

**“AUSTRALOPITHECUS AFARENSIS” AND A. AFRICANUS:  
CRITIQUE AND AN ALTERNATIVE HYPOTHESIS**

by

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**ABSTRACT**

During the seventies, a succession of East African discoveries has been claimed to represent the “true” ancestral line of modern man, thus relegating *A. africanus*, and especially its Transvaal subspecies, to a subordinate role in hominid phylogeny. The latest such attempt has been the claim of Johanson and his co-workers that the 3,7–2,6 My-old hominids of Laetoli in Tanzania and of Hadar in Ethiopia represent a new species, “*A. afarensis*”, which led to *H. habilis*, whilst *A. africanus* represents early stages in a specialized side-branch leading to *A. robustus* and *A. boisei*. A critique of the diagnostic criteria of “*A. afarensis*” reveals that on the available evidence, the Laetoli and Hadar fossils cannot be distinguished at specific level from *A. africanus transvaalensis*. Furthermore, it is by no means clear that the pooling for statistical and comparative purposes of the Hadar and Laetoli fossils is justified. Hominids from the two sites are separated by about 800 000 years and about 1 600 km as well as by morphometric differences. As an alternative hypothesis, it is proposed that the Laetoli and Hadar hominids belong to the same lineage as that represented by the hominids of Makapansgat Members 3 and 4 and of Sterkfontein Member 4. Moreover, it is hypothesized that the Laetoli and Hadar hominids cannot be separated morphologically from *A. africanus* and that they represent two new subspecies of that species. Since “*A. afarensis*” is tied to a Laetoli specimen as holotype, only the Laetoli specimens should be designated *A. africanus afarensis* (though *A. africanus tanzaniensis* suggested by the author in 1978 would have been a more appropriate nomen) and the Hadar fossils *A. africanus aethiopicus*. These newest East African discoveries afford strong confirmation of the hypothesis that *A. africanus* is the common ancestor of the two later hominid lineages, *A. robustus/boisei* and *Homo*, leading from *H. habilis* through *H. erectus* to *H. sapiens*.

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**INTRODUCTION**

In the first 25 years after R.A. Dart (1925) published an account of the Taung australopithecine skull, few scientists believed that this fossil, or those ancient hominoid specimens discovered shortly before and after World War II at Sterkfontein, Kromdraai, Makapansgat and Swartkrans,

represented species that should be classified in the Hominidae. Fewer still were those who accepted that these South African forms included any that were directly ancestral to later taxa of man, namely *Homo erectus* (known then as *Pithecanthropus erectus*) and *Homo sapiens*.



## THE EMERGING PARADIGM ON HOMINID PHYLOGENY

A change of attitude came gradually in the late forties and early fifties. The cardinal factors heralding the new consensus of the ensuing quarter of a century (1950–75) may be listed as follows:

- the accumulation of new australopithecine specimens from the four Transvaal caves and from a growing number of East African sites;
- the publication of the Transvaal Museum Memoirs in which R. Broom and his co-workers, J.T. Robinson and G.W.H. Schepers, presented for the first time detailed accounts of the fossils' structure;
- the studies of S. Zuckerman and his co-workers, especially E.H. Ashton, on the cranial and postcranial skeletal morphology of the great apes — and, though their aim seems to have been to show that the Transvaal australopithecines were no more than apes, in the event nothing proved more effectively than their data that the australopithecines fell outside the family Pongidae and within the Hominidae;
- J.T. Robinson's systematization of the gracile and robust australopithecines in respect of form, function, systematic and phyletic status and, especially, their dental morphology; and
- W.E. Le Gros Clark's meticulous appraisal of the cranial, dental and pelvic morphology of the australopithecines.

As a result, a substantial consensus was attained and has been sustained for several decades. On this paradigm all australopithecines are seen as hominids and, for a majority of palaeo-anthropologists, as belonging to a single genus of micrencephalic hominids called *Australopithecus*. To this genus are assigned those fossils that have previously been named *Australopithecus*, *Paranthropus*, *Paraustralopithecus*, *Plesianthropus*, *Praeanthropus* and *Zinjanthropus*. A second aspect of the paradigm is that some populations of *Australopithecus* are considered to have been ancestral to the genus *Homo*, particularly those of the less-specialised species, *A. africanus*.

Mayr (1970: 360) states the concept in broad terms: "... it is now quite evident that man's ancestors must have passed through an *Australopithecus*-like stage." More explicitly, Campbell (1974: 94–5) speaks of "... our ancestor, *Australopithecus*", and he adds, "The fossils that fall into this genus represent two species (*A. africanus* and *A. robustus*) ... One lineage, *Australopithecus africanus*, leads on toward man ...". The ultimate expression of the closeness of this relationship was the submission of Robinson (1966, 1972) that the fossils assigned to *A. africanus* should be taken out of the genus *Australopithecus* and reclassified in the genus *Homo* as *Homo africanus*.

Further elaboration of the pattern of hominid phylogeny has resulted from finds of fossil hominids at Olduvai, Peninj and other East African sites and of their placement in chronological sequence by the K-Ar and  $^{40}\text{Ar}/^{39}\text{Ar}$  dating tech-

niques, fission-tracking and palaeomagnetic determinations. It has been shown that the robust and hyper-robust australopithecines, as well as the earliest species of *Homo*, called by Leakey *et al.*, (1964) *H. habilis*, were later in time than *A. africanus* (fig. 1). Hence, there emerged a third aspect of the paradigm, namely that for considerable periods of time (from about 2.3 to about 1.0 My B.P.) at least two hominid lineages co-existed: indeed, they were not only synchronic but also sympatric in both South and East Africa.

As a corollary, a fourth feature of the paradigm was that an early and little-specialised species of *Australopithecus*, such as *A. africanus*, provides the likeliest claimant to have been the common ancestor to both the *Homo* lineage and the *A. robustus/A. boisei* lineage. In other words *Australopithecus africanus*, or a species close to it, was probably the common ancestral hominid (Tobias 1967, 1975, 1978a) (fig. 2).

DISTRIBUTION OF HOMINID TAXA IN TIME (1979)

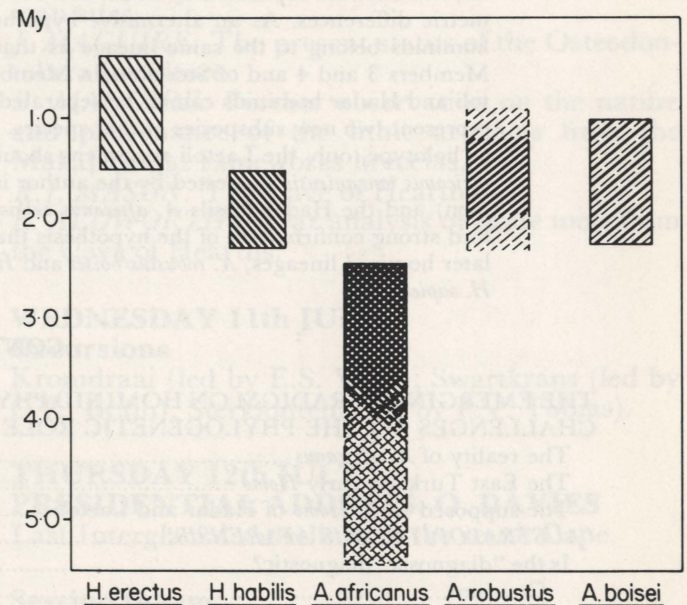


Figure 1. The approximate distribution in time of five major extinct taxa of the Hominidae. This chart shows the dating of three species belonging to the genus *Australopithecus* and two species of the genus *Homo*. The two species on the right — *A. robustus* in the Transvaal and *A. boisei* in East Africa — are considered to be on a lineage which became extinct about a million years ago. The species on the left — the earlier *Homo habilis* and the later *Homo erectus* — are believed to be chronospecies on the lineage leading to the third species of *Homo*, namely *H. sapiens*. *Homo sapiens* is not shown on this chart, but its beginnings are set by various workers at 500 000 to 250 000 years B.P. *Australopithecus africanus*, in which the author believes the fossils of Laetoli and Hadar should be included, is the oldest species of hominid widely recognised as such today. It is the probable common ancestor to the progressive lineage on the left leading to modern man, and to the conservative lineage on the right that led to an evolutionary cul-de-sac.



## PROVISIONAL SCHEMA OF HOMINID PHYLOGENY 1979

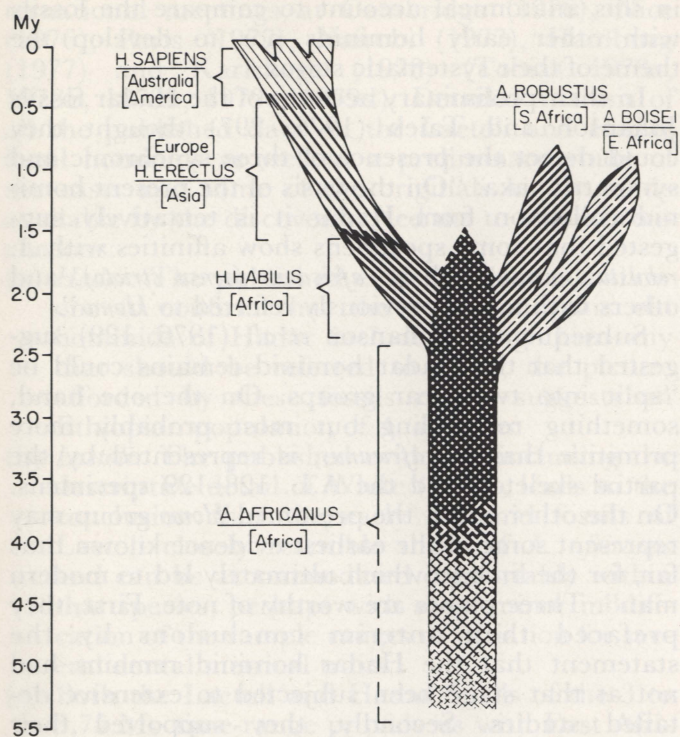


Figure 2. Provisional phylogenetic tree of the Hominidae according to the latest information available in mid-1979. The lightly shaded lower part of the common trunk represents a part of the fossil record where specimens are rare and not absolutely diagnostic, namely Kanapoi and Lothagam in northern Kenya. The geographical zones indicated on the *Homo* lineage are areas into which hominids moved from their presumed African source-area.

Until recently, it had seemed that the pattern of hominid evolution had been progressively revealed by the researches of the fifties and sixties. A major degree of consensus was evident at international gatherings, though there remained differences of opinion, mainly on nomenclature and systematics and on relative dating, especially of the South African sites. For little more than the last five years, however, new African finds and especially some of the interpretations offered have led several workers to cast serious doubts on what a few of them are already calling "the classical view" or "the conventional wisdom", that *Australopithecus* is man's ancestor. These alternative views have had the effect also of minimizing the role of the Transvaal australopithecines in hominid phylogeny. There follows an examination of this new development of the seventies, which we may jocularly dub "the assault on *Australopithecus africanus*".

### CHALLENGES TO THE PHYLOGENETIC ROLE OF AUSTRALOPITHECUS AFRICANUS

#### The reality of *A. africanus*

After the revelation of the existence of *Homo habilis* as a form intermediate in some key morphological characters between *A. africanus* and *H. erectus*, the reality and validity of *A. africanus transvaalensis* was on several occasions questioned

by one or two colleagues. They claimed that some of the Sterkfontein Member 4 specimens of *A. africanus* were, in fact, *H. habilis*; furthermore, the occurrence at Makapansgat of some robustly-built specimens of *A. africanus* was considered by them to connote the presence of *A. robustus* in Member 3 at that site. The argument then followed these lines: "Take away from the supposed hypodigm of *A. africanus* those elements that are really *H. habilis* and *A. robustus*, and what is left of *A. africanus*?" However, this line suggested a measure of unfamiliarity with the immense collection of fossils of *A. africanus transvaalensis*, and we have not heard it repeated in the last few years. It may be noted that, save for *A. robustus crassidens* of Swartkrans, *A. africanus transvaalensis* from Sterkfontein Member 4 and from Makapansgat Members 3 and 4 remains the largest, well-described taxon of very early fossil hominids, documented in great detail in numerous articles and monographs by Broom, Dart, Robinson, Schepers, Le Gros Clark, Sperber, Wallace, Clarke, Tobias and others. The abundance of the hypodigm of *A. africanus transvaalensis* has been made clear in the section on South African fossils (Tobias et al., 1977) in the second edition of the *Catalogue of Fossil Hominids, Part I: Africa* (Oakley et al., 1977).

#### The East Turkana early *Homo*

A more serious problem was posed by the dates originally assigned to the cranium KNM-ER 1470 found in the lower member of the Koobi Fora Formation in 1972 (Leakey et al., 1978). This cranium was assigned to *H. habilis* (Leakey 1973, 1976). The dates claimed initially were "pre-2,6 million years" and even 2,9 My.

Although Cooke (1970) had assigned a faunal date of 2,5–3,0 My to Sterkfontein and Makapansgat, being supported in this by Maglio (1973), it was not generally known for some time that so high an antiquity had been proposed for the Transvaal australopithecines. Hence, the supposedly 2,9 million-year-old *Homo* specimen from Koobi Fora was deemed by many workers to have antedated the Transvaal samples of *A. africanus*. If *Homo* was already in existence before *A. africanus transvaalensis*, the latter was unlikely to have been on the direct human line. This led an anonymous correspondent to claim in *Nature* (1975) that "all previous theories of the origin of the lineage which leads to modern man must now be totally revised", a claim which has recurred recently. Oxnard (1975) proposed specifically to deny to *Australopithecus* "a direct place in the human lineage".

The validity of this supposed refutation of current hypotheses on hominid evolution depended almost entirely on two premises, namely that ER-1470 was a member of *Homo* and that it was as old as had been claimed. On the first point there is much agreement that the calvario-facial morphology and the cranial capacity of 770–775 cc (Holloway, cited by Day et al., 1975) mark ER-



1470 as a member of *Homo habilis* (e.g. Walker and Leakey 1978, Tobias 1979a). However, some newer estimates of its age have claimed a dating of 2,4 My for the overlying KBS tuff (Hurford *et al.*, 1976, Fitch *et al.*, 1976), instead of the 2,6 My earlier proposed. Moreover, the work of Curtis *et al.* (1975) and the recent demonstration that more than one tuff has, apparently in error, been called the KBS tuff (Cerling *et al.*, 1979) have produced a date of 1,8 My for the tuff that overlies the discovery-site of ER-1470. On this basis early *Homo* at Koobi Fora is no older than *H. habilis* from Olduvai (Hay 1976), nor than that from the Shungura Formation at Omo (Boaz and Howell 1977). This is in keeping with the faunal evidence from Koobi Fora, notably that furnished by the suids (White and Harris 1977). Since 1470 man is not as old as the dates arrived at on faunal and palaeomagnetic grounds for Makapansgat and Sterkfontein, the claim that ER-1470 seriously challenges the place of *A. africanus* on the human lineage has fallen away. As Boaz and Howell (1977) put it, pre-*erectus* *Homo* appears in the fossil record no earlier than 2,3 My.

#### The supposed early *Homo* of Hadar and Laetolil

The next claims for the existence of much earlier *Homo* in East Africa were made in 1976. The fossils in question came from the Laetolil Beds at Laetoli in the southern Serengeti Plains of northern Tanzania and from the Hadar site in the Afar depression of north-eastern Ethiopia. The hominid-bearing Laetolil Beds have been provisionally placed stratigraphically between volcanic strata dated by the conventional K-Ar method and, in one instance, the  $^{40}\text{Ar}/^{39}\text{Ar}$  method, to average ages of 3,77 My and 3,59 My (Leakey *et al.*, 1976). The geochronology and palaeomagnetism suggest for the Hadar Formation and its fauna a Gauss Epoch age that spanned a period from somewhat more than 3,1 My ago (just older than the Mammoth Event) to somewhat less than 2,6 My ago (Aronson *et al.*, 1977). This palaeomagnetic sequence coincides with that for upper Member 2 to Member 4 at Makapansgat (Brook 1977, Partridge 1979, McFadden *et al.*, 1979).

From both Laetoli and Hadar fossils have emerged that were initially claimed to show affinities with *Homo*. The first publication on the Laetoli fossils claimed, "Preliminary assessment indicates strong resemblance between the Laetolil hominids and later radiometrically-dated specimens assigned to the genus *Homo* in East Africa. Such assessment suggests placement of the Laetolil specimens among the earliest firmly dated members of this genus" (Leakey *et al.*, 1976). However, the same work likened the Laetoli fossils to hominid fossils from South Africa, including Sts 3, 24, 50, 51, 52 and MLD 11. All of these fossils belong to the hypodigm of *A. africanus* though this escaped mention in the paper cited. Subsequently, a careful, detailed description of the Laetoli fossils was

published by White (1977). No attempt was made in this anatomical account to compare the fossils with other early hominids nor to develop the theme of their systematic status.

In their preliminary account of the Hadar fossils Johanson and Taieb (1976: 297) thought they could detect the presence of three synchronic and sympatric taxa: "On the basis of the present hominid collection from Hadar it is tentatively suggested that some specimens show affinities with *A. robustus*, some with *A. africanus* (*sensu stricto*), and others with fossils previously referred to *Homo*".

Subsequently, Johanson *et al.* (1976: 129) suggested that the Hadar hominid remains could be "split into two clear groups. On the one hand, something resembling but most probably more primitive than *A. africanus*, is represented by the partial skeleton and the A.L. 128-129 specimens. On the other hand, the presumed *Homo* group may represent some of the earliest evidence known thus far, for the lineage which ultimately led to modern man". Three points are worthy of note. First, they prefaced their interim conclusions by the statement that the Hadar hominid remains had not at that stage been subjected to extensive detailed studies. Secondly, they supported their claim that *Homo* was represented at Hadar by "the closeness in morphology of certain mandibles . . . with OH 7 (jaw of the type specimen of *H. habilis* from Olduvai) and the new Laetolil specimens . . ." (Johanson *et al.*, 1976: 129) (*italics mine*). The case for the latter belonging to *Homo* was then, and is now, unproven; so the comparisons with Laetoli could not be taken to strengthen their claims for the presence of *Homo* at Hadar. Thirdly, they again drew attention to robust elements in certain of the Hadar fossils (Johanson *et al.*, 1976: 128-9):

" . . . it is possible that A.L. 211-1 and A.L. 166-9 may represent an early occurrence of a robust australopithecine lineage. The somewhat atypically robust character of the temporal may be considered as consistent with the idea that the early stages of the robust lineage are being sampled."

These remarks are especially interesting in view of the later claim of Johanson and White (1979) that the Transvaal *A. africanus* (but *not* the Hadar fossils) is already on the robust lineage.

However, Johanson *et al.* (1976: 129) went on to say, "For the moment a strong case cannot be made for the presence of a robust hominid in Hadar and should be considered as a preliminary suggestion".

Thus the original claim that there were three elements, including *Homo*, at Hadar, had in the same year been replaced by a proposal that there were effectively "two clear groups". A year later Coppens and Johanson (1977) indicated that they were prepared to entertain the hypothesis that all of the Hadar hominid material could have belonged to a single taxon though they did not specify which taxon.

The view that *Homo* was present at Laetoli and



Hadar was strongly contested at a number of international meetings at Cambridge (1976), Nice (1976), Paris (1977), Nairobi (1977), Hamburg (1977) and Karlskoga (1978) (Tobias 1978a, 1978b, 1979b, 1979c, 1979d). Detailed analysis of all the published data on the Laetoli and Hadar fossil hominids as well as a preliminary study of the casts and some of the originals kindly made available by the discoverers, led me to several conclusions:

- (a) *Hadar*: The published evidence does not allow one to confirm that the 3 million years old hominids of Hadar include among them any that should be referred to *Homo*; the picture afforded by these fossils rather suggests an Ethiopian population of *A. africanus*.
- (b) *Laetoli*: The published evidence, including the descriptive detail of White (1977), leads to the conclusion that the early hominid fossils of Laetoli closely resemble those of *A. africanus* and can be accommodated comfortably within that species, perhaps with some minor modification of the sample ranges of variation for several dental metrical traits.
- (c) Both the Laetoli and Hadar fossils of the 3 to 3.75 My time-range provide us with East African samples of *A. africanus* very similar to and approximately contemporary with, or slightly older than, the Transvaal populations of that species.
- (d) The place of *A. africanus* in time and space is now confirmed and strengthened by the Hadar and Laetoli finds, which have added greatly to the probability that *A. africanus* was the ancestor of both the later forms, the robust australopithecines and the earliest species of *Homo* (Tobias 1978b).

By 1978 Johanson, Coppens and White had dropped the idea that *Homo* was represented at either Laetoli or Hadar and had accepted the view that the hominids from the two sites belonged in the genus *Australopithecus* and that they were close to, if not identical with, the southern African taxon *A. africanus transvaalensis*.

#### **"AUSTRALOPITHECUS AFARENSIS"**

Although recognising that the Hadar and Laetoli fossils are very similar to *A. africanus*, Johanson and Coppens (1978) formally proposed that these fossils be placed in a separate species, "*A. afarensis*". The first preliminary account of the postulated new species was published on 1st June 1978 by Hinrichsen (1978), but its formal diagnosis was subsequently published over the names of Johanson, White and Coppens (1978). Further details were published by Johanson and White (1979). The remainder of this article is devoted to a critique of this proposal.

#### **Is the "Diagnosis" diagnostic?**

An anonymous "Palaeoanthropology Correspondent" pointed out in *Nature* (29 March 1979) that the success of Johanson and White "in

demonstrating the morphological distinctiveness of *A. afarensis* is by no means clear". The correspondent added that "very few characters of *A. afarensis* are not also found in *A. africanus*". Moreover, "there are very few features said to be characteristic of *A. afarensis* which are, in fact, distinctive of that group".

This coincides with the view I reached after I had examined every feature in the published diagnosis and compared it with the corresponding trait in the Sterkfontein and Makapansgat fossils of *A. africanus*. A suite of eight cranial, five mandibular and eight dental features from the published diagnosis is examined here.

#### *Cranium*

It is claimed that "*A. afarensis*" has "strong alveolar prognathism with convex clivus". Marked alveolar prognathism is a well-known feature of Sterkfontein crania as exemplified by TM 1511, TM 1512, Sts 5 and Stw 13. Convexity of the clivus is a continuously varying trait, and it is present in diverse degrees in Sterkfontein maxillae such as TM 1512, Sts 17, Sts 71 and Stw 73. The convexity in the latter specimens is both transverse and vertical, as in the Hadar maxillae of A.L. 200-1a (fig. 3).

"Dental arcade (of "*A. afarensis*") long, narrow, straight sided". There are few complete palates from Sterkfontein or Makapansgat, but it is clear from those preserved that the same description would have pertained to these. There are of course markedly varying degrees of prognathism and so of palatal lengthening within early hominid taxa.

"Compound T/N crest in larger specimens". Such a crest is well-known in *A. boisei* (Tobias 1976, Day *et al.*, 1976) and its probable development in larger Transvaal gracile australopithecines was hinted at by the position in MLD 1, the first hominid specimen from Makapansgat, in which the least distance apart of the inferior temporal and superior nuchal lines is 1 mm. As the latter specimen is probably mature though not aged, it is likely that with further development of the individual a small compound T/N crest would have formed, just as it is possible that this cranium might have developed a sagittal crest had the subject lived longer into middle life. Tobias (1967: 23-4) pointed out that compound T/N crests should be expected in australopithecines generally, especially adult males with big teeth and heavy musculature. The presence of a compound T/N crest in the strongly-muscled A.L. 333-45 (though not on the less robust A.L. 288-1) is precisely what one would have expected in a well-muscled, small-brained australopithecine and what is likely to have developed in MLD 1 and others of the Transvaal *A. africanus* in the event of survival to older adulthood. This developmental variable cannot be accepted as a specific diagnostic feature.

"Shallow mandibular fossae, with weak articular eminences placed only partly under braincase". All three of these features are absolutely





Figure 3. Maxillae of australopithecines seen from above. On both specimens the floor of the nasal cavity is present in the centre, flanked on either side by the floor of the maxillary sinus.  
 Left: Stw 73, a specimen of *A. africanus* from Member 4 at Sterkfontein.  
 Right: A.L. 200-1a, a specimen of "*A. afarensis*" (or in the author's view *A. africanus aethiopicus*) from Hadar.  
 In both specimens the sub-nasal or naso-alveolar clivus is well-rounded, from above downwards and from side to side. A convex clivus has been included by Johanson *et al.* (1978) as diagnostic of "*A. afarensis*".

characteristic of australopithecines in general and indeed do not serve to distinguish among *A. africanus*, *A. robustus* and *A. boisei* (Tobias 1967, 1979a) let alone "*A. afarensis*".

"Occipital condyles with strong ventral angulation". Such high convexity of the condyles characterises *A. boisei* and other australopithecines (Tobias 1967: 27).

#### Mandible

"Ascending ramus of mandible broad, not high". Unfortunately, in this as in other such "diagnostic" traits, no measurements have been given in the diagnosis. Nevertheless, broad rami of moderate height are characteristic of *A. africanus* as, for example, are shown by Sts 36 (and see Dart 1954, 1955).

"Moderate superior transverse torus". This very variable character is to be found in a number of Transvaal *A. africanus* jaws (e.g. Broom *et al.*, 1950, Dart 1954).

"Low rounded inferior transverse torus". This description fits extremely well most *A. africanus* mandibles.

"Anterior corpus rounded and bulbous". This variable trait characterises the symphyseal region

of a number of the Transvaal australopithecine mandibles.

"Strong posterior angulation of symphyseal axis". Again, no measurements of the symphyseal angle are cited; once more this is a variable trait. Yet strong posterior angulation of the symphysis certainly characterises most *A. africanus* and *A. robustus* jaws (e.g. Broom *et al.*, 1950: 35, Dart 1955, Tobias 1976).

#### Dentition

"Upper central incisors relatively and absolutely large": Johanson and White (1979) have published means, standard deviations and ranges of both crown diameters for each tooth type in the combined Hadar plus Laetoli sample. Sample sizes are given, but it is not clear whether this refers to the number of individuals, or the number of teeth. If both teeth are present in a single jaw (e.g. the two upper central incisors in the maxilla of A.L. 200-1a), then in an overall small sample this one specimen may bias the mean if both teeth are included in the sample each in its own right. A common practice in such cases is to use the mid-values for the calculation of the means, though of course the maximum or minimum individual values are used in



statements of the sample range. Furthermore, the explanation of Table 1 of Johanson and White (1979) makes clear that the M.D. diameters for postcanine teeth have been corrected for interproximal attrition, "except in cases where that was impossible". It would appear from this wording that the authors have included data for some postcanine teeth that they were unable to correct for interproximal attrition: if so, their inclusion would lower the means for postcanine teeth. Moreover, since it is usually possible without difficulty to correct for interproximal attrition on incisors and canines, the authors' failure to do so might have introduced a small bias to the mean, which may affect comparisons with mean metrical traits of other samples.

Table 1 compares the published mean data for the combined Laetoli-Hadar sample of upper central incisors with the corresponding means for the *A. africanus transvaalensis* sample based upon Sterkfontein Member 4 and Makapansgat. In the Transvaal sample all teeth have been corrected for interproximal attrition. Where a pair of antimeres is involved, the mid-value between the left and right teeth is used for computation of the mean and the pair of such teeth counts as only one item in the given "n" where "n" refers to individuals.

**TABLE 1**  
Size of Upper Central Incisors  
Sample Ranges and Means of Metrical Characters

		M.D.	B.L.	Module
		Diameter	Diameter	(M.D. + B.L.)
		(mm)	(mm)	2
<i>A. africanus</i>		9,3-c12,0	8,2-c9,6	8,80-c10,70
	$\bar{x}$	10,60	8,93	9,77*
(4 teeth)	n	3	2	2
" <i>A. afarensis</i> "		9,0-11,8	7,1-8,6	—
	$\bar{x}$	10,36	8,16	9,26*
	n	4	5	(4-5)

\* The mean module for *A. africanus* refers to the mean of the modules of individual teeth, but for "*A. afarensis*" it is the module of the means, since the diameters for all individual teeth have not been published.

Small as are the samples, the data in the Table show that the supposed large size of the Laetoli-Hadar I<sup>1</sup> does not distinguish it from that of *A. africanus*; if anything, on the available evidence, the I<sup>1</sup> of the latter is slightly larger. If the M.D. diameters of the Hadar I<sup>1</sup> were corrected for approximal attrition, and the published illustration suggests that at least some correction is necessary (Johanson and White 1979: fig. 2), this would bring the Hadar mean slightly nearer to parity with that of the Transvaal series though the mean B.L. diameter would remain in arrears. In a word the supposed relatively and absolutely large size of the I<sup>1</sup> does not distinguish "*A. afarensis*" from *A. africanus*.

"Diminutive lateral incisors". Table 2 shows that small upper lateral incisors characterise both the Sterkfontein-Makapansgat sample and the Laetoli-Hadar sample. On the available samples,

**TABLE 2**  
Size of Upper Lateral Incisors  
Sample Ranges and Means of Metrical Characters

		M.D.	B.L.	Module
		Diameter	Diameter	
<i>A. africanus</i>		5,8-c7,5	5,6-c7,3	5,70-c7,90
9 teeth	$\bar{x}$	6,77	6,89	6,83*
(1 immature, excluded)	n	6	6	6
" <i>A. afarensis</i> "		6,7-8,2	6,2-8,1	—
		(worn)		
	$\bar{x}$	7,65	7,18	7,41*
	n	6	8	(6-8)

\* "Mean module" for *A. africanus* refers to mean of modules and for "*A. afarensis*" module of means.

the *A. africanus* lateral incisors are somewhat smaller than those of "*A. afarensis*".

"Strong variation in canine size, canines asymmetric, lowers with strong lingual ridge": To take the two latter morphological features first, both asymmetric canines and strong lingual ridges are characteristics of *A. africanus* (fig. 4) which Robinson (1956) long ago brought to notice. For example, he illustrated and pointed out the asymmetry of the crowns of maxillary canines (Robinson 1956: 45) and of mandibular canines (p. 49) of *A. africanus*; and he drew special attention to the lingual ridge which he said "appears to be a prominent feature of the Sterkfontein mandibular canines" (pp. 49-50). Strong variation in size has been

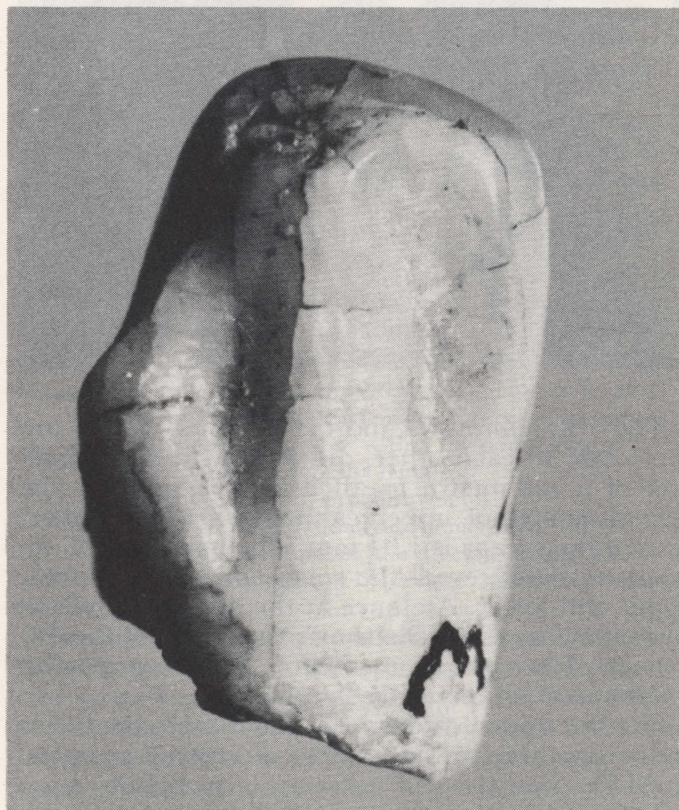


Figure 4. Lingual aspect of the crown of mandibular left canine Stw 21, of *A. africanus* from Sterkfontein Member 4. Note the obvious asymmetry of the crown and the strong lingual ridge, both of which features are said to be diagnostic of "*A. afarensis*" (Johanson et al., 1978).



shown to be a mark especially of canines, in most primates, including modern man (Gonda 1959, Mijsberg 1931) and the australopithecines (Wolpoff 1975, 1976); and it is known that the canine is generally the most sexually dimorphic tooth. Therefore the amount of variability in canine size in a fossil hominid sample may be influenced greatly by the sexual composition of the sample. This would be especially likely with the small samples that palaeo-anthropologists generally have at their disposal.

Using the means and S.D.s furnished by Johanson and White (1979) and mindful of the aforementioned uncertainty whether bilaterally represented teeth have been counted twice or only as a mid-value in the calculation of the mean, I estimated the coefficient of variation for crown diameters of upper and lower canines in the Laetoli-Hadar sample, in *A. africanus transvaalensis* and in *A. robustus crassidens* (Swartkrans Member 1) (table 3).

TABLE 3  
Canine Variability

Upper Canines	Mean mm	S.D.	C.V. %
<i>M.D. diameter</i>			
<i>A. africanus transvaalensis</i>	9,61 (6)	0,60	6,24 (6)
" <i>A. afarensis</i> "	9,92 (10)	0,74	7,46 (10)
<i>A. robustus crassidens</i>	8,54 (12)	0,40	4,68 (12)
<i>B.L. diameter</i>			
<i>A. africanus</i>	9,90 (6)	1,16	11,72 (6)
" <i>A. afarensis</i> "	10,94 (10)	1,11	10,15 (10)
<i>A. robustus crassidens</i>	9,38 (12)	0,94	10,02 (12)
<i>Lower Canines</i>			
<i>M.D. diameter</i>			
<i>A. africanus</i>	9,11 (10)	0,45	4,94 (10)
" <i>A. afarensis</i> "	9,16 (5)	1,54	16,81 (5)
<i>A. robustus crassidens</i>	8,01 (4)	0,33	4,12 (4)
<i>B.L. diameter</i>			
<i>A. africanus</i>	9,93 (11)	0,64	6,45 (11)
" <i>A. afarensis</i> "	10,17 (9)	1,15	11,31 (9)
<i>A. robustus crassidens</i>	8,53 (4)	0,62	7,27 (4)

The "*A. afarensis*" and *A. africanus* means are very close to each other, differing by a small fraction of a millimetre in all instances save for the B.L. diameter of upper canines where the difference of the means is 1,04 mm. The means for *A. robustus crassidens* reveal the small size of its canines, upper and lower. A glance at the differences of the means and at the S.D.s shows that none of the differences between the means of "*A. afarensis*" and *A. africanus* is statistically significant.

For the upper canines the Laetoli-Hadar C.V.s are comparable to those of the Transvaal samples: in M.D. diameter "*A. afarensis*" is slightly more variable than *A. africanus*, and the reverse is true for the B.L. diameters. In keeping with previous studies that have shown the greatest degree of dimorphism to be in the B.L. diameter, for each of the three taxa the C.V. for B.L. diameter is greater than for M.D. diameter in the maxillary canines.

When one turns to the lower canines, however, "*A. afarensis*" shows an astonishingly high value for the C.V. of the M.D. diameter, not only higher than any other C.V. in the entire table, but contrary to expectation higher also than the C.V. for the B.L. diameter of the same sample. This high C.V. of 16,81 flows from the very high S.D. of 1,54 for a sample of M.D. diameters stated to be only 5, whereas the sample for B.L. diameters of lower canines from Laetoli-Hadar is given as 9. The high S.D. is obviously related, in part, to the small sample size. There is a clear-cut discrepancy within the Laetoli-Hadar sample, the M.D. diameters being more highly variable than the B.L. diameters, whereas the opposite is the case for all other sets of data in Table 3 and in most previous studies. It is difficult to resolve this problem, since with a few exceptions the original measurements for individual Hadar teeth have not been published. Secondly, we are told that the M.D. diameters of the front teeth have not been corrected — and it is a set of M.D. diameters of canines that have yielded the discrepant results. Thirdly, we do not know whether and to what extent the results have been influenced by the inclusion of both members of a pair of antimeres in the calculation of the mean, such as the two lower canines in the Hadar jaw A.L. 400-1a. Fourthly, one questions whether the high C.V.s for the mandibular teeth of Laetoli-Hadar do not betray that more than one population has been sampled, a not unreasonable query, since the data quoted by Johanson and White are for two site-samples that have been pooled — *vide infra*. Lastly, the internal discrepancy compels one to ask whether a computational or typographic error might have crept in to their published table of means.

Save for this discrepant value, the morphology and variability of the canines do not distinguish between "*A. afarensis*" and *A. africanus*.

"P<sub>3</sub> occlusal outline elongate oval in shape with main axis mesiobuccal to distolingual at 45°-60° to tooth row, dominant . . . buccal cusp, small lingual cusp often expressed only as inflated lingual ridge": The shape as described is exactly as we find it in many of the Sterkfontein and Makapansgat P<sub>3</sub>s. Here are Robinson's (1956: 72-73) very words as he describes the Sterkfontein P<sub>3</sub>s: "The crown thus has a skewed appearance in occlusal view, with the longest diameter running from the distolingual to the mesiobuccal angle".

It would have been helpful to know what number of Laetoli-Hadar P<sub>3</sub>s had moderate, small and very small lingual cusps: since this is a most variable feature in populations of early hominids. Of seven excellent casts of Hadar mandibles kindly made available by Dr. Johanson, all of which show the unworn lingual cusps of P<sub>3</sub>, two show moderately high lingual cusps: of these it is highest in A.L. 333W-1a where the buccal and lingual cusps are sub-equal; the pattern is similar to that in the Sterkfontein jaw SL 52b. The lingual cusp is moderately high on both left and right in A.L. 400-1a.



Only two of the seven mandibles have  $P_3$ s with very low lingual cusps: A.L. 128-23 and A.L. 288-11. Coppens (1977: 1301) singles out the latter as being "pratiquement monocuspide". These observations suggest that the expression of the lingual cusp in the Hadar population is very variable, as in *A. africanus transvaalensis*. On the three Laetoli  $P_3$ s Wolpoff (1979) speaks of "a dominant buccal cusp, a weaker somewhat lower lingual cusp", which implies a better developed lingual cusp than the form Johanson *et al.* (1978) describe as "often expressed only as inflated lingual ridge".  $P_3$ s with very small lingual cusps are to be found in the Transvaal samples; for example the  $P_3$ s of MLD 2, the first jaw of *A. africanus* found at Makapansgat (Dart 1948a). Of course there may be a difference in the frequency of small lingual cusps between the three populations, but this would have to be very marked before it could be regarded as a diagnostic trait. On presently available evidence the range of characteristics of the  $P_3$ s of Hadar and Laetoli do not distinguish between "*A. afarensis*" and *A. africanus*.

"Postcanine (mandibular) teeth aligned in straight rows". This feature is to be found in *A. africanus transvaalensis*, for example Sts 7 (Broom *et al.*, 1950), MLD 18 (Dart 1962) and Stw 14 (Tobias 1973b). It is therefore not diagnostic.

#### Summation on diagnosis

Feature after feature listed in the "Diagnosis" of "*A. afarensis*" by Johanson *et al.*, (1978) has proved to be not diagnostic; and working systematically through the remaining half-dozen enumerated traits, I have been led to the same conclusion about them. In a word "*A. afarensis*" cannot be separated from *A. africanus* on the characters that have been adduced as the diagnosis.

From the tooth measurements for Laetoli published separately by White (1977) the author was able to show that there are indeed some slight odontometric differences between the fossils of Laetoli and those of *A. africanus*. The only such differences are that the teeth of Laetoli are slightly larger on the average, and the mandibular premolars of Laetoli, though larger, are longer and narrower than those of *A. africanus* (Tobias 1979d). These tenuous differences seem to me to be insufficient evidence on which to separate the Laetoli hominids from Transvaal *A. africanus* at the species level. There may well be a case to separate them at the subspecies level, since, aside from their small dental differences, they are 0.6-1.0 My earlier than Makapansgat Member 3 and Sterkfontein Member 4 and 200-2500 km apart.

Other descriptive details have been placed on record by Johanson *et al.*, (1978) though without these points being listed as part of the formal diagnosis. These traits, too, do not strengthen the case for separate specific status. As was pointed out in the anonymous comment in *Nature*, such additional features as the "waisted" capitate bone, the lack of a styloid process on the third metacar-

pal and the features of the pelvis of "Lucy" (A.L. 288-1) are extremely similar to corresponding traits from Sterkfontein. The same applies to the strong molar size gradient  $M3 > M2 > M1$  which typifies *Australopithecus*. Strong dimorphism in body size is said to characterise the Hadar collection, but it is true too of the Transvaal australopithecines. Wolpoff (1975) was led to conclude that in the gracile australopithecines of the Transvaal the male is considerably larger than the female. Apart from the evidence adduced by him we may point to the great variation of vertebral size between the very small vertebrae of the putative female Sts 14 and the much larger ones comprising the still articulated spine Stw 8/41, derived from the same Member 4 at Sterkfontein: these vertebrae point to a strong degree of sexual dimorphism in body size (bulk) in *A. africanus transvaalensis* (fig. 5).



Figure 5. These two partial vertebral columns of *A. africanus* from Sterkfontein Member 4 reveal the great size dimorphism present within the population. Left: Sts 14, probably female. Right: Stw 8/41, probably male. Marked sexual dimorphism has been claimed to be a special feature of the Laetoli-Hadar fossils for which the nomen "*A. afarensis*" has been proposed.

In short the Laetoli and Hadar hominids seem to have provided us with the first good East African populations of *A. africanus*, for it has been a curious feature of the record of discovery that the luxuriant fossil sites of East Africa have until lately not yielded any series that bears direct and close comparison with *A. africanus*, save for isolated teeth from Omo and possibly for the incomplete mandible of Lothagam and humeral fragment from Kanapoi. The claims for their distinctiveness notwithstanding, the Laetoli and Hadar fossils seem at last to have filled this gap.



### Is the pooling of the Laetoli and Hadar fossil hominids justified?

In creating the supposed taxon "*A. afarensis*" and in further justifying it, Johanson and his co-workers have pooled the two site-samples of Hadar and Laetoli. In vindication of this procedure, they speak of "The strong morphological and chronological continuity" between these two site-samples (Johanson and White 1979: 321).

The supposed chronological continuity is not immediately apparent. For the Hadar Formation Aronson *et al.*, (1977: 327) have arrived at a range of dates which extends "from somewhat more than 3,1 My ago to somewhat less than 2,6 My ago". The ages of the hominid-bearing strata at Laetoli have been bracketed between 3,59 and 3,77 My B.P. (M.D. Leakey *et al.*, 1976).

Thus the latest hominid at Laetoli and the oldest at Hadar are separated in time by something like 0,4 My. If we take the mid-value of the range of datings for each site, we have values of about 3,68 My at Laetoli and of about 2,85 My at Hadar, these mid-range values being separated by 0,83 My.

Even within the Hadar Formation the hominids are distributed in three Members of different ages. At a rough estimate based on the lists of specimens published by Johanson, White and Coppens (1978), some 11 % of Hadar hominids are derived from the Sidi Hakoma Member. This is the oldest member, and its dating is said to be older than c3,0 My, but less than c3,3 My. Thus, only a small minority of the oldest Hadar fossils are within about 0,4 My of the most recent date for the Laetoli fossil hominids.

Most of the Hadar hominids are derived from the two younger Members, Denan Dora and Kada Hadar, both of which are dated to younger than c3,0 My though not more recent than c2,6 My. The older of the two, the Denan Dora Member, is the one that is richest in hominids, including the supposed family group that constituted one of the more remarkable finds at Hadar. At a rough estimate, 85 % of the Hadar hominid specimens come from this Denan Dora Member. The remaining Kada Hadar member seems to be 2,8 My old, or just less, and has yielded one hominid individual, the 40 % complete skeleton of A.L. 288-1 known as Lucy.

There is thus a range in time of at least 0,5 My between the oldest and the youngest hominids from Hadar. This is comparable with the minimum estimate of the lapse of time between Members 4 and 5 at Sterkfontein and much less than the interval between Members 1 and 2 at Swartkrans. Although the Hadar hominids are dispersed through these three Members, they have been pooled and treated as one sample by Johanson and his co-workers. Then, this entire site-sample has been pooled with the still earlier hominids of Laetoli, the oldest of which may be 1,0 My older than the youngest from Hadar. That is, the combined sample encompasses a million years of possible

morphological change — and even within a single evolving lineage this may be appreciable. For such pooling to be justified, it would be necessary for the hominids from each Member in the Hadar Formation to be first analysed separately; it would need to be shown that no appreciable morphological differences distinguished the hominids in the earlier and later parts of the half million years or more that elapsed during the deposition of the various Members of the Hadar Formation. This might have been done by Johanson and his colleagues, but nothing to this effect is mentioned in any relevant publication. Also, the data from each Hadar Member sub-sample have not been presented separately with a statistical evaluation of the mean measurable characters and of the significance of any differences that may be detected by such analyses. Once it had been shown that the fossil hominids from the three Members at Hadar were indeed "poolable", one should then by a similar procedure evaluate the morphology and measurable differences between the Hadar sample *in toto* and that of Laetoli: if the differences were sufficiently small, it could be adjudged that the two site-samples could be pooled. In this way each of the site-samples of Sterkfontein and Makapansgat was analysed separately, and only after it was proved that they shared a common morphological pattern did Robinson (1954) formally propose that they be grouped as two sub-sets of a single subspecies, *A. africanus transvaalensis*.

With "*A. afarensis*", there are no published indications, data nor statistical analyses to show that such a procedure has been followed. Early and late sub-samples and site-samples have simply been pooled and treated as one population, comprising a supposedly distinctive lineage and taxon. Had the describers of the proposed new taxon *manifestly* followed this time-honoured and well-validated procedure, and, had statistical tests not militated against such pooling, the case for a new taxon would have been more convincing.

To the chronological difficulties just mentioned should be added their geographical separation by 1 600 km, a sufficiently great distance for geographical subspeciation or "racciation" to have occurred even if the two groups had been synchronic. With major differences of time and space between the Hadar sub-samples and the Laetoli assemblage, the chances of the two site-samples belonging at least to different subspecies are very great. However, only the morphological analysis of the various sub-samples will be able to prove whether subspeciation had indeed occurred.

The manner in which the preliminary morphological accounts of the Hadar fossils have been published makes it difficult to determine what differences exist between the Tanzanian and Ethiopian samples. Although some Laetoli fossils have been described in detail (White 1977), the data published separately for the earlier-discovered Hadar specimens do not allow metrical comparison with the Laetoli fossils. For example, it is not clear



whether the published mesiodistal diameters of the Hadar teeth had been corrected for approximal attrition (Johanson and Taieb 1976, Johanson, Coppens and Taieb 1976); yet without such corrections comparisons of dental measurements of hominids are largely vitiated (Wolpoff 1971, Tobias 1978b).

The present appraisal has already referred to the large coefficient of variation of the mesiodistal diameters of lower canines of the Laetoli-Hadar combined sample, and the query was raised whether in fact more than one population has been sampled.

It has proved possible to calculate approximate means for some dental traits for the Hadar populations alone (table 4) from published data (White 1977, Johanson and White 1979). In the Table only metrical traits based on cheek-tooth measurements have been used, since these are the only ones for which Johanson and White (1979) have made corrections for approximal attrition. The approximate Hadar means in the Table differ appreciably from the Laetoli means, whether we consider mesiodistal or buccolingual diameters, crown areas or the sum of crown areas, or shape index values (M.D./B.L.  $\times$  100%). It is noteworthy that for all metrical characters cited in the Table the

**TABLE 4**  
Some Estimates of Odontometric Contrasts Between Laetoli and Hadar\*

	<i>A. africanus</i>	Laetoli	Hadar	Laetoli-Hadar	
	<i>transvaalensis</i>			" <i>A. afarensis</i> "	
Mandibular Tooth Material (P <sub>3</sub> -M <sub>3</sub> )	860,66	868,61	c732,52	748,61	
M.D. diam. P <sub>3</sub>	9,61 (5)	11,60 (2)	c9,16	9,51	(14)
B.L. diam. M <sup>1</sup>	13,8 (15)	14,5 (3)	c12,60	13,23	(9)
B.L. diam. M <sub>3</sub>	14,2 (14)	c14,2 (1)	c13,14	13,23	(12)
Crown Area P <sup>3</sup>	114,10 (15)	120,08 (2)	c95,12	102,25	(7-8)
Crown Area M <sub>1</sub>	181,01 (9)	181,02 (3)	c158,13	162,17	(16-18)
Shape Index P <sub>3</sub>	82,57 (5)	112,45 (2)	c85,93	89,72	(14)
Shape Index P <sub>4</sub>	83,04 (8)	94,46 (3)	c85,38	87,65	(12-13)

\* The means for *A. africanus transvaalensis* are the latest results estimated by me and based upon enlarged samples that include most of the newest finds from the Transvaal sites. The means for Laetoli above have been prepared by me from mean diameters given by White (1977). The mean diameters for Laetoli-Hadar are taken from Johanson and White (1979), and the derived measures and indices have been based upon the published means. The values for Hadar have been estimated from those for Laetoli-Hadar combined and Laetoli alone, since data for individual Hadar teeth are generally not available, and those published might not have been corrected for interproximal attrition. Mandibular tooth material is my modification of Howes's (1954) tooth material concept: it is the sum of the crown areas (M.D.  $\times$  B.L.) of the five mandibular permanent cheek-teeth (P<sub>3</sub>-M<sub>3</sub>). In parentheses "n" refers in the first two columns not to the total number of teeth available, but to the number of individuals from each of whom one or two measurable representatives of the tooth-type in question are available. For Laetoli-Hadar "n" is as published; it is not known if it refers to teeth or to individuals.

means for Laetoli, as computed for White's (1977) individually recorded tooth measurements, give higher values than the means cited by Johanson and White (1979) or derived from their mean values for the Laetoli-Hadar combined sample. Thus, the mean values for measures of size of the Hadar teeth alone are all smaller than the means for the combined sample.

The relatively small size of the Hadar teeth in turn must have a major effect on means for the combined sample, at least 80% of which seems to comprise Hadar teeth. Their smallness is vividly portrayed when one compares the Cheek-Tooth Material (summed crown areas of P<sub>3</sub> to M<sub>3</sub>) for various fossil populations (table 5). Laetoli alone has a mandibular tooth material of 868,61, very close to the mean for *A. africanus* (860,66).

**TABLE 5**  
Cheek-Tooth Material of Hominids Summed Crown Areas of P<sub>3</sub> to M<sub>3</sub>

	Maxillary	Mandibular
<i>A. boisei</i> (several E. African sites)	1 230,88	1 312,00
<i>A. robustus crassidens</i> (Swartkrans)	990,67	960,13
<i>A. robustus robustus</i> (Kromdraai)	929,08	882,10
Laetoli	—*	868,61
<i>A. africanus transvaalensis</i> (Sterkfontein and Makapansgat)	819,70	860,66
<i>H. habilis</i> (several E. African sites)	743,48	786,59
Laetoli-Hadar	734,39	748,61
Hadar	686,61†	732,52†
<i>H. erectus erectus</i>	641,13	695,34
<i>H. erectus mauritanicus</i>	—	665,03
<i>H. erectus pekinensis</i>	577,07	607,66
<i>H. erectus heidelbergensis</i>	—	543,65
<i>H. sapiens sapiens</i>	471,80	484,83

\* No measurements for a P<sup>4</sup> from Laetoli have been published, so it has not been possible to compute its maxillary tooth material.

† Figures for Hadar have been computed from estimates based on the means for the combined Laetoli-Hadar sample and for the separately-published Laetoli teeth.

The values for Laetoli-Hadar combined and those estimated for Hadar are so low as to set them below the tooth-material of *H. habilis*. This position is decidedly odd when one notes that the Laetoli component of the combined sample has tooth material somewhat larger than that of *A. africanus*. These relative placements make the combined sample look positively heterogeneous. Again one has cause to ponder the "poolability" of Hadar and Laetoli and to consider whether they do not represent different populations.

In five out of six size parameters (table 4), the means for Laetoli alone are closer to the *A. africanus transvaalensis* means than are the estimated means for Hadar alone. There is near identity between the Laetoli means and the Transvaal means for mandibular tooth material, buccolingual diameter of M<sub>3</sub> and the Crown Area of M<sub>1</sub>; the values are close for the buccolingual diameter of M<sup>1</sup> and the Crown Area of P<sup>3</sup>. Only for the mesiodistal diameter of P<sub>3</sub> is the Hadar estimated mean closer to the *A. africanus* mean. On the other hand, as men-



tioned above, in shape measures the mandibular premolars of Laetoli differ appreciably from those of *A. africanus*, and the values estimated for Hadar are very similar to those for the Transvaal.

Approximate as is this method for the testing of metrical similarity between Laetoli and Hadar, it does at least confirm what the variability had earlier shown, namely that there is a strong *prima facie* case to examine more closely the characteristics of the Laetoli and Hadar samples and subsamples separately. It provides us with some justification for the feeling already voiced that the two site-samples may be samples of different populations. How different those populations might have been is altogether another question; the dental metrical differences may bespeak no more than geographical and chronological subspeciation within a single lineage. Nevertheless the differences between Laetoli and Hadar are great enough to deter us from easily accepting the pooling of the two site-samples for purposes of statistical evaluation or for taxonomic appraisal.

### THE PHYLOGENETIC SYSTEM ERECTED BY JOHANSON AND WHITE (1979)

Johanson (1978a) and Johanson and White (1979) have proposed that "*A. afarensis*" is directly ancestral to (a) *H. habilis* and (b) a branch leading via *A. africanus* to *A. robustus*. That is, they consider that *A. africanus* is off the main line of hominid evolution leading to *Homo*, and they regard it as already differentiated in the direction of the robust australopithecines. This view involves judgements on both the morphology and the dating of the Transvaal hominids. Attention will here be drawn to these two aspects.

#### The dating of the Transvaal sites

Opinions on the dating of the Transvaal sites of Sterkfontein and Makapansgat have been shown in the family trees published by Johanson (1978a, 1978b) and by Johanson and White (1979). Although aware of the known difficulties in dating these sites in the absence of radiometric ages, Johanson and White place Sterkfontein at about 2,3 My and Makapansgat at about 2,4–2,5 My B.P. In one of the phylogenetic charts *A. africanus* is actually shown as a direct contemporary of *H. habilis* (Johanson 1978b). In the light of all the evidence that has accumulated the promoters of "*A. afarensis*" have assigned too young an age to the Transvaal gracile australopithecines.

As a result of numerous faunal analyses (e.g. Cooke 1970, 1974, Cooke and Maglio 1972, Maglio 1971, Collings *et al.*, 1976, White and Harris 1977) and of the newest palaeomagnetic dating for Makapansgat (Brock 1977, Partridge 1979, McFadden *et al.*, 1979), Sterkfontein Member 4 is dated on faunal grounds to 2,5 to 3,0 My (fig. 6) with "a fairly probable minimum of about 2,5 m.y." (Cooke 1974). Palaeomagnetic results for Sterkfontein are not yet available. Makapansgat Member 3, the stratum that has yielded all but

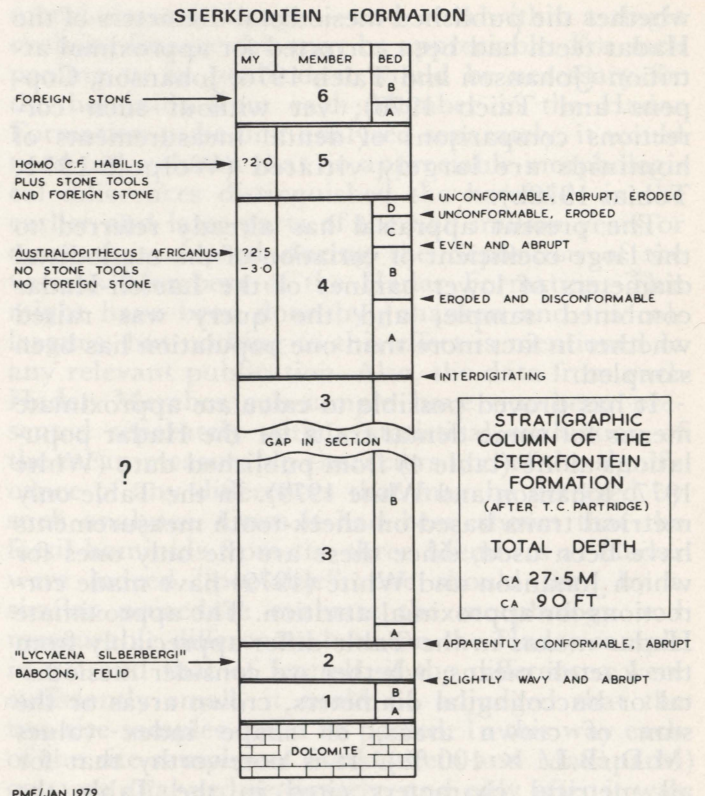


Figure 6. Schema of the stratigraphic sequence at Sterkfontein based on Partridge (1978). The *A. africanus* Member 4 is dated by the associated fauna to 3,0–2,5 My B.P.; palaeomagnetic data are not yet available.

one of the australopithecines from that site, is dated faunistically as somewhat older than Sterkfontein Member 4 and palaeomagnetically as either just over 2,9 My or just over 3,06 My (fig. 7), according to which sequence applies (McFadden *et al.*, 1979, and this volume).

The latest palaeomagnetic dating for Makapansgat was announced by Brock as long ago as 1977 and supersedes the preliminary datings published by Brock *et al.* (1977).

The faunal datings are based independently on a variety of faunal elements, including suids, proboscideans, felids and hyaenids, whilst bovids have not so far provided definitive indications (Vrba 1974, 1975). It is noteworthy that White and Harris (1977: 19) have equated the Makapansgat suids (of Member 3) with Omo Shungura Members B and C though on p. 20 they mention only Member C. The approximate time equivalent of Shungura B and C spans a period from just under 3,0 My to about 2,4 My (Brown and Shuey 1976). Cooke (1978) has contested the suid phylogenetic and correlative scheme of White and Harris (1977) as oversimplified, and he has proposed an alternative. None the less, he has made clear that the "taxonomic and phylogenetic differences do not have any significant effect on the stratigraphic interpretations offered by White and Harris" (Cooke 1978: 460). In view of all this faunal and palaeomagnetic evidence, some of which White himself has ad-







lation of gracile hominids included polymorphically some robust-like features that seem to have been part and parcel of the same population and doubtless expressions of a markedly sexually dimorphic phase of the hominid lineage.

## CONCLUSION AND PROPOSAL OF AN ALTERNATIVE HYPOTHESIS

### Laetoli

The published evidence, including the detailed description by White (1977) and the observational contact I have been allowed to enjoy with the originals and casts, have led me to conclude that the early hominid fossils of Laetoli closely resemble those of *A. africanus*. Indeed, no convincing morphological evidence has been presented that the fossils of Laetoli belong to a different lineage and are any more than subspecifically distinct from *A. africanus transvaalensis*. From the information at my disposal I believe that the Laetoli hominids can be accommodated comfortably within the species *A. africanus*, perhaps with some minor modifications of the ranges of variation for several dental metrical traits. On the basis that the Laetoli teeth are very slightly larger and the mandibular premolars somewhat longer and narrower than those of the Transvaal *A. africanus*, and since the Laetoli fossils are 0.6–1.0 My older and geographically well-removed from *A. africanus transvaalensis*, there may well be a case to separate the Laetoli hominids at the subspecies level. At the same 1978 Nobel symposium at which Johanson formally announced the proposal to establish a new species, "*A. afarensis*", I suggested in my paper that the Laetoli hominids should be regarded as the Tanzanian subspecies of *A. africanus* under the nomen of *A. africanus tanzaniensis* (Tobias 1979d). Appropriate as this name would be for the Tanzanian geographical subspecies of *A. africanus*, the claimed new species "*A. afarensis*" has since been published. Even though its authors drew its name from the Ethiopian Afar depression, they have chosen as its type specimen one of the Laetoli mandibles (L.H. 4). Thus the name *afarensis* remains inseparably linked to the Laetoli holotype. This would remain true even were "*A. afarensis*" to be relegated to the status of a subspecies within *A. africanus*. For the proposed subspecies represented by the Laetoli fossils the correct name would then be *A. africanus afarensis*. The other two subspecies of *A. africanus* formally recognised are *A. africanus africanus* for the Taung type skull and *A. africanus transvaalensis* for the gracile australopithecines of Sterkfontein and Makapansgat (Robinson 1954, Campbell 1962)\*

\* Campbell (1972, 1973) has more recently propounded a hominid classification in which the Transvaal robust australopithecines, *Homo habilis* and the Mojokerto hominid are regarded as representing other subspecies of *A. africanus*, namely *A. africanus robustus*, *A. a. habilis* and *A. a. modjokertensis*, respectively. His proposed scheme has not yet gained acceptance.

### Hadar

Neither the published evidence, nor the personal acquaintance I have had with the originals and casts of some of the fossils, allows me to confirm that the hominids of Hadar are so different that they — or even some of them — should be referred to any new species of *Australopithecus*. The picture afforded by most of these fossils suggests an Ethiopian population or sequence of populations in the *A. africanus* lineage. We need close further study, including statistical analysis of metrical traits, of the Ethiopian remains (from both the earlier members of Omo and the various members at Hadar), before it can be determined whether the various sub-sets of Hadar hominids, severally or collectively, should be referred to (a) the same subspecies as their southern African contemporaries, *A. africanus transvaalensis*; (b) the same subspecies as the earlier Tanzanian hominids from Laetoli; or (c) a separate fourth subspecies of *A. africanus*, for which a name other than *A. africanus afarensis* would have to be sought if the latter name remained tied to the Laetoli fossils.

One morphological trait to which attention has not been drawn is incurvation of the M<sup>3</sup>s of the superb Hadar palate and dental arcade, A.L. 200–1a, manifest on the cast and illustrations (e.g. Johanson and White 1979: fig. 2). This gives a maxillary bidental width at M<sup>3</sup> which is less than that at M<sup>2</sup>. This feature has not been found on a small series of australopithecine dental arcades of *A. africanus*, *A. robustus* or *A. boisei* (Tobias 1980), nor does it appear to characterize the more fully adult specimen A.L. 199–1. If it is a real adult trait of A.L. 200–1a, and not the consequence of its young adult status, it may follow that this individual possessed the structural basis to have developed a helicoidal occlusal plane (Tobias 1980). The presence of this structural and functional complex, along with the probable tendency to smaller teeth, and perhaps a few other odontoscopic special features, may signal sufficient differences to justify recognition of the Hadar hominids, and perhaps the *A. africanus*-like teeth of Omo (Howell 1969, Coppens 1975), as representative of a distinct geographic subspecies of *A. africanus*. If further close morphological and statistical analysis confirms the presence of these small marks of distinction, it may be necessary to recognize and name a separate subspecies within the evolving and polytypic lineage of *A. africanus*. As the name *afarensis* would be pre-occupied by the Laetoli fossils, then it would be most appropriate to suggest an alternative regional or territorial soubriquet: I propose *Australopithecus africanus aethiopicus* as a suitable name for this Ethiopian taxon.

### Summation

No adequate morphological, chronological or other evidence has been provided that would refute the alternative hypothesis, namely that both the Laetoli and Hadar samples and the Omo teeth allocated to *A. africanus* or *A. aff. africanus* belong to



the same lineage as *A. africanus transvaalensis* and, moreover, constitute earlier and later populations of the long-elusive East African representative of *A. africanus*. It is here proposed that the Laetoli and Hadar fossils and those of Omo of the 3,7–2,5 My time-range provide us, at last, with East African samples of *A. africanus* very similar to the Transvaal populations of that species, partly contemporary with and partly older than the Transvaal counterparts.

On the view propounded here the place of *A. africanus* in time, space and phylogeny is confirmed and strengthened by the valuable new finds of Laetoli and Hadar. These early East African hominids have added greatly to the probability that *A. africanus* was a polytypic species, part of an evolving lineage of ancestral hominids from at least 3,7 to about 2,5 My B.P. These hominids occupied a late-Pliocene time-slot, earlier than the appearance of both the robust australopithecines (*A. robustus* and *A. boisei*) and the earliest members of the genus *Homo* which first emerge in the fossil record about 2,3 My B.P. In this sense *A. africanus* from the Transvaal, Tanzania and Ethiopia is most likely to have been the common ancestor of both later lineages of hominids.

One derivative lineage retained micrencephaly, developed its teeth and masticatory apparatus to a very marked degree, became on the average heavier though not necessarily taller, evolved perhaps a greater degree of sexual dimorphism and apparently did not show marked dependence on implements: *A. robustus*, a modestly robust offshoot known thus far only from the Transvaal; and *A. boisei*, a hyper-robust branch so far represented only in the end-Pliocene and early-Pleistocene fossil assemblages of Tanzania, Kenya and Ethiopia.

The other seemingly derivative lineage was characterized by allometric brain enlargement: meso-encephaly in its early stages, as in *Homo habilis*; macrencephaly in the subsequent grade, *H. erectus*; and gigantencephaly in *H. sapiens*. It was marked, too, by reduction of the dentition and masticatory apparatus, a probable diminution in the degree of sexual dimorphism and increasing dependence on implemental activity and an ever-

more-diversified programme of cultural behaviour. To this derivative lineage has been given the name *Homo*, and the varied morphological grades it traversed are designated *H. habilis*, *H. erectus* and *H. sapiens*, more or less in succession.

This alternative hypothesis underlines a view that I have long held: it is not the South African fossils alone, nor yet the East African fossils alone, that may be expected to lay bare the secrets of human evolution. Accidents of preservation and of discovery have decreed that our early African fossils are sundered into these two geographical groups with a palaeo-anthropological no-man's-land separating them. None would doubt, however, that the distributions of the early hominids embraced the intervening region: unfortunately, J. Desmond Clark's searches in the vicinity of Lake Malawi about half-way between the northern Tanzanian sites and those of the Transvaal have not yielded the hoped-for early hominids. It is, however, most likely that they are there and will still be discovered. My point is that only by the careful study of all South and East African early hominids may we expect to find an approximation to the truth, for the birth of the hominids was a pan-African phenomenon. The uncovering of those birth-stages requires a pan-African approach, free of regional or territorial preconceptions and predilections.

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#### REFERENCES

- AGUIRRE, E. (1970). Identificación de "Paranthropus" en Makapansgat. *Crónica del XI Congreso Nacional de Arqueología, Mérida 1969*, 98–124.
- ANONYMOUS CORRESPONDENT (1975). Ethiopian fossil hominids. *Nature*, Lond., **253**, 232–233.
- ARONSON, J.L., SCHMITT, T.J., WALTER, R.C., TAIEB, M., TIERCELIN, J.J., JOHANSON, D.C., NAESER, C.W. and NAIRN, A.E.M. (1977). New geochronologic and paleomagnetic data for the hominid-bearing Hadar Formation of Ethiopia. *Nature*, Lond., **267**, 323–327.
- BOAZ, N.T. and HOWELL, F.C. (1977). A gracile hominid cranium from Upper Member G of the Shungura Formation, Ethiopia. *Am. J. phys. Anthropol.*, **46**, 93–108.
- BROCK, A. (1977). Paper presented to Pan-African Congress on Prehistory and Quaternary Studies, Nairobi, Sept. 1977.
- BROCK, A., McFADDEN, P.L. and PARTRIDGE, T.C. (1977). Preliminary palaeomagnetic results from Makapansgat and Swartkrans. *Nature*, Lond., **266**, 249–250.
- BROOM, R., ROBINSON, J.T. and SCHEPERS, G.W.H. (1950). Sterkfontein ape-man *Plesianthropus*. *Transv. Mus. Mem.*, **4**, 1–117.
- BROWN, F.H. and SHUEY, R.T. (1976). Magnetostratigraphy of the Shungura and Usno Formations, Lower Omo Valley, Ethiopia. In: Coppens Y., Howell F.C., Isaac G.L. and Leakey R.E.F., Eds., *Earliest Man and Environments in the Lake Rudolf Basin*. University of Chicago Press, 64–78.
- CAMPBELL, B.G. (1962). The systematics of man. *Nature*, Lond., **194**, 225–232.
- — — (1972). Conceptual progress in physical anthropology: fossil man. *Ann. Rev. Anthropol.*, **1**, 27–54.



- — — (1973). A new taxonomy of fossil man. *Yearbook of Phys. Anthropol.*, **17**, 194–201.
- — — (1974). *Human Evolution, an Introduction to Man's Adaptations* (2nd ed.). Chicago, Aldine Publishing Co., 1–469.
- CERLING, T.E., BROWN, F.H., CERLING, B.W., CURTIS, G.H. and DRAKE, R.E. (1979). Preliminary correlations between the Koobi Fora and Shungura Formations, East Africa. *Nature*, Lond., **279**, 118–121.
- COLLINGS, G.E., CRUICKSHANK, A.R.I., MAGUIRE, J.M. and RANDALL, R.M. (1976). Recent faunal studies at Makapansgat Limeworks, Transvaal, South Africa. *Ann. S. Afr. Mus.*, **71**, 153–165.
- COOKE, H.B.S. (1970). Notes from members. *Bull. Soc. Vertebrate Paleont.*, **90**, 2.
- — — (1974). Plio-Pleistocene deposits and mammalian faunas of Eastern and Southern Africa. *Proc. V<sup>e</sup> Congrès Néogène Méditerranéen, Lyon 1971*. Paris: B.R.G.M., Memoir **78**, 99–108.
- — — (1978). Suid evolution and correlation of African hominid localities: an alternative taxonomy. *Science*, **201**, 460–463.
- COOKE, H.B.S. and MAGLIO, V.J. (1972). Plio-Pleistocene stratigraphy in East Africa in relation to proboscidean and suid evolution. In: Bishop, W.W. and Miller, J.A., eds., *Calibration of Hominoid Evolution*. Edinburgh, Scottish Academic Press, 303–329.
- COPPENS, Y. (1975). Évolution des hominidés et de leur environnement au cours du Plio-Pléistocène dans la basse vallée de l'Omo en Éthiopie. *C.R. Acad. Sci. Paris*, **281**, 1693–1696.
- — — (1977). Évolution morphologique de la première prémolaire inférieure chez certains Primates supérieurs. *C.R. Acad. Sci.*, **285**, 1299–1302.
- COPPENS, Y. and JOHANSON, D.C. (1977). Paper presented to Pan-African Congress on Prehistory and Quaternary Studies, Nairobi, Sept. 1977.
- CURTIS, G.H., DRAKE, R.F., CERLING, T.E., CERLING, B.L. and HAMPEL, J.M. (1975). Age of KBS tuff in Koobi Fora Formation, East Rudolf, Kenya. *Nature*, **258**, 395–398.
- DART, R.A. (1925). *Australopithecus africanus*: the man-ape of South Africa. *Nature*, Lond., **115**, 195–199.
- — — (1948a). The adolescent mandible of *Australopithecus prometheus*. *Am. J. phys. Anthropol.*, n.s. **6**, 391–412.
- — — (1948b). The Makapansgat proto-human *Australopithecus prometheus*. *Am. J. phys. Anthropol.*, n.s. **6**, 259–284.
- — — (1954). The adult female lower jaw from Makapansgat. *Nature*, Lond., **173**, 286.
- — — (1955). Extinct and extant human mandibles. *S. Afr. J. Sci.*, **51**, 258–262.
- — — (1962). A cleft adult mandible and the other nine lower jaw fragments from Makapansgat. *Am. J. phys. Anthropol.*, n.s. **20**, 267–286.
- DAY, M.H., LEAKEY, R.E.F., WALKER, A.C. and WOOD, B.A. (1975). New hominids from East Rudolf, Kenya, I. *Am. J. phys. Anthropol.*, **42**, 461–476.
- — — (1976). New hominids from East Turkana, Kenya. *Am. J. phys. Anthropol.*, **45**, 369–436.
- FITCH, F.J., HOOKER, P.J. and MILLER, J.A. (1976). <sup>40</sup>Ar/<sup>39</sup>Ar dating of the KBS tuff in Koobi Fora Formation, East Rudolf, Kenya. *Nature*, Lond., **263**, 740–744.
- GONDA, K. (1959). On the sexual difference in the dimensions of human teeth. *J. Anthrop. Soc. Nippon*, **67**, 151–163.
- HAY, R.L. (1976). *Geology of the Olduvai Gorge*. University of California Press, 1–203.
- HINRICHSSEN, D. (1978). How old are our ancestors? *New Scientist*, **78**, 571.
- HOWELL, F.C. (1969). Remains of Hominidae from Pliocene/Pleistocene formations in the lower Omo basin, Ethiopia. *Nature*, Lond., **223**, 1234–1239.
- HOWES, A.E. (1954). A polygon portrayal of coronal and basal arch dimensions in the horizontal plane. *Amer. J. Orthod.*, **40**, 811–831.
- HURFORD, A.J., GLEADOW, A.J.W. and NAESER, C.W. (1976). Fission-track dating of pumice from the KBS tuff, East Rudolf, Kenya. *Nature*, Lond., **263**, 738–740.
- JOHANSON, D.C. (1978a). A new species of man, *Australopithecus afarensis* from Eastern Africa stimulates major revisions in understanding human origins. *Further Evidence*, **1**, 5–8.
- — — (1978b). Our roots go deeper. *Science Year 1979, Worldbook Childcraft International Inc.*, 43–45.
- JOHANSON, D.C., COPPENS, Y. and TAIEB, M. (1976). Pliocene hominid remains from Hadar, Central Afar, Ethiopia. In: Tobias, P.V. and Coppens, Y. eds., *Les Plus Anciens Hominidés*, U.I.S.P.P., Nice. C.N.R.S., 120–137.
- JOHANSON, D.C. and COPPENS, Y. (1978). Paper presented to Nobel Symposium on "Current Argument on Fossil Man", Karlskoga (in press).
- JOHANSON, D.C. and TAIEB, M. (1976). Plio-Pleistocene hominid discoveries in Hadar, Ethiopia. *Nature*, Lond., **260**, 293–297.
- JOHANSON, D.C., WHITE, T.D. and COPPENS, Y. (1978). A new species of the genus *Australopithecus* (Primates: Hominidae) from the Pliocene of eastern Africa. *Kirtlandia*, **28**, 1–14.
- JOHANSON, D.C. and WHITE, T.D. (1979). A systematic assessment of early African hominids. *Science*, **202**, 321–330.
- LEAKEY, L.S.B., TOBIAS, P.V. and NAPIER, J.R. (1964). A new species of the genus *Homo* from Olduvai Gorge. *Nature*, Lond., **202**, 7–9.
- LEAKEY, M.D., HAY, R.L., CURTIS, G.H., DRAKE, R.E., JACKES, M.K. and WHITE, T.D. (1976). Fossil hominids from the Laetolil Beds. *Nature*, Lond., **262**, 460–466.
- LEAKEY, R.E.F. (1973). Evidence for an advanced Plio-Pleistocene hominid from East Rudolf, Kenya. *Nature*, Lond., **242**, 447–450.
- — — (1976). Hominids in Africa. *Amer. Scientist*, **64**, 174–178.
- LEAKEY, R.E.F., LEAKEY, M.G. and BEHRENSMEYER, A.K. (1978). The hominid catalogue. In: Leakey, M.G. and R.E.F., eds., *Koobi Fora Research Project*, Vol. **1**, Oxford, Clarendon Press, 86–182.
- McFADDEN, P.L., BROCK, A. and PARTRIDGE, T.C. (1979). Palaeomagnetism and the age of the Makapansgat hominid site. *Earth Planet. Sci. Lett.*, **44**, 373–382.
- MAGLIO, V.J. (1973). Origin and evolution of the Elephantidae. *Trans. Amer. Phil. Soc.*, n.s. **63**, 1–149.
- MAYR, E. (1970). *Populations, Species and Evolution*. Cambridge, Mass., Harvard University Press, 1–453.
- MIJSBERG, W.A. (1931). On sexual differences in the teeth of the Javanese. *Konink. Akad. Wetensch.*, Amsterdam, **34**, 1111–1115.
- OAKLEY, K.P., CAMPBELL, B.G. and MOLLESON, T.I., eds. (1977). *Catalogue of Fossil Hominids. Part I: Africa* (2nd ed.). London, British Museum (Nat. Hist.), 1–223.
- OXNARD, C.E. (1975). The place of the australopithecines in human evolution, grounds for doubt? *Nature*, Lond., **258**, 389–395.
- PALAEOANTHROPOLOGY CORRESPONDENT (1979). Difficulties in the definition of new hominid species. *Nature*, Lond., **278**, 400–401.
- PARTRIDGE, T.C. (1978). Re-appraisal of lithostratigraphy of Sterkfontein hominid site. *Nature*, Lond., **275**, 282–287.
- — — (1979). Re-appraisal of lithostratigraphy of



- Makapansgat Limeworks hominid site. *Nature*, Lond., **279**, 484-488.
- ROBINSON, J.T. (1954). The genera and species of the Australopithecinae. *Am. J. phys. Anthrop.*, **12**, 181-200.
- (1956). The dentition of the Australopithecinae. *Mem. Transv. Mus.*, **9**, 1-179.
- (1966). Comment on "The distinctiveness of *Homo habilis*". *Nature*, Lond., **209**, 957-950.
- TOBIAS, P.V. (1967). Olduvai Gorge, Vol. 2, *The Cranium and Maxillary Dentition of Australopithecus (Zinjanthropus) boisei*. Cambridge University Press, 1-264.
- (1969). Commentary on new discoveries and interpretations of early African fossil hominids. In: Genoves, S., ed., *Yearbook of Phys. Anthrop. 1967*, **15**, 24-30.
- (1973a). New developments in hominid paleontology in South and East Africa. *Ann. Rev. Anthrop.*, **2**, 311-334.
- (1973b). A new chapter in the history of the Sterkfontein early hominid site. *J. S. Afr. biol. Soc.*, **14**, 30-44.
- (1975). New African evidence on the dating and phylogeny of the Plio-Pleistocene *Hominidae*. In: Suggate, R.P. and Cresswell, M.M. Eds., *Quaternary Studies*, Bull. No. 13, Royal Society of New Zealand, Wellington, 289-296.
- (1976). Incomplete or delayed closure of the symphysis menti in early hominids and a possible mechanism. *Yugoslav Anthropol. Soc. Special Publications*, Vol. **3**, 23-32.
- (1978a). The place of *Australopithecus africanus* in hominid evolution. In: Chivers, D.J. and Joysey, K.A., Eds., *Recent Advances in Primatology*, Vol. **III**, *Evolution*. London, Academic Press, 373-394.
- (1978b). Position et rôle des australopithécins dans la phylogénèse humaine, avec étude particulière de *Homo habilis* et des théories controversées avancées à propos des premiers hominidés fossiles de Hadar et de Laetolil. In: *Les Origines Humaines et les Époques de l'Intelligence*. Paris, Masson, 38-77.
- (1979a). Olduvai Gorge, volume 4, *Homo habilis* (in preparation).
- (1979b). Recent palaeontological studies in southern Africa: new discoveries at Sterkfontein, 1968-1976. *Proc. IXth Congr. U.I.S.P.P., Nice* (in press).
- (1979c). *Australopithecus* and early *Homo*. *Proc. VIII Pan-Afr. Congr. Prehist. Quatern. Stud., Nairobi* (in press).
- (1979d). A survey and synthesis of the African hominids of the late Tertiary and early Quaternary periods. *Proc. 41st Nobel Symposium, Karlskoga* (in press).
- (1980). The natural history of the helicoidal occlusal plane and its evolution in early *Homo*. *Am. J. phys. Anthrop.*, **53**, 173-187.
- TOBIAS, P.V., COPLEY, K. and BRAIN, C.K. (1977). South African entries in *Catalogue of Fossil Hominids, Part I: Africa* (2nd edn.), Oakley, K.P., Campbell, B.G. and Molleson, T.I., Eds., London, Brit. Mus. (Nat. Hist.), 95-151.
- VRBA, E.S. (1974). Chronological and ecological implications of the fossil Bovidae at the Sterkfontein australopithecine site. *Nature*, Lond., **250**, 19-23.
- (1975). Some evidence of chronology and palaeoecology of Sterkfontein, Swartkrans and Kromdraai from the fossil Bovidae. *Nature*, Lond., **254**, 301-304.
- WALKER, A. and LEAKEY, R.E.F. (1978). The hominids of East Turkana. *Sci. Amer.* **239**, 54-66.
- WALLACE, J.A. (1975). Dietary adaptations of *Australopithecus* and early *Homo*. In: Tuttle, R.H., Ed., *Paleoanthropology, Morphology and Paleoecology*. The Hague, Mouton, 203-223.
- WHITE, T.D. (1977). New fossil hominids from Laetolil, Tanzania. *Am. J. phys. Anthrop.*, **46**, 197-230.
- WHITE, T.D. and HARRIS, J.M. (1977). Suid evolution and correlation of African hominid localities. *Science*, **198**, 13-21.
- WOLPOFF, M.H. (1971). Interstitial wear. *Am. J. phys. Anthrop.*, **34**, 205-228.
- (1975). Sexual dimorphism in the australopithecines. In: Tuttle, R.H., ed., *Paleoanthropology, Morphology and Paleoecology*. The Hague, Mouton, 245-284.
- (1976). Some aspects of the evolution of early hominid sexual dimorphism. *Curr. Anthrop.*, **17**, 579-606.
- (1979). Anterior dental cutting in the Laetolil hominids and the evolution of the bicuspid P<sub>3</sub>. *Am. J. phys. Anthrop.*, **51**, 233-234.