) and Toth and Schick (1993) distinguish between chimpanzee implemental activities and those manifested by the Oldowan practitioners. Toth and Schick argue that "it may be beyond the cognitive capabilities of chimpanzees to modify stones in an Oldowan manner...the seeking out of acute angles or overhangs on cobbles and cores, as well as the judgment of the correct angle and force of impact required to effectively flake stone, may well be beyond the capabilities of chimpanzees even in the best cases of Pavlovian classical conditioning" (op. cit., p. 351). They give a number of other features of the Oldowan activities which differentiate their fabricators from chimpanzees. For example, the distances over which raw materials were transported; a major subsistence dependence on meat and marrow, involving the carrying of stone or even, as Potts (1984, 1988) has suggested, the caching or stockpiling of rock resources; and the heavy concentrations of tools and technological by-products at early hominid sites, more than in any chimpanzee tool-using localities reported thus far.

Clearly, there are wide and deep disparities between the views cited. We need more studies on higher primates and more archaeological analyses of the kinds that Isaac, Toth, Schick and Potts have been making – and more conversation between palaeo-anthropologists and primatologists – before a consensus arrives.

It has long been my view that the greater the cognitive component in cultural activities, the more likely it would have been that its successful transmission to younger generations would have required a more efficient mechanism than imitation. From the cultural and inferred social aspects of the lifeways of *H. habilis*, coupled with the testimony of the endocasts, spoken language would seem to have been a logical necessity in the members of that species.

EVIDENCE OF CONCOMITANCE OF BRAIN ENLARGEMENT AND SPEECH AREAS

The earliest endocasts attributable to H. habilis agree in showing striking differences from those of apes and of Australopithecus: they are larger in absolute and in relative size, they show the presence of protrusions in the Broca and Wernicke areas and they have a human sulcal pattern, especially in the frontal lobe. There has been much discussion on what the selective advantage of increasing brain size might have been and many selective pressures have been proposed (e.g. Gabow, 1977; Tobias, 1981a, 1994). In proposing a deviation-amplifying, auto-catalytic relationship to link brain size, spoken language and culture, as well as eyes and hands, I laid stress on the special development of certain areas of the cerebral cortex, rather than on a generalised enlargement of the brain as a whole. The evolutionary benefits of a larger brain, I proposed, lay in having very large parietal lobes (and especially the inferior parietal lobule on the left), inferior frontal and superior temporal convolutions. The ape's brain already has much localisation of functions; therefore, in the hominid lineage, the whole brain enlarged for the sake of the highly desirable increase of certain areas. The very areas that have shown the most striking enlargement are those that are related to spoken language.

In a word, enlargement of certain areas of the brain went handin-hand with the development of an increasingly complex culture, as a revolutionary new survival kit (Figures 9 & 10). 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. As Eccles (1990) put it, in defending my viewpoint (Tobias, 1990) at the Pontifical Academy of Sciences in 1988, "The important question is: how did the brain grow so rapidly in hominid evolution? It must have been because of the tremendous advantage of a developed language in natural selection. There is no other explanation." (Eccles, 1990, p. 18).

WHAT CAME BEFORE THE SPEECH AREAS?

We referred at the beginning to the extreme difficulty we encounter when we try to reduce the emergence and evolution of language to basic building stones. There is a dramatic suddenness in the appearance of the cortical speech areas in *H. habilis* or in the antecedent advanced *A. africanus*. As Eccles puts it, "We are presented with a most extraordinary evolutionary phenomenon. Evolutionary change normally occurs by development of structures already in existence, perhaps with a different, but related function. It appears to be otherwise with areas 39 and 40 [the angular and supramarginal gyri, respectively], which grew out of the superior bank of the superior temporal lobe in a kind of efflorescence that was incredibly fast in evolutionary time..." (Eccles, 1989. pp. 91-92).

There are at least three competing views about the emergence and evolution of language, one which relates it to a prior, nonlinguistic, motor function; one which connects it to a prior, non-communicative sensory function, the building of a world image; and one which sees language emerging as a vehicle of communication from the beginning.

Wilkins and Wakefield (1995) postulate that these areas were initially evolved to fulfil a function other than linguistic and they suggest that skilled manipulative activities constituted these nonlinguistic functions. They suggest that these areas were subsequently redeployed - by what they call evolutionary reappropriation - for linguistic purposes. If Wilkins and Wakefield (1995) are correct, the pre-linguistic development of Broca's area and Wernicke's area would have occurred in the australopithecines. We have no evidence of stone culture associated with A. africanus, so we are unable to confirm directly the manipulations to which they were applying their postulated, new-found, skilled, control mechanisms. Indirectly, A. africanus would have been capable of at least as many learned, manipulative activities as chimpanzees. Their cultural skills might have been plied in perishable media such as bark, twigs, leaves, which would normally not be preserved in the fossil record (Tobias, 1965, 1971).

Against this background, it is possible that Broca's area and Wernicke's parieto-occipitotemporal complex (POT) emerged at a pre-linguistic phase among some australopithecines, but without earlier (6.0-3.0 mya) endocasts and tools, it is impossible for us to confirm or refute the Wilkins-Wakefield hypothesis.

There is another difficulty about the reappropriation hypothesis. The essence of reappropriation is that the cells and their connections initially subserving one function were taken over for the novel linguistic function and ipso facto were no longer available to control the prior non-linguistic functions. If manipulative skills and feedback circuits governing eye-hand co-ordination were advantages in the pre-linguistic evolution of Broca's area and POT, and if these areas and their connections were subsequently reappropriated for linguistic purposes, what would have happened after that to the neural control of these manipulative and coordinative functions? Did some other neural complex take over control of later manipulative evolution? Or were the "language areas and connections" reappropriated for linguistic functions only in part? = so that the cognitive aspects of skilled manipulations and of spoken language remained under the control of the same architectonic areas?

While the Wilkins-Wakefield hypothesis endeavours to relate the evolution of the language centres to alternative, non-linguistic, *motor* activities, Jerison (1977, 1991) has offered an interesting speculative analysis which sees the initial evolution of language, not as a communication system, but as a *supersensory* system. "From an evolutionary point of view," says Jerison, "the initial evolution of language is more likely to have been as a supplement to other sensory systems for the construction of a real world. This would be consistent with the other evolutionary changes in mammalian neural adaptations and would not require the sudden appearance of an evolutionary novelty. The suggestion is that our ancestors evolved a more corticalized auditory sense that was coupled with the use of vocal capacities for which almost all living primates are notorious..." (1977, p. 55).

The third view about the development of spoken language is

that it emerged as a vehicle of communication from the beginning. Eccles (1989) illustrates this view when, speaking of the earliest hominids, the australopithecines, he states, "There would have been the challenge to develop a language of sounds for communication. Tobias (1983a, b, 1987) regards *Homo habilis* as the initiator of spoken language because of the evidence from endocasts for the existence of the anterior and posterior speech areas. Such a momentous development must have had some preliminary happening in the primitive sound signalling that resulted from a genetic coding building a brain giving increased survival. It could be classed as an example of evolutionary gradualism. ...I would suggest the beginning of a language [in the australopithecines] (Eccles, 1989, p. 95).

These three prevailing concepts – which may be summed up as motor re-deployment, sensory re-deployment and linguistic *ab initio* – address the question posed at the outset: on what substrate did natural selection go to work to produce the speech centres in the cerebral cortex? Testability is considered the hallmark of a good, rigorous hypothesis. It will test the ingenuity of palaeo-neurobiologists well into the 21st century to convert these three notions into testable hypotheses – and to test them!

THE ROLE OF THE PERIPHERAL INSTRUMENTALITIES OF SPEECH

Apart from the neuro-anatomical and -physiological cerebral mechanisms, the faculty of speech requires a suite of peripheral instrumentalities, which can fulfil a complex co-ordinated activity of the lips, palate, tongue, pharynx, larynx and respiratory apparatus. These parts are not preserved in the fossil record, but several investigators have drawn inferences from the degree of flexion of the basicranium about the degree of development of one part of this complex vocal tract, namely the nasopharynx. From this one part of the vocal tract, in turn, they have made deductions about the capacity for speech (Lieberman and Crelin, 1971; Lieberman, 1975; Laitman and Heimbuch, 1982; Laitman 1984, 1985). The main thrust of these investigations has been that a greatly expanded supralaryngeal portion of the pharynx enhances the ability of the pharynx to modify laryngeal sounds, over the capacity of non-human mammals or newborn human babies (Laitman and Heimbuch, 1982; Laitman, 1985). "In essence", states Laitman, "it is this expanded pharynx which gives us the unique ability to produce a full range of speech sounds" (1985).

Many criticisms of these morphological studies on the supralaryngeal vocal tract and speech capacities of fossil hominids have been published (e.g. Carlisle and Siegel, 1974: Falk, 1975; Le-May, 1975; Wind, 1978, Arensburg et al., 1990; Houghton, 1993, 1994). I too, have long expressed difficulty with the farranging inferences drawn from the basicranium about the capacity for speech (e.g. Tobias, 1991b). Even if there were a valid and consistent relationship between the basicranial flexion and the location and size of the vocal tract, as seems still to be asserted (e.g. Lieberman, 1994a, 1994b), a peripheral anatomical "limitation" on the range of speech sounds - in the presence of the language centres in the brain - would merely modify the kind of language, its phonetic range and versatility; it would surely not deny such populations the faculty of language. It is the author's contention that some form of speech is possible even with an incomplete range of speech sounds. From this shaky association, the proponents of this view went on to make an even more chancy inference, namely that the Neandertalers, who were the unfortunate objects of their scrutiny, had no capacity for spoken language! These investigators seemed to ignore, or to minimise, the role of the brain in speech and language. Moreover, they seemed to disregard the cognitive complexity of the concepts and culture Neandertalers transmitted to their children. In this respect, they must have drawn comfort from some archaeological studies which tended to minimise the cognitive and symbolic

competency of Middle Palaeolithic people (e.g. Chase and Dibble, 1987, 1992; Dibble, 1989).

I was among those who found it difficult to accept the idea that the concept of a language would stand or fall by the ability to pronounce the sounds 'i', 'a' and 'u'. The languages of modern mankind vary enormously in the range of sounds which they utilize. For instance, whereas biassed earlier observers likened the languages of the Kalahari San (or Bushmen) to the 'barks and grunts of baboons', Traill, an authority on San languages, has no hesitation in declaring that, "From the phonetic point of view, these are the world's most complex languages. To speak one of them fluently is to exploit human phonetic ability to the full." (Traill, 1978, p. 139). From this rich phonemic repertoire of the San languages, modern tongues range through the smaller set of sounds in the languages of Europe, to the impoverished languages of the Pacific. Goodenough (1992) points out that Hawaiian has only 11 phonemes and Gilbertese only 12, yet they qualify as fully functioning languages. Moreover, Goodenough reminds us that children can make vowel sounds before their larynges are mature or have descended.

Clearly, it makes no difference whether a modern human spoken language is phonemically rich or poor: it remains a functioning language.

In the face of such views, those who seem to be bent on robbing Neandertalers of speech have shifted their ground: instead of asserting that they could not speak (as originally claimed), they declare rather that the Neandertalers had poor or defective spoken language. Under pressure, they have progressively pushed back the frontier of language, even to *H. erectus* (Laitman, 1985). In my opinion, they have not gone far enough and should move the goalposts back further to *H. habilis*, whose endocasts tell us that they possessed the neurological basis of spoken language two million years ago. In sum, the peripheral instrumentalities are, of course, important. For instance, our phonation is greatly helped by our mobile tongues, in contrast with the constrained tongues of apes. But it is not the executive instrument that determines the essence of language: those determinants are the controlling centres in the brain. To repeat, it is the lesson of neurophysiology that we speak with our brains, not with our tongues.

THE RECEPTION OF THE CLAIM THAT H. HABILIS COULD SPEAK

At first, my view was unsupported by any of my colleagues. I began to wonder whether my claim was turning out to be an example of a *premature discovery*, in the sense of Stent (1972), just as the initial announcements of *A. africanus* by Dart (1925) and of *H. habilis* by Leakey et al. (1964) had been premature by 25 and 20 years respectively (Tobias, 1992b, 1995b).

The first person who supported my view in print was Falk (1983) when her own study of KNM-ER 1470 led her to the same conclusion as I had reached in 1979, namely that *H. habilis* probably had spoken language.⁷ I was grateful for her support and for nearly a decade it was the only backing that the concept received.

Next, the idea was adopted by Sir John Eccles and strongly supported at the Study Week on The Principles of Design and Operation of the Brain, held at the Pontifical Academy of Sciences in October 1988 (through illness, my paper was presented *in absentia*). In "Evolution of the Brain: Creation of the Self", Eccles (1989) accepts that *H. habilis* was capable of spoken language. He even suggests the possibility that the putative ancestor of *H. habilis, A. africanus,* with its cortical protrusion in the Broca area (Schepers, 1946), had the beginning of a language. Andrews and Stringer (1993), Deacon (1994) and Wilkins and Wakefield (1995) most recently accept the probability that *H. habilis* had spoken language of at least a rudimentary form. As Andrews and Stringer say, *"Homo habilis* cannot have developed the full range of sounds that a modern human brain and voice box can produce, but even a limited combination of vowels and consonants, reinforcing facial expressions and manual signals, must have offered practical advantages that paid off the higher running costs of a bigger brain with better food and improved survival chances." (op. cit., p. 241). Even one of the exponents of the basicranial flexion approach has come to accept that *H. habilis* had a voice box that was equal to the demands of spoken language (J. Laitman, personal communication, 17th November 1992).

It may fairly be claimed, just over 20 years after attention was first drawn to the speech areas on the endocasts of H. *habilis*, that the hypothesis that this ancient species of *Homo* used spoken language is gaining appreciable support.

THE MILIEU OF THE EARLIEST SPOKEN LANGUAGE

Spoken language must have developed in a social and cultural milieu, but these aspects are beyond the scope of this lecture. I should like to make brief mention of the physical environment within which this enormous leap was made.

The species *H. habilis* emerged at a time when survival in Africa was becoming more and more difficult. Conditions were cooler, drier and more exacting. The great wet forest of middle Africa was retreating and being replaced by woodland and, beyond that, by a spreading savanna.⁹ There was a vigorously changing biota among which *H. habilis* is numbered. Against this background, the emergence of spoken language, as a new kind of social cohesive, information transmitter and survival facilitater,

must have bestowed immense advantages on the newfound speakers.

LANGUAGE, CLADOGENESIS AND AUTAPOMORPHISM

Many scholars agree that about $2\frac{1}{2}$ mya, or a little earlier, there was a great cladogenetic split in hominid phylogeny. Hominids were faced by one of those evolutionary choices. The derivative lineages were one or more lines of robust australopithecines and the genus *Homo*. The question I should like to raise – as my final heresy – is this: Did brains capable of articulated language appear before or after the late Pliocene split?

If the faculty for spoken language arose only following the cladogenesis, then we should see this propensity as a special, uniquely derived trait, an autapomorphy, of the genus *Homo*.

We have however to countenance another possibility, that this faculty might have appeared before, rather than after, the bifurcation. If it arose in the last common ancestor of the derivative lineages, say in an advanced A. africanus in the sense of Skelton et al., (1986), then it is likely that the propensity to speak would have been handed on to both or all lineages derived from the split. On at least one line of evidence, it seems that the rudiments of a speech centre were present already before the great cladogenesis. We have seen that a Broca's cap was observed in A. africanus endocasts almost fifty years ago (Schepers, 1946) and this has been confirmed by later workers. As regards the inferior parietal lobule, Schepers (1946) reported that area 40 (supramarginal gyrus) was "large" in the A. africanus endocasts and area 39 (angular gyrus) "quite large" (op. cit., p. 253). But neither I nor, to the best of my knowledge, any other scholar has been able to confirm this. In a single A robustus endocast from Swartkrans, SK 1585, Holloway (1972) reported that the inferior frontal convolution "suggests an advanced disposition of the socalled Broca's region... this area appears larger and more rounded than in pongid brain endocasts" (p. 177). Similarly, he reported that the endocast gave the strong impression that the inferior parietal lobule "is certainly more expanded than in any pongid brain" (p. 177). Holloway added," ..it cannot be claimed that this hominid was capable or incapable of language. The minimal statement that can be made is that there is nothing in the cortical morphology of the endocast which necessarily precludes language ability, and much is in its favour." (op. cit., p. 182). If we assume that, of the two well known hominid species found in the Swartkrans formation, SK 1585 is indeed the endocast of a specimen of *A. robustus*, then this is an item of evidence supporting the hypothesis that speech areas were *banded on* from the common ancestor to the *A. robustus* descendant. We already have the signs of the speech cortical areas in early *Homo*.

In this case, both sets of offshoots would have inherited the capacity for spoken language. Already there is suggestive evidence from Swartkrans that, it has been claimed, associates *A. robustus* with fire-making and implemental activities, but as the genus *Homo* is there present, synchronically and sympatrically, along with the robust australopithecine, it is doubtful whether we can at this stage be certain about the fire- and tool-maker. It could be argued that the endocast SK 1585 might have belonged to either *A. robustus* or to the Swartkrans *Homo*. However, the fact that Holloway found considerable resemblance between this endocast and that of the Olduvai *A. boisei* type specimen (OH 5) – which some would unite in the same genus *Paranthropus* with *A. robustus* from Swartkrans and Kromdraai – argues in favour of SK 1585 having belonged to a robust australopithecine.

If indeed the second scenario turns out to be closer to the facts, that is, that advanced *A. africanus*, the presumptive common ancestor, already showed the propensity for spoken language, then it would very likely follow that this faculty was inherited

by both, or all, derivative lineages. We know that language became entrenched in the *Homo* lineage and persisted up to *H. sapiens*: we could infer that language became *obligate* (or habitual) in the *Homo* line, but probably it remained only *facultative* (or occasional) in the robust australopithecines.

While at present the emergence of spoken language before the cladogenesis seems to be supported by several pieces of evidence, we need endocasts (natural or artificial) of late *A. africanus* and more examples of *A. robustus* endocasts in order to refute or confirm this hypothesis.

A corollary of the problem we have posed is this: if language emerged before the cladogenesis, then it would have formed part of the milieu within which the splitting of the hominids occurred. In that event, its emergence might have been a part of the nexus of causal factors that generated or precipitated the cladogenesis. If, on the other hand, the rise of spoken language followed the split, it would have done so as an autapomorphy of *Homo* and as one of the outcomes of the split. Either way its inferred emergence close to the time of the cladogenesis is a provocative happening of the highest importance.

One is led to conclude that the species *H. habilis* was not only the earliest culture-bound primate, but on presently available evidence, the first language-bound hominid. So a new set of sounds, those of articulate speech, must have been heard in Africa from 2.5-2.0 mya – and a new level of organisation was attained in the evolution of life on earth.

NOTES

- I. I am honoured to have been invited by the Stichting Nederlands Museum voor Anthropologie en Praehistorie, Amsterdam, to deliver the seventeenth Kroon Lecture. I am especially grateful to Dr. W.H. De Vries-Metz for her kind help with the arrangements for my visit to The Netherlands. My gratitude is extended to the University of the Witwatersrand, Johannesburg, and especially the Department of Anatomy and Human Biology, the Palaeo-Anthropology Research Unit and the Palaeo-Anthropology Scientific Trust. My sincere thanks are extended to Mrs. Heather White, Mr. Peter Faugust, Dr. Ronald J. Clarke, and Mr. Terry Borain.
- 2. Throughout the Lecture, I have used the name Australopithecus robustus for the robust australopithecines from South Africa and Australopithecus boisei for the hyper-robust australopithecines from East Africa. Some investigators prefer to place both taxa in the genus Paranthropus, as P. robustus and P. boisei respectively. A compromise systematic dispensation is to regard Paranthropus as a sub-genus within the genus Australopithecus, as I formally proposed in 1967 and 1968. The South African form would then be designated Australopithecus (Paranthropus) robustus and the East African species, Australopithecus (Paranthropus) boisei. As originally proposed, the East African subgenus was (Zinjanthropus), the hyper-robust species then being dubbed Australopithecus (Zinjanthropus) boisei. No international accord or consensus has yet been reached on these nomenclatural differences. I find it convenient to group all of the small-brained hominids in the genus Australopithecus, but I occasionally use the subgeneric appellation. However, a number of workers in the field use the generic nomen Paranthropus, largely, it seems, on cladistic grounds.
- 3. Specimens of *A. africanus* stem from Sterkfontein Member 4, Makapansgat Members 3 and 4, and Taung, in South Africa. It is still a moot point whether this species is represented in any of the East African collections of fossil hominids.
- 4. To this generalisation, the oldest *A. boisei* endocast, that of KNM-WT 17000, and the second oldest, that of Omo L338y-6, may be exceptions see Holloway (1981a, 1988).
- As in modern humans, there are exceptions to this combination among the early hominids (LeMay 1976, 1984, Holloway and De LaCoste-Lareymondie 1982; LeMay et al. 1982; Tobias 1987; Holloway, 1988).

- 6. Wernicke's field includes a large region of the inferior parietal and the superior temporal lobes and it corresponds approximately to Brodmann's areas 40 (supramarginal gyrus), 39 (angular gyrus) and 22 (part of the superior temporal gyrus). It is sometimes known as the sensory speech cortex and it is believed to be a prerequisite for the understanding and the formulating of coherent, propositional speech. It was "Wernicke's aphasia" an impairment of communication that first drew Wernicke's attention to the importance of this region. He realised that there was a significant relationship between lesions in it and aspects of spoken communication, especially word deafness and anomia (an inability to name objects even though they are perceived).
- 7. A third speech centre, the supplementary motor area, Msll, lies on the medial surface of the frontal lobe of the cerebral hemisphere: since this surface does not impinge upon the endocranium, its presence cannot be detected on an endocast.
- 8. So enthusiastically has Falk adopted the concept that, in her new book, *Braindance*, she claims that "Phillip Tobias and I independently concluded that [*H. habilis*] may have been capable of some rudimentary form of language" (Falk, 1992, p. 145). While this would be a delightful example of synchronicity, it is slain by an ugly fact, namely that my claim had been published in seven articles and chapters by 1983 when Falk first published her interpretation of 1470 man!
- 9. Among the faunal changes that became evident in Africa from about 2.5 mya, the first baboons of the genus *Papio* made their appearance. Some elephantids, suids and archaic bovids disappeared, being replaced by later suids and many modern species of bovids. Hexaprotodont hippopotami gave way to tetraprotodont forms. Machairodonts (sabre-toothed cats) left the scene; some rodents vanished; some new ones made their debut. The genus *Homo* announced itself.

REFERENCES CITED

Andrews, P. & Stringer, C. (1993) The primates' progress. In: S. J. Gould, ed. *The Book of Life*. New York: Ebury Hutchinson, pp. 219-251

Arensburg, B., Schepartz, L. A., Tillier, A. M., Vandermeersch, B. and Rak, Y. (1990) A reappraisal of the anatomical basis for speech in middle palaeolithic hominids. *Am. J. Phys. Anthrop.* 83:137-146.

Armstrong, E. (1981) A look at relative brain size in mammals. Neurosc. Lett. 34:101-104.

Armstrong, E.(1983) Relative brain size and metabolism in mammals. *Science* 220:1302-1304.

Armstrong, E.(1984) Allometric considerations of the adult mammalian brain with special emphasis on primates. In: W. L. Jungers, ed. *Size and Scaling in Primate Biology*. New York: Plenum, pp. 115-147.

Bailey, P., von Bonin, G. & McCulloch, W.S. (1950) The Isocortex of the Chimpanzee. Urbana: University of Illinois Press.

Bear, D., Schiff, D., Saver, J., Greenberg, M. and Freeman, R. (1986) Quantitative analysis of cerebral asymmetries: frontooccipital correlation, sexual dimorphism and association with handedness. *Arch. Neurol.* 43:598-603.

Brainerd, C.J. (1979) Recapitulationsim, Piaget, and the evolution of intelligence: déjà vu. *The Behavioral and Brain Sciences* 2:381-382. Carlisle, R.C. & Siegel, M.I. (1974) Some problems in the interpretation of Neandertal speech capabilities: a reply to Lieberman. Am. Anthropol. 76:319-322.

Chase, P.G. & Dibble, H.L. (1987) Middle Paleolithic symbolism: a review of current evidence and interpretations. *J. Anthropol. Archaeol.* 6:263-296.

Chase, P.G. & Dibble, H.L. (1992) Scientific archaeology and the origins of symbolism: a reply to Bednarik. *Cambridge Archaeol. J.* 2(1):43-51.

Clark, W.E. Le Gros (1964) The Fossil Evidence for Human Evolution: an Introduction to the Study of Paleoanthropology. 2nd edit., Chicago: University of Chicago Press.

Connolly, C.J. (1950) External Morphology of the Primate Brain. Springfield: Charles C. Thomas.

Critchley, M. (1953) The Parietal Lobes. London: Edward Amold.

Cunningham, D.J. (1892) Contribution to the surface anatomy of the cerebral hemispheres. *Roy. Irish Acad. Sci. Cunningham Mem.* VII. Dublin.

Dart, R.A. (1925) Australopithecus africanus: the man-ape of South Africa. Nature 115:195-199.

Deacon, T. (1994) Interview cited in R. Caird, Ape Man: the Story of Human Evolution. London: Boxtree, pp. 99-101.

Dibble, H.L. (1989) The implications of stone tool types for the presence of language during the Lower and Middle Palaeolithic. In: P. Mellars and C. Stringer, eds. *The Human Revolution*. Edinburgh: Edinburgh University Press, pp. 415-432. Dingwall, W.O. (1979) Reconstruction of the Parker/Gibson 'model' for the evolution of intelligence. *The Behavioral and Brain Sciences* 2:383-384.

Eccles, J.C. (1989) Evolution of the Brain: Creation of the Self. London and New York: Routledge.

Eccles, J.C. (1990) Discussion following paper by P.V. Tobias (1990), *Pontificiae Academiae Scientiarum Scripta Varia* 78:17-23.

Falk, D. (1975) Comparative anatomy of the larynx in man and chimpanzee: implications for language in Neandertal. *Am. J. Phys. Anthropol.* 43:123-132.

Falk, D. (1983) Cerebral cortices of East African early hominids. *Science* 222:1072-1074.

Falk, D. (1989) Ape-like endocast of "ape-man" of Taung. Am. J. Phys. Anthropol. 80:335-339.

Falk, D. (1992) Braindance. New York: Henry Holt.

Falk, D., Hildebolt, C. and Vannier, M.W. (1989) Reassessment of the Taung early hominid from a neurological perspective. *J. Hum. Evol.* 18:485-492.

Gabow, S.L. (1977) Population structure and the rate of hominid brain evolution. *J. Hum. Evol.* 6:643-665.

Galaburda, A.M. (1984) Anatomical asymmetries. In: N. Geschwind and A.M. Galaburda, eds. *Cerebral Dominance: The Biological Foundations.* Cambridge, Mass.: Harvard University Press, pp. 11-25.

Geschwind, N. (1965) Disconnexion syndromes in animals and man. Brain 88:237-294, 585-644.

Gibson, K.R. (1983) Comparative neurobehavioral ontogeny: the constructionist perspective in the evolution of language, object manipulation and the brain. In: E. de Grolier, ed. *Glossogenetics: The Origin and Evolution of Language.* New York & Paris: Harwood Academic Publishers, pp. 52-82.

Gibson, K.R. (1993) Tool use, language and social behavior in relationship to information processing capacities. In: K.R. Gibson and T. Ingold, eds. *Tools, Language and Cognition in Human Evolution.* Cambridge: Cambridge University Press, pp. 251-278.

Gibson, K.R. (1994) Continuity theories of human language origins versus the Lieberman model. *Language and Communication* 14:97-114.

Goodall, J. (1963) Feeding behaviour of wild chimpanzees: a preliminary report. Symp. Zool. Soc. Lond. 10:39-48.

Goodenough, W.H. (1992) Language origin. Language and Society 21:145-147.

Gould, S. J. (1979) Panselectionist pitfalls in Parker and Gibson's model for the evolution of intelligence. *The Behavioral and Brain Sciences* 2:385-386.

Harvey, P.H. and Mace, G.M. (1982) Comparisons between taxa and adaptive trends: problems of methodology. In: King's College Research group (eds.) *Current Problems in Sociobiology*. Cambridge: Cambridge University Press, pp. 343-361. Hemmer, H. (1985) What the australopithecine brain tells about the australopithecine biology: state of decoding. Johannesburg: Taung Diamond Jubilee International Symposium: Book of Abstracts, p. 17.

Hewes, G.W. (1993) A history of speculation on the relation between tools and language. In: K.R. Gibson and T. Ingold, eds. *Tools, Language and Cognition in Human Evolution*. Cambridge: Cambridge University Press, pp. 20-31.

Hofman, M.A. (1982) Encephalization in mammals in relation to the size of the cerebral cortex. *Brain Behav. Evol.* 20:24-96.

Holloway, R.L. (1970) Neural parameters, hunting, and the evolution of the human brain. In: C.R. Noback and W. Montagna, eds. *Advances in Primatology* Vol. 1: *The Primate Brain.* New York: Appleton-Century-Crofts, pp. 299-310.

Holloway, R.L. (1972) New australopithecine endocast, SK 1585, from Swartkrans, South Africa. Am. J. Phys. Anthrop. 37:173-185.

Holloway, R.L. (1974) The casts of fossil hominid brains. *Scient. Am.* 231:106-115.

Holloway, R.L. (1975) Early hominid endocasts: volumes, morphology and significance for hominid evolution. In R.H. Tuttle, ed. *Primate Functional Morphology and Evolution*. The Hague: Mouton, pp. 393-413.

Holloway, R.L. (1983) Cerebral brain endocast pattern of *Australopithecus afarensis* hominid. *Nature* 303:420-422.

Holloway, R.L. (1985) The past, present and future significance of the lunate sulcus in early hominid evolution. In: P.V. Tobias, ed. *Hominid Evolution: Past, Present and Future.* New York: Alan R. Liss, Inc., pp. 47-62.

Holloway, R.L. (1988) "Robust" australopithecine brain endocasts: some preliminary observations. in: F.E. Grine ed. *Evolutionary History of the "Robust" Australopithecines.* New York: Aldine de Gruyter, pp. 95-105.

Holloway, R.L. and Post, D.G. (1982) The relativity of relative brain measures and hominid mosaic evolution. In: E. Armstrong and D. Falk, eds. *Primate Brain Evolution: Methods and Concepts.* New York, London: Plenum, pp. 57-76.

Houghton, P. (1993) Neandertal supralaryngeal vocal tract. Am. J. Phys. Anthrop. 90:139-146.

Houghton, P. (1994) Neandertal supralaryngeal vocal tract: a reply to Dr. Lieberman (1994). *Am. J. Phys. Anthrop.* 95:450-452.

Isaac, G.L. (1978) The archaeological evidence for the activities of Africa hominids. In: C.J. Jolly, ed. *Early Hominids of Africa*. London: Duckworth, pp. 219-254.

Jerison, H. (1977) Evolution of the brain. In: M.C. Wittrock et al. eds. *The Human Brain*. Englewood Cliffs, N.J.: Prentice Hall, pp. 39-62.

Jerison, H. (1991) Brain Size and the Evolution of Mind. New York: American Museum of Natural History.

Jungers, W.L. (1984) Aspects of size and scaling in primate biology with special reference to the locomotor skeleton. *Yrbk. Phys. Antbrop.* 27:73-97.

Jungers, W.L. (1985) Size and Scaling in Primate Biology. New York: Plenum.

Kempler, D. (1993) Disorders of language and tool use: neurological and cognitive links. In: K.R. Gibson and T. Ingold eds. *Tools, Language and Cognition in Human Evolution.* Cambridge: Cambridge University Press, pp. 193-215

Laitman, J.T. (1984) The anatomy of human speech. Nat. Hist. 93:20-27.

Laitman, J.T. (1985) Evolution of the hominid upper respiratory tract: the fossil evidence. In: P.V. Tobias, ed. *Hominid Evolution: Past, Present and Future.* New York: Alan R. Liss, Inc., pp. 281-286.

Laitman, J.T. and Crelin, E.S. (1980) Developmental change in the upper respiratory system of human infants. *Perinatol. Neona-tol.* 4:15-22.

Laitman, J.T. and Heimbuch, R.C. (1982) The basicranium of Plio-Pleistocene hominids as an indicator of their upper respiratory systems. *Am. J. Phys. Anthropol.* 59:323-343

Lande, R. (1985) Genetic and evolutionary aspects of allometry. In. W.L. Jungers, ed. *Size and Scaling in Primate Biology*. New York: Plenum Press, pp. 21-32.

Leakey, L.S.B. (1960) Recent discoveries at Olduvai Gorge. *Nature* 88:1050-1052.

Leakey, L.S.B. (1961) The juvenile mandible from Olduvai. *Nature* 191:417-418. Leakey, L.S.B., Tobias, P.V. and Napier, J.R. (1964) A new species of the genus *Homo* from Olduvai Gorge. Nature 202:7-9.

Leakey, M.D. (1971) Olduvai Gorge: Excavations in Beds I and II, 1960-1963. Vol. III. Cambridge: Cambridge University Press.

LeMay, M. (1975) The language capability of Neanderthal man. Am. J. Phys. Anthrop. 42:9-14.

LeMay, M. (1976) Morphological cerebral asymmetry of modern man, fossil man and nonhuman primates. *Ann. NY Acad. Sci.* 280:348-366.

LeMay, M. (1977) Asymmetries of the skull and handedness. J. Neurol. Sci. 32:243-253.

LeMay, M. and Culebras, A. (1972) Human brain: morphologic differences in the hemispheres demonstrable by carotid arteriography. New Eng. J. Med. 287:168-170.

Lieberman, P. (1975) On the evolution of language: a unified view. In: R.H. Tuttle, ed. *Primate Functional Morphology and Evolution.* The Hague: Mouton, pp. 501-540.

Lieberman, P. (1994a) Hyoid bone position and speech: reply to Arensburg et al., (1990). *Am. J. Phys. Anthrop.* 94:275-278.

Lieberman, P. (1994b) Functional tongues and Neanderthal vocal tract reconstruction: a reply to Dr. Houghton (1993). *Am. J. Phys. Anthrop.* 95:443-452.

Lieberman, P. and Crelin, E.S. (1971) On the speech of Neanderthal Man. *Linguistic Inquiry* 11:203-222. Lock, A. (1993) Human language development and object manipulation: their relation in ontogeny and its possible relevance for phylogenetic questions. In: K.R. Gibson and T. Ingold, eds. *Tools, Language and Cognition in Human Evolution.* Cambridge: Cambridge University Press, pp. 279-299.

Martin, R.D. (1980) Adaptation and body size in primates. Z. Morph. Anthrop. 71:115-124.

Martin, R.D. (1981) Relative brain size and basal metabolic rate in terrestrial vertebrates. *Nature* 293:57-60.

Martin, R.D. (1982) Allometric approaches to the evolution of the primate nervous system. In. E. Armstrong and D. Falk, eds. *Primate Brain Evolution: Methods and Concepts.* New York: Plenum, pp. 39-56.

McGrew, W.C. (1993) The intelligent use of tools: twenty propositions. In: K.R. Gibson and T. Ingold, eds. *Tools, Language and Cognition in Human Evolution*. Cambridge, Cambridge University Press, pp. 51-170

Meltzoff, A.N. (1988) *Homo imitans.* In: T.R. Zentall and B.G. Galef, eds. *Social Learning, Psychological and Biological Perspectives.* Hillsdale, N.J.: Lawrence Erlbaum, pp. 319-342.

Meltzoff, A.N. and Moore, K.M. (1983). The origins of imitation in infancy: paradigm, phenomena, and theories. In: L.P. Lipsett, ed. *Advances in Infancy Research*, Vol. 2. Norwood, N.J.: Ablex, pp. 265-301.

Miller, J.A. (1991) Does brain size variability provide evidence of multiple species in *Homo habilis? Am J. Phys. Anthrop.* 84:385-398

Mountcastle, V.B., Lynch, J.C., Georgopoulos, A., Sakata, H. and Acuna, A. (1975) Posterior parietal association cortex of the monkey. *J. Neurophysiol.* 38:871-908.

Mountcastle, V.B., Motter, B.C., Steinmetz, M.A. and Duffy, C.J. (1984) Looking and seeing: the visual functions of the parietal lobe. In: G.M. Edelman, W.E. Gall and W.M. Cowan, eds. *Dynamic Aspects of Neocortical Function*. New York: Wiley, pp. 159-193.

Parker, S.T. and Gibson, K.R. (1979) A developmental model for the evolution of language and intelligence in early hominids. *Behavioral and Brain Sciences* 2:367-381.

Potts, R. (1984) Home bases and early hominids. Am. Scient. 72:338-347.

Potts, R. (1988) *Early Hominid Activities at Olduvai*. New York: Aldine de Gruyter.

Reynolds, P.C. (1983) Ape constructional ability and the origin of linguistic structure. In: E. DeGrolier, ed. *Glossogenetics: The Origin and Evolution of Language.* New York and Paris: Harwood Academic Publishers, pp. 185-200.

Roland, P.E. (1985) Cortical activity in man during discrimination of extrinsic patterns and retrieval of intrinsic patterns. In C. Chagas, R. Gattass and C. Gross, eds. *Pattern Recognition Mechanism.* Vatican City: *Pontificiae Academiae Scientiarum Scripta Varia* 54:215-246.

Saban, R. (1983) Les veines meningées des australopithèques. Bull. Mem. Soc. Anthrop. Paris 10:313-324. Schepers, G.W.H. (1946) The endocranial casts of the South African ape-men. In: R. Broom and G.W.H. Schepers, *The South African Fossil Ape-man, the Australopithecinae.* Transv. Mus. Mem. 2:153-272.

Schepers, G.W.H. (1950) The brain casts of the recently discovered Plesianthropus skulls. In: R. Broom, J.T. Robinson and G.W.H. Schepers, *Sterkfontein Ape-man, Plesianthropus.* Transv. Mus. Mem. 4:85-117.

Skelton, R.R., McHenry, H.M. and Drawhorn, G.M. (1986) Phylogenetic analysis of early hominids. *Curr. Anthrop.* 27:21-43.

Smith, G.E. (1907) On the asymmetry of the caudal lobes of the cerebral hemispheres and its influence on the occipital bone. *Anat. Anz.* 30:574-578.

Snowdon, C.T. and French, J.A. (1979) Ontogeny does not always recapitulate phylogeny. *Behavioral and Brain Sciences* 2:397-398.

Stent, G.S. (1972) Prematurity and uniqueness in scientific discovery. *Sci. Amer.* 227:84-93.

Tobias, P.V. (1965) Australopithecus, Homo habilis, tool-using and tool-making. S. Afr. Archaeol. Bull. 20:167-192.

Tobias, P.V. (1967) Olduvai Gorge, Vol. 2: The Cranium and Maxillary Dentition of Australopithecus (Zinjanthropus) boisei. Cambridge: Cambridge University Press.

Tobias, P.V. (1968) The pattern of venous sinus grooves in the robust australopithecines and other fossil and modern hominids. In: K. Saller Festschrift Anthropologie und Humangenetik. Stuttgart: Gustav Fischer Verlag, pp. 1-10.

Tobias, P.V. (1971) *The Brain in Hominid Evolution*. New York, London: Columbia University Press.

Tobias, P.V. (1975) Brain evolution in the Hominoidea. In: R.H. Tuttle, ed. *Primate Functional Morphology and Evolution*. The Hague: Mouton Publishers, pp. 353-392.

Tobias, P.V. (1979) Men, minds and hands: cultural awakenings over two million years of humanity. *S. Afr. Archaeol. Bull.* 34:85-92.

Tobias, P.V. (1980) L'évolution du cerveau humain. *La Recherche* 11: 282-292.

Tobias, P.V. (1981a) Evolution of the Human Brain, Intellect and Spirit. Adelaide, Australia: University of Adelaide.

Tobias, P.V. (1981b) The emergence of man in Africa and beyond. *Phil. Trans. Roy. Soc.* 292:43-56.

Tobias, P.V. (1981c) From palaeo-anatomy to culture. The 10th International Congress of Prehistoric and Protohistoric Sciences, Mexico, 19th-24th October 1981. *Actas* 120-148.

Tobias, P.V. (1982) The antiquity of man: human evolution. In: B. Bonné-Tamir, ed. *Progress in Clinical and Biological Research.* Part A, *Human Genetics.* New York: Alan R. Liss, Inc., pp. 195-214. Tobias, P.V. (1983a) Recent advances in the evolution of the hominids with especial reference to brain and speech. *Pontifical Academy of Sciences Scripta Varia* 50:85-140.

Tobias, P.V. (1983b) Hominid evolution in Africa. Can. J. Anthrop. 3:163-190.

Tobias, P.V. (1987) The brain of *Homo habilis*: a new level of organization in cerebral evolution. J. Hum. Evol. 16:741-761.

Tobias, P.V. (1990) Some critical steps in the evolution of the hominid brain. *Pontifical Academy of Sciences Scripta Varia* 78:1-16

Tobias, P.V. (1991a) Olduvai Gorge, Vols. 4A and 4B. The Skulls, Endocasts and Teeth of Homo habilis. Cambridge: Cambridge University Press.

Tobias, P.V. (1991b) The emergence of spoken language in hominid evolution. In: J. Desmond Clark, ed. *Cultural Beginnings: Approaches to Understanding Early Hominid Life-Ways in the African Savanna.* Bonn: Dr. Rudolf Habelt GMBH, pp. 67-78.

Tobias, P.V. (1992a) Il Bipede Barcollante: Corpo, Cervello, Evoluzione Umana. Torino, Italy: Giulio Einaudi Editore s.p.a.

Tobias, P.V. (1992b) The species *Homo habilis*: example of a premature discovery. Ann. Zool. Fennici 28:371-380.

Tobias, P.V. (1994) The craniocerebral interface in early hominids. In: R.S. Corruccini and R.L. Ciochon, eds. *Integrative Paths to the Past.* Englewood Cliffs, N.J. Prentice Hall, pp. 185-203.

Tobias, P.V. (1995a) Thoughts on *Homo erectus* and its place in human evolution *Vertebrata PalAsiatica*/Acta Anthropologica Sinica (Accepted).

Tobias, P.V. (1995b) Premature discoveries in science with especial reference to Australopithecus and Homo habilis. Proc. Am. Philos. Soc. (submitted).

Tobias, P.V. and Symons, J. (1992) Functional, morphogenetic and phylogenetic significance of conjunction between cardioid foramen magnum and enlarged occipital and marginal venous sinuses. *Perspectives in Human Biology 2/Archaeology in Oeania* 27:120-127.

Toth, N. and Schick, K. (1993) Early stone industries and inferences regarding language and cognition. In: K.R. Gibson and T. Ingold, eds. *Tools, Language and Cognition in Human Evolution.* Cambridge: Cambridge University Press, pp. 346-362.

Traill, A. (1978) The languages of the Bushmen. In: P. V. Tobias, ed. *The Bushmen: San Hunters and Herders of Southern Africa*. Cape Town and Pretoria: Human & Rousseau, pp. 137-147.

Visalberghi, E. (1993) Capuchin monkeys: a window into tool use in apes and humans. In: K.R. Gibson and T. Ingold. eds. *Tools, Language and Cognition in Human Evolution.* Cambridge: Cambridge University Press, pp. 138-150.

Wilkins, W.K. and Wakefield, J. (1995) Brain evolution and neurolinguistic preconditions. *Behavioral and Brain Sciences* (in press).

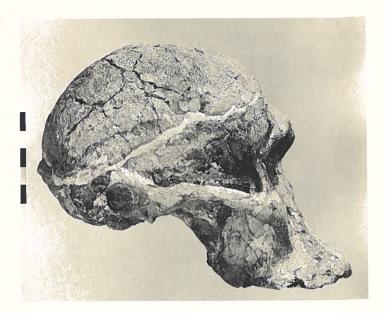
Wind, J. (1978) Fossil evidence for primate vocalizations? In: D.J. Chivers and K.A. Joysey, eds. *Recent Advances in Primatology*. New York: Academic Press, pp. 87-91.

Wood, B.A. (1991) Koobi Fora Research Project, Vol. 4: Hominid Cranial Remains. Oxford: Clarendon Press. Wynn, T. (1981) The intelligence of Oldowan hominids. J. Hum. Evol. 10:529-541.

Wynn, T. (1993a) Layers of thinking in tool behavior. In: K.R. Gibson and T. Ingold, eds. *Tools, Language and Cognition in Hu-man Evolution.* Cambridge: Cambridge University Press, pp. 389-406.

Wynn, T. (1993b) What artefacts reveal about the mind of *Homo* erectus. Pithecanthropus Centennial 1893-1993 International Scientific Congress, Leiden, The Netherlands.

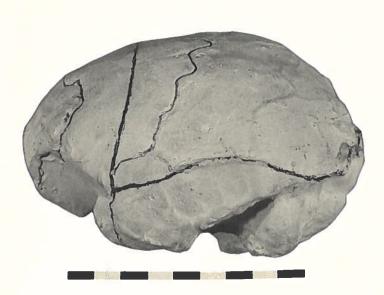
Wynn, T. and McGrew, W.C. (1989) An ape's view of the Oldowan. *Man* 24:383-398.



Right lateral view of the splendidly preserved cranium of Sts 5 ('Mrs Ples'): a specimen of *Australopithecus africanus* discovered by R. Broom and J.T. Robinson on 18th April 1947 in Member 4 of the Sterkfontein Formation. Like other australopithecines, this specimen was possessed of a small cranium with a capacity of 485cm¹. However, no natural endocast had formed, probably because the cranium landed in the deposit the right way up, so sandy matrix could not gain access to the inside of the calvaria through the foramen magnum (see Figure 2).



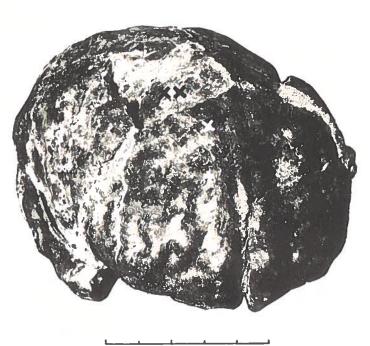
The well-preserved base of the interior of the brain-case of an *Australopithecus africanus* cranium (Sterkfontein Hominid 5). The calvaria was empty, no natural endocast having formed.



Artificial endocast of the type specimen of Australopithecus (Paranthropus) boisei: left lateral view.



The Taung skull, type specimen of *Australopithecus africanus*, with its natural endocast in position. Right lateral view.



CMS

Figure 5

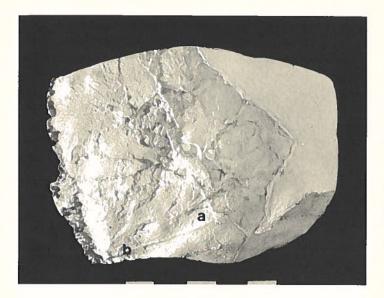
Natural endocast of a hominid from Member 4, Sterkfontein, almost certainly of Australopithecus africanus, seen from anterosuperior aspect. X is the *limen coronale*, the coronally orientated impression marking the junction between the lower part of the endocast where the gyral impressions are well marked, and the upper part where they are poorly imprinted. XX marks a depressed fracture of the calvaria inflicted before the endocast was formed.



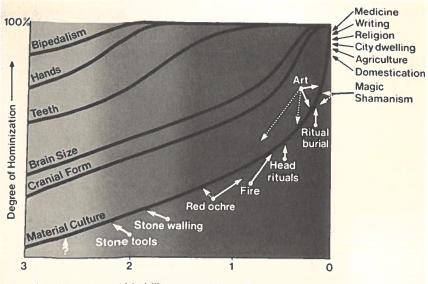
Partial natural endocast of *Australopithecus africanus* from Sterkfontein Member 4, seen from above and behind. A is the clear marking of the sagittal suture and B that of the lambdoid suture. Just below the lambdoid suture on each side is the impression of the lower part of the occipital pole of the cerebral hemisphere (traversed by the line leading from B to the rough linear marking of the lambdoid suture). Below that again, on each side, part of the impression of the cerebellar hemisphere is evident.



Partial artificial endocast of Olduvai hominid 13, a probable female specimen of *Homo habilis*. In the lower half of the endocast, running in the median plane (vertically downwards) is the impression of the groove for the superior sagittal venous sinus. Flanking it on either side is the impression of the superior parietal lobule.



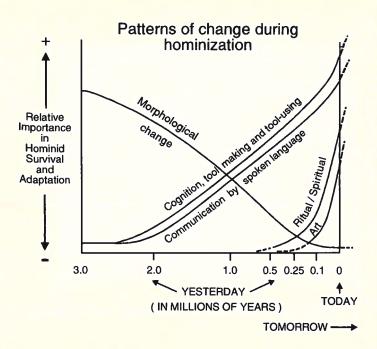
Partial artificial endocast of the left side of the calvaria of Olduvai hominid 7; part of the type specimen of *Homo habilis*. In the lower part of the endocast is the highlighted impression of the superior temporal gyrus (a). Above the gyrus is the impression of the lateral (Sylvian) fissure, running from below left, gently upwards and to the right, parallel to the superior temporal gyrus. Below the gyrus is part of the marking of the superior temporal sulcus. The lateral fissure and the gyrus are crossed almost transversely by the impression of the posterior branch of the middle meningeal artery (b).



A. africanus - H. habilis -- H. erectus -- + H. sapiens

Figure 9

Diagram of the degrees of hominisation shown by various parts of the evolving hominid bodily structure and by the phases of material cultural advancement.



The relative importance in hominid adaptation and evolution, of certain broad modalities of change, between 3 million years ago and the present. The diagram suggests that morphological changes, though still occurring, have played a decreasingly important role in hominid survival and adaptation during the last 3 million years, whereas functional, cognitive and linguistic behaviour has come to dominate hominid evolutionary adaptation in the last 2.5 million years. A close correlation in time is indicated between tool-using and linguistic communication. The possible nature of future hominid evolution is suggested by the extrapolation of the curves beyond the o point towards 'Tomorrow'.

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