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TAXONOMIC STATUS OF THE SKULL A.L.444-2 FROM THE PLIOCENE OF HADAR, ETHIOPIA

by

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ABSTRACT

A nearly complete hominid skull, A.L.444-2, from the Pliocene of Hadar in Ethiopia, has been attributed to *Australopithecus afarensis* Johanson, White & Coppens 1978. Comparative morphological analysis indicates that it may not conform to this species. Cranial and dental morphology and measurements of A.L.444-2 agree more closely with those of *A. africanus* Dart 1925, to which it could be reassigned.

KEYWORDS: "*Australopithecus afarensis*"; *Australopithecus africanus*; Hadar.

INTRODUCTION

In 1980 Tobias suggested that the Hadar/Laetoli fossil hominoids which had been described as a new species, "*A. afarensis*", might rather belong to *A. africanus*. Several authors have since questioned the validity of "*A. afarensis*" as representing a single species (Leakey 1981; Ferguson 1983, 1986, 1987, 1989, 1992a,b; Schmid, 1983; Falk & Conroy 1983; Olson 1985; Zihlman 1985; Senut & Tardieu 1985, Shipman 1986).

A complete skull of "*A. afarensis*" was not found and so a composite skull was reconstructed by White (Johanson & Edey 1981). A new fossil skull, A.L.444-2, dated at 3 Myr from Hadar, has been identified as belonging to a male "*A. afarensis*" (Kimbel *et al.* 1994). Its identification was based primarily on mandibular, facial and calvarial features without a detailed analysis of the dentition, which is important in recognizing species.

Kimbel *et al.* (1994) assert that the morphology of A.L.444-2 is consistent with that of White's composite reconstruction of a purported male "*A. afarensis*" skull (Figure 1), and that it refutes suggestions that "*A. afarensis*" represents more than one species.

The purpose of this study is to test whether skull A.L.444-2 really confirms the validity of "*A. afarensis*" as a single species, or if it might conform more closely to *A. africanus*.

MATERIAL AND METHODS

A.L.444-2 comprises a partial mandible, right zygomatic, most of the nasal bones and frontal with attached anteromedial segments of the parietals, the left parietal, the occiput with attached posterior right parietal, and both temporals (Figure 1c; Kimbel *et al.* 1994). The anterior cranial base and most of both temporal squamae are missing. The frontal, maxilla and zygomatic are without contacts and their positions relative to each other are uncertain. There is post depositional deformation of the palate, which is compressed along the midline. The right side of the frontoparietal fragment and supraorbital are uplifted. The left zygomatic arch is twisted and the right elevated. The nuchal plane is pushed into the cranial cavity. The endocranial capacity has not yet been determined.

Dentition consists of the right mandibular fragmentary left and right incisors, partial right C and damaged P_4-M_1, the maxillary right I^1, C, P^4-M^3 and left I^1, C, P^3-M^3. Measurements have been obtained for the better preserved maxillary teeth, RC, LP^4, and LM^1-LM^3.

In this study A.L.444-2 is compared with White's composite reconstruction of "*A. afarensis*" and Sts 5 (representing *A. africanus* from Sterkfontein, South Africa) (Figure 1). The data used includes the same information used by Kimbel *et al.* (1994) in identifying A.L.444-2.

The problem in comparing A.L.444-2 with "*A. afarensis*" is that the hypodigm for the latter may comprise more than one species, denial not withstanding (Kimbel *et al.* 1994). Johanson & Taieb (1976) referred some specimens from Hadar to *A. aff. africanus*. In 1979, Johanson and White acknowledged that single specimens can be similar to specimens representing other species. Several specimens have features and measurements that conform to those of "*A. africanus*" (Tobias 1980; Ferguson 1987).

RESULTS AND DISCUSSION

According to Kimbel *et al.* (1994) the character complex of "*A. afarensis*" has a greater number of symplesiomorphies than in any species within the Australopithecinae, and that the attribution of A.L.444-2 to "*A. afarensis*" is "warranted by its primitive constellation of mandibular, facial and calvarial characters". Taxonomic assignment to a new species, however, is not usually based only on symplesiomorphic features, but also on apomorphic or derived characters (Mayr *et al.* 1953). The reason for

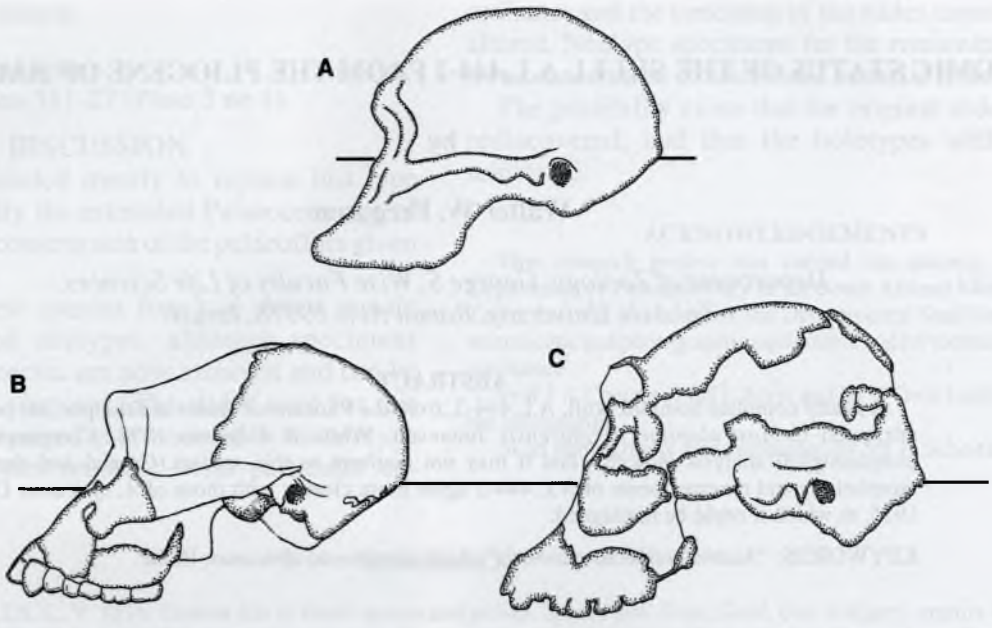


Figure 1: Hominid skulls (left *norma lateralis*). A) *A. africanus*, Sts 5, female; B) Composite reconstruction of male "*A. afarensis*" (after White); C) Reconstruction of male A.L.444-2 (reversed after Johanson & Edgar, 1996). Same relative scale.

the greater number of primitive features in "*A. afarensis*" may not be due so much to its early age, but the possibility that the hypodigm is comprised of pongid as well as hominid fossils (Ferguson 1983, 1986, 1992a,b).

In this study I wish to comment on the primitive mandibular and calvarial features on which Kimbel *et al.* (1994) base their identification of A.L.444-2 as belonging to "*A. afarensis*". Only a single dental feature is given to show its affinity to this "species".

1) Strong prognathism relative to both calvaria (no metrical expression given) and to the P^4-M^1 origin of the zygomatic process of the maxilla. *Comment*: prognathism is strong in *A. africanus* (Tobias 1967), especially in Sts 5.
2) P^4-M^1 origin of the zygomatic process of the maxilla. *Comment*: on "*A. afarensis*" it is also above P^4-M^1 (Kimbel *et al.* 1982); in *A. africanus* the origin of the zygomatic process is variable, above P^4 (Walker *et al.* 1986) or M^1 (Tobias 1967).
3) Marked projection of sagittally and transverse convex premaxilla anterior to the bicanine plane. *Comment*: this is also found in *A. africanus* (Tobias 1980).
4) Nasoalveolar clivus horizontally inclined. *Comment*: not diagnostic for "*A. afarensis*" (Johanson *et al.* 1978).
5) Extensive intranasal component of the premaxilla with step-down to nasal cavity floor. *Comment*: not diagnostic for "*A. afarensis*" (Johanson *et al.* 1978).
6) Inferior lateral nasal aperture margins sharp. *Comment*: this is sometimes found in *A. africanus* (Tobias 1967; Rak 1983).
7) "Canine fossae". *Comment*: such fossae are also found in *A. africanus* (Rak 1983).
8) Zygomaticoalveolar crests curved. *Comment*: this is speculation since the critical parts are missing; in *A. africanus* the crests are straight or slightly curved (Tobias 1967).
9) Palate flat anteriorly. *Comment*: in *Australopithecus* the palate is shallow anteriorly (Tobias 1991).
10) Diastemata 1^2-$\underline{C}$ + C-P_3. *Comment*: this is frequent or common in "*A. afarensis*" (Johanson *et al.* 1982), but not always present. Diastemata are rare in hominids (Le Gros Clark 1972).
11) Temporal lines posteriorly convergent. *Comment*: in "*A. afarensis*" temporal lines converge anteriorly (Johanson & White 1979); in *A. africanus* MLD 1 or MLD 37-38 from Makapansgat temporal lines coverage anteriorly (Tobias 1991).
12) A low, probably bifid, posterior saggital crest. *Comment*: this could occur in large *A. africanus* males (Tobias 1980, 1991).
13) Compound temporal/nuchal crest. *Comment*: this is also found in *A. africanus* (Tobias 1980).
14) Mastoid process massive and inflected beneath the cranial base with tips independent of occipital crests. *Comment*: Kimbel *et al.* (1994) make no mention of a flat posterolateral face as seen in "*A. afarensis*"; the mastoid process is well developed in known australopithecines (Le Gros Clark 1963); rather small in [female] *A. africanus* (Tobias 1991), but would be larger in males. Inferomedial inflection is not diagnostic for "*A. afarensis*" (Johanson *et al.* 1978).
15) Mandibular fossa shallow. *Comment*: it is also shallow in *H. habilis* and *A. africanus* (Tobias 1991), and in KNM-WT 17000 (Walker *et al.*

1986) attributed to "*A. aethiopicus* Arambourg & Coppens 1968", but described as a new species, *A. walkeri* Ferguson 1989.

16) Tubular tympanic plates that sit completely posterior to large postglenoid process. *Comment*: according to Walker *et al.* (1986), the postglenoid in KNM-WT 17000 is anterior to tympanic; in *A. africanus* the tympanic is intermediate and the position of the postglenoid process is variable (Walker *et al.* 1986); the feature is not diagnostic for "*A. afarensis*" (Johanson *et al.* 1978).

17) Maxillary incisors procumbent. *Comment*: this feature is not indicated in "*A. afarensis*" A.L.333-2 (Kimbel *et al.* 1982), and not diagnostic for the species (Johanson *et al.* 1978).

Mandible

Sexual differences in *H. sapiens* are more marked in the mandible than in the cranium (De Villiers 1963). The same may be true in Plio-Pleistocene hominids. Mandibles of presumed males in "*A. afarensis*" are much larger than those attributed to females of the same species, reflecting a high degree of sexual dimorphism (Johanson & White 1979). White (Johanson & Edey, 1981) argues that there is no difference between the large and small jaws from Hadar due to continuous variation. This argument is distorted and undermines the reality of differences between them. Since there is no sharp division, it is claimed there are no differences.

The variation in mandibular corpus robusticity (height/breadth index) in "*A. afarensis*" ranges from 45.5-63.8 per cent, which suggests distinct sexual dimorphism, yet the index of the male A.L.444-2-b (50.9 per cent) is virtually the same as that of the "female" A.L.417-1a (50 per cent). The lack of difference in robusticity between these two specimens does not support strong sexual dimorphism, but may indicate similar robusticity in males of two different-sized species (Table 1).

TABLE 1.
Mandible corpus metrics and index of robusticity of A.L.444-2b compared to those of "*A. afarensis*".

Hominids	Breadth (mm)	Height (mm)	Robusticity (%)
A.L.444-2b	22.0	43.2	50.9
"*A. afarensis*"			
A.L.417-1a.	18.0	36.0	50.0
Hadar sample 1970s	n=13	n=11	n=11
Range	15.6-22.4	28.0-40.5	45.5-63.8

Measured at P_4/M_3 position. Metrics after Kimbel *et al.* (1994).

In *Australopithecus* large, broad teeth are related to large masseter muscles which, in turn, are related to large, high, ascending mandibular rami (Pilbeam, 1972). A.L.444-2 is the largest *Australopithecus* cranium on record (Kimbel *et al.* 1994). The back teeth (P^4-M^3) of A.L.444-2 are 824.80 mm^2, distinctly larger than the maximum for "*A. afarensis*", 708.6 mm^2, and larger than the maximum for *A. africanus*, 733.8 mm^2. It is safe to infer that the ascending ramus of A.L.444-2 would have been at least as large as the maximum for "*A. afarensis*" and within the range of. *A africanus*. The ascending ramus of the female A.L.288-1 is within the lower range of *H. sapiens* (Kimbel *et al.* 1984). If A.L.444-2 and A.L.288-1 were conspecific as claimed, the range of sexual dimorphism of the ascending ramus height in "*A. afarensis*" (31.0-55.0) exceeds those of *A. robustus* (57.0-64.0), *A. boisei* (47.0-65.0) and *H. sapiens* (30.3-41.0).

Endocranial capacity

Tobias (1991) gives the 95 per cent limits of population range of "*A. afarensis*" as 352 - ?493 cm^3, mean ?413.5 cm^3, and *A. africanus* as 391 - 492 cm^3, mean 441.2 cm^3. With the maximum virtually the same, but the mean of *A. africanus* distinctly larger, we may assume that the maximum of *A. africanus* is probably larger than that of "*A. afarensis*". The endocranial capacity of A.L.444-2 probably exceeded 500 cm^3 (Johanson 1996), larger than in "*A. afarensis*".

Frontal

Kimbel *et al.* (1994) note that the frontal is a taxonomically important region, and that "*A. afarensis*" has many primitive features. The frontal in A.L.444-2, however, is not primitive. The supraorbital torus is vertically thick laterally and the low squama and supraorbital sulcus are unlike those of a chimpanzee. As in *A. africanus*, it has no frontal

TABLE 2.
Selected cranial metrics of fossil hominids.

	Postorbital constriction	Biasterionic breadth chord	Difference between max. & min.
A.L.444-2	77.0	106.0	
"*A. afarensis*"			26.8
A.L.162-28	-	79.2	
A.L.333-45	-	94.5	
A. africanus			10.0
MLD 1	-	85.0	
MLD 37/38	-	79.5	
Sts 5	65.5	76.0	
Sts 25	-	?77.0	
Sts 71	71.5	c86.0	
A. boisei			10.8
OH5	-	89.2	
KNM-ER 406	-	c100.0	
H. habilis			24.0
OH 13	-	84.0	
OH 16	75.5	c108.0	
OH 24	74.2	c96.0	
KNM-ER 1470	c80.0	c99.0	
H. erectus			17.0
	-	?113.0-130.0	

Metrics for "*A. afarensis*" after Kimbel *et al.* (1981); A.L.444-2 after Kimbel *et al.* (1994). The rest after Tobias (1967, 1991).

trigon, but the postorbital constriction is as advanced as in *H. habilis* (Table 2).

The postorbital constriction in *H. habilis* is described as moderately developed (Howell 1972). Since the postorbital constriction of A.L.444-2 falls within the range of *H. habilis*, and is greater than in known *A. africanus* (Tobias 1991), it indicates brain expansion, unlike "*A. afarensis*".

Biasterionic breadth

The biasterionic chord breadth gives a good measure of the capacity of the posterior part of the endocranium (Tobias 1991). Although "*A. afarensis*" is supposedly ancestral to *A. africanus* and shows no brain expansion, its biasterionic breadth is on average greater than that of *A. africanus*. This may be due to a sampling error since there are only two values for "*A. afarensis*" and the *A. africanus* sample is mostly females. The biasterionic breadth of A.L.444-2 falls in between *A. africanus* and *H. habilis* (Table 2), and clearly indicates endocranial expansion.

Johanson claims that the brain of "*A. afarensis*" is comparable in size to that of chimpanzees (Johanson & Edey 1981). The marked transverse expansion of the frontal and biasterionic breadth in A.L.444-2 indicates brain expansion greater than that of chimpanzees.

Frontobiorbital breadth index

The frontobiorbital breadth index is the postorbital breadth (constriction) in relation to superior facial breadth. The value for the frontobiorbital index in A.L.444-2 is higher than in any australopithecine or *H. habilis* crania for which data are tabulated, and closest to that of *H. habilis* (Table 3). The index for "*A. afarensis*" is unknown.

Zygomatic

In A.L.444-2 the enormous face, large, flaring cheekbones, and the bone shelf that reflects massive chewing muscles are typical of a 'robust' hominid (McAuliffe 1994). Large, flaring zygomatics are an advanced, not primitive, feature that characterizes the australopithecine lineage, including the least 'robust' member, *A. africanus*. There is no evidence or reason to believe that this specialization arose twice independently in different genera. Its presence in A.L.444-2 is clear evidence of its position early on a 'robust' branch of the Hominidae and more advanced than "*A. afarensis*". It is inconsistent with the claim that "*A. afarensis*" is the most primitive and undifferentiated of hominids (Johanson & White 1979).

Two new species of hominoids older and more primitive than "*A. afarensis*" have recently been described. The first, *Ardipithecus ramidus* (White, Suwa & Asfaw, 1994) from Ethiopia, was mistakenly classified as an *Australopithecus*, but is generally regarded as an ape and was renamed. The second is *Australopithecus anamensis* Leakey, Feibel, McDougall & Walker, 1995 from Kenya, whose holotype is an *apelike* jaw and teeth. To my mind, the only evidence for its being a hominid is a partial tibia anatomically *unassociated* with the jaws and teeth.

TABLE 3.
Frontobiorbital breadth index of hominids.

Hominids	per cent
A.L.444-2	80
A. africanus	
Sts 5	c63.4
A. robustus	
SK 48	c71.7
A. boisei	
KNM-ER 732	65.2
KNM-ER 406	56.0
OH 5	60.1
H. habilis	
OH 24	c74.2

After Tobias (1991); A.L.444-2 after Kimbel *et al.* (1994).

TABLE 4.
Dental metrics of A.L.444-2 compared to those of "*A. afarensis*" and *A. africanus*.

Hominids	C	P^3	P^4	M^1	M^2	M^3
A.L.444-2						
M/D*	10.4	-	10.6	13.7	14.2	14.9
B/L	11.5	-	14.5	15.0	15.8	16.2
"*A. afarensis*"						
M/D	8.9-11.6	7.2- 9.3	7.6- 9.7	10.8-13.7	12.1-13.5	11.4-14.3
B/L	9.3-12.5	9.8-13.4	11.1-12.6	11.2-15.0	13.4-15.0	13.1-15.55
A. africanus						
M/D	8.8-11.2**	8.5-10.0	8.2- 9.9	11.0-14.4	12.7-16.0	11.6-16.4
B/L	8.7-11.8**	10.7-14.5	12.4-13.8	12.6-15.	13.8-18.0	13.9-18.2

*Estimated (Kimbel *et al.*, 1994). *A. africanus* after Tobias (1991).
** Estimated for Sts 3 by Robinson (1956). A.L.444-2 after Kimbel *et al.* (1994); "*A. afarensis*" after Johanson & White (1979).

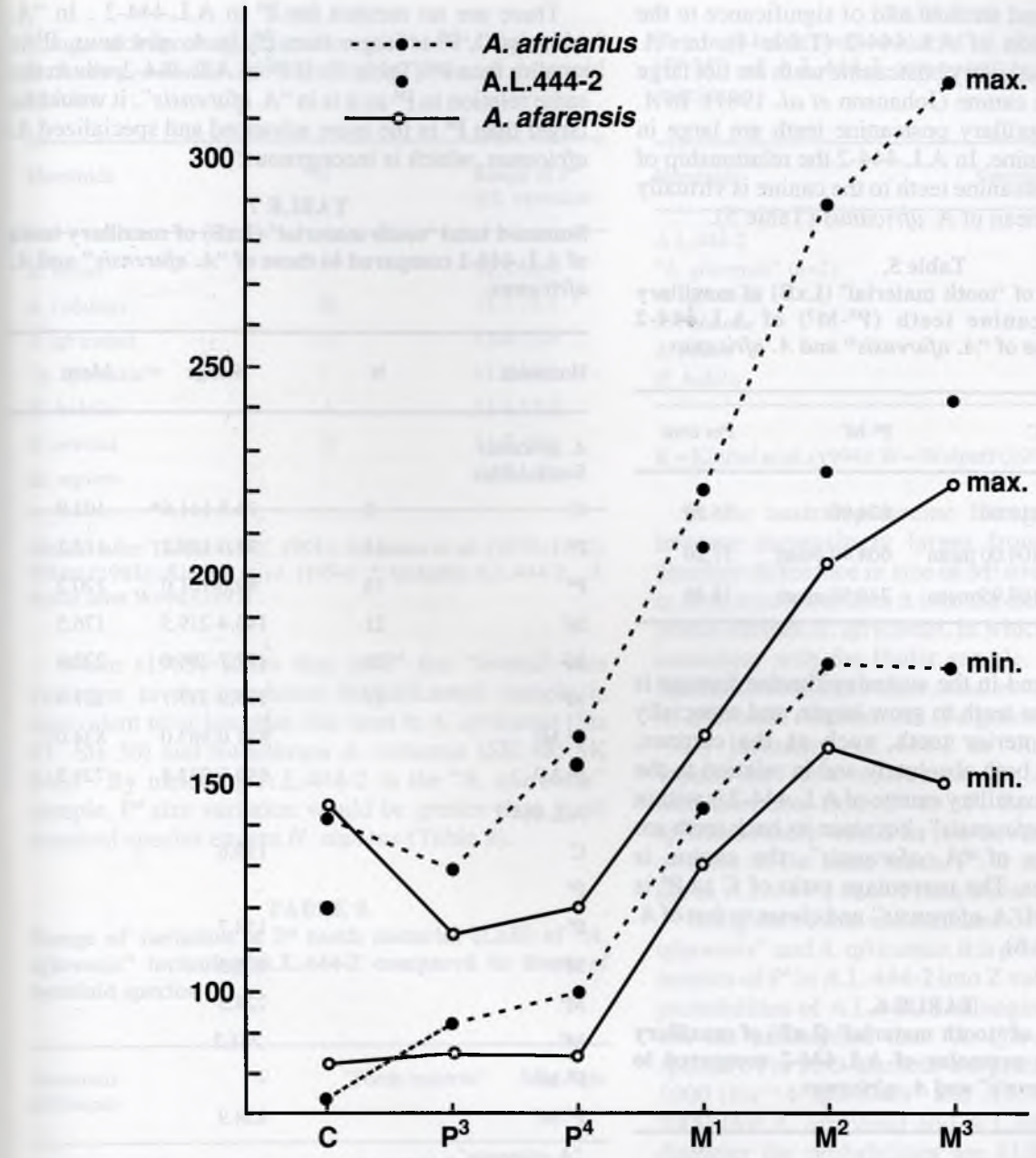


Figure 2: Graphs of maxillary 'tooth material' (C-M^3) of A.L.444-2 compared to the range of variation of *A. africanus* and "*A. afarensis*". Note that A.L.444-2 is in the upper range of *A. africanus*, whereas P^4-M^3 are above the maximum for "*A. afarensis*".

Maxilla

The maxilla and zygomatic fragments of A.L.444-2 are without contacts. In the preliminary reconstruction of A.L.444-2 the maxilla shows greater facial prognathism than in the composite reconstruction of "*A. afarensis*". It seems to be oriented incorrectly, thus creating an apelike nasoalveolar contour and an occlusal line that is unnaturally convergent with the Frankfort Horizontal anteriorly, as in the composite reconstruction of "*A. afarensis*" (Ferguson 1983). If the maxilla would be restored so that the nasoalveolar profile was straighter, then the occlusal line would take its natural, more horizontal inclination and there would be less facial prognathism.

Similarly, the zygomatic has been restored so that in relation to the maxilla the zygomaticoalveolar crest would be curved. Since the critical part is missing, it could just as well have been restored with the zygomaticoalveolar crest straight or slightly curved.

Dentition

Dentition is particularly important in hominid taxonomy. It is surprising, therefore, that apart from noting that the incisors are procumbent, the dentition of A.L.444-2 is dismissed in a single sentence by Kimbel *et al.* (1994) stating, "although the maxillary postcanine teeth are larger than any of those in the limited Hadar and Laetoli sample from the 1970s, relative to canine size they are not unusual". This is not true (Figure 2). The upper postcanine teeth are not only larger than those of "*A. afarensis*" in all M/D and B/L metrics except M^1, but are large in relation to the

canine, thus indeed unusual and of significance to the systematic position of A.L.444-2 (Table 4). In *"A. afarensis"*, the maxillary postcanine teeth are not large in relation to the canine (Johanson *et al.* 1981). In *A. africanus* the maxillary postcanine teeth are large in relation to the canine. In A.L.444-2 the relationship of the maxillary postcanine teeth to the canine is virtually identical to the mean of *A. africanus* (Table 5).

Table 5.
Percentage ratio of 'tooth material' (LxB) of maxillary canine to postcanine teeth (P^4-M^3) of A.L.444-2 compared to those of *"A. afarensis"* and *A. africanus*.

Hominids	C	P^4-M^3	Per cent
A.L.444-2	119.60	824.80	14.50
"A. afarensis"	104.00 mean	604.49 mean	17.20
A. africanus	107.95 mean	746.50 mean	14.46

The dental trend in the australopithecine lineage is for the postcanine teeth to grow larger, and especially broader. The anterior teeth, such as the canines, become smaller, both absolutely and in relation to the back teeth. The maxillary canine of A.L.444-2 is within the range of *"A. afarensis"*, but since its back teeth are above the range of *"A. afarensis"*, the canine is relatively smaller. The percentage ratio of C to P^4 is well below that of *"A. afarensis"* and closer to that of *A. africanus* (Table 6).

TABLE 6.
Percentage ratio of 'tooth material' (LxB) of maxillary canine to fourth premolar of A.L.444-2 compared to those of *"A. afarensis"* and *A. africanus*.

Hominids	C	P^4	Per cent
A.L.444-2	119.6	153.7	77.8
"A. afarensis" Hadar	104.0	100.4	96.0 mean
A.L.199-1	82.7	84.3	98.1
A.L.200-1a	102.5	101.2	101.2
A.L.333-1	124.0	112.8	90.9
A.L.333-2	(?)106.8	113.4	94.1
A. africanus	74.3-141.6	96.6 mean	85.0* mean

Tobias (1967; Table 37) gives the mean for *A. africanus* at 77.0; *A. africanus* after Wolpoff (1978). * Estimated by Robinson (1956:44).

There are no metrics for P^3 in A.L.444-2 . In *"A. afarensis"*, P^3 is larger than P^4. In *A. africanus*, P^3 is smaller than P^4 (Table 7). If P^3 in A.L.444-2 was in the same relation to P^4 as it is in *"A. afarensis"*, it would be larger than P^4 in the more advanced and specialized *A. africanus*, which is incongruous.

TABLE 7.
Summed total 'tooth material' (LxB) of maxillary teeth of A.L.444-2 compared to those of *"A. afarensis"* and *A. africanus*.

Hominids	N	Range	Mean
A. africanus South Africa			
C	7	74.3-141.6*	102.9
P^3	15	92.0-129.2	112.7
P^4	13	99.6-161.0	120.2
M^1	21	143.4-219.5	176.5
M^2	20	177.7-288.0	222.4
M^3	17	177.0-317.7	227.4
P^3-M^3		811.0-863.0	834.0
P^4-M^3		599.6-733.8	721.3
A.L.444-2			
C		119.6	
P^3		-	
P^4		153.7	
M^1		205.5	
M^2		224.3	
M^3		241.3	
P^3-M^3		-	
P^4-M^3		824.9	
"A. afarensis"			
C	10	82.7-145.0	113.8
P^3	7	84.7-124.6	107.8
P^4	6	84.3-119.7	104.1
M^1	9	129.6-162.2	145.9
M^2	3	158.1-210.8	184.4
M^3	5	149.3-215.9	182.6
P^3-M^3		606.0-833.2	724.8
P^4-M^3		521.3-708.6	617.0

Metrics of *A. africanus* after Wolpoff (1978); * Estimated by Robinson (1956); A.L.444-2 after Kimbel *et al.* (1994); *"A. afarensis"* after Johanson *et al.* (1979, 1982).

The buccolingual diameter of P^4 in A.L.444-2 is not only broader than the maximum for *"A. afarensis"* (Table 4), it even reaches the minimum of the range of variation for *A. boisei*, the most specialized of all australopithecines (Table 8).

TABLE 8.
Range of buccolingual metrics of P^4 of "*A. afarensis*" including A.L.444-2 compared to those of hominid species.

Hominids	N	Range of P^4 B/L variation
A. boisei	7	14.3-18.0
A. robustus	20	13.7-16.5
A. africanus	11	12.4-13.9
"*A. afarensis*"*	7	11.1-14.5
H. habilis	4	11.4-12.5
H. erectus	12	11.0-12.3
H. sapiens	-	8.5-10.1

Metrics after Tobias (1967, 1991); Johanson *et al.* (1979, 1982); White (1985); Kimbel *et al.* (1994). * Includes A.L.444-2 . *A. boisei* after Wood (1991).

White (1985) states that in P^4 the "overall size variation in the combined Hadar/Laetoli sample is equivalent to or less than that seen in *A. africanus* (Sts 47; Sts 30) and Swartkrans *A. robustus* (SK 48; SK 845)". By including A.L.444-2 in the "*A. afarensis*" sample, P^4 size variation would be greater than in all hominid species except *H. sapiens* (Table 9).

TABLE 9.
Range of variation of P^4 tooth material (LxB) of "*A. afarensis*" including A.L.444-2 compared to those of hominid species.

Hominids difference	N	'Tooth material'	Max-Min
"*A. afarensis*"*	5	84.3-153.7	69.4
A. africanus	13	99.6-161.0	61.4
A. robustus	30	112-5-181.0	65.5
A. boisei	5	150.9-208.9	58.0
H. habilis Olduvai	10	91.7-103.7	12.0
H. sapiens modern	318	38.5-109.8	71.3

Metrics for "*A. afarensis*" Johanson *et al.* (1979, 1982); * Includes A.L.444-2. *H. habilis* after Tobias (1991); The rest after Wolpoff (1978).

In the primitive "*A. afarensis*" the postcanine teeth average smaller than in *A. africanus*. The back teeth of A.L.444-2, however, are not only significantly larger than in "*A. afarensis*", they are well above the mean for *A. africanus* and even slightly above the mean for *A. robustus* (Table 10), but within the range of *A. africanus* (Table 7).

TABLE 10.
Summed total 'tooth material' (LxB) of maxillary teeth (P^4-M^3) of A.L.444-2 compared to those of hominid species.

Hominids	Summed crown areas (P^4-M^3)
A.L.444-2	824.8[K]
"*A. afarensis*" (n=2)	604.49 mean[K]
A. africanus	746.5 mean[W]
A. robustus	798.5 mean[W]
A. boisei	1161.3 mean[W]
H. habilis	681.24 mean[T]

K = Kimbel *et al.* (1994); W = Wolpoff (1978); T = Tobias (1991).

In the australopithecine lineage molars tend to become increasingly larger from M^1 to M^3. The absolute difference in size of M^2 over M^1 in A.L.444-2 is 18.8, much less than it is in the mean of the nominate South African *A. africanus*, in which it is 45.9. This is consistent with the Hadar sample, part of which has been described as an older, smaller-toothed subspecies, *A. africanus miodentatus* (Ferguson 1987).

By including A.L.444-2 in "*A. afarensis*" there would be new extremes in six out of eight measurements from P^4 to M^3. By including it in *A. africanus* there would be two new extremes, and both of them in the same tooth, P^4. It is obvious to which taxon A.L.444-2 shows the closest dental affinity.

Using the means and standard deviation of P^4 of "*A. afarensis*" and *A. africanus*, it is possible to convert the metrics of P^4 in A.L.444-2 into Z values which give the probabilities of A.L.444-2 belonging to either species (on the assumption that "*A. afarensis*" is a single species). For M/D diameter the probabilities are 11.9 in 1000 (for "*A. afarensis*" and A.L.444-2) and 0.47 in 1000 (for *A. africanus* and A.L.444-2). For the B/L diameter the probabilities are 11.9 in 1000 (for "*A. afarensis*" and A.L.444-2) and 1 in 1000 (for *A. africanus* and A.L.444-2). It may be concluded that on the basis of the standard deviation, it is most improbable that A.L.444-2 belongs to either taxon. One must take into account if the sample of "*A. afarensis*" is not homogenous, the results could be skewed.

In this case the statistics appear to contradict morphological facts. "*A. afarensis*" is claimed to be one of the most primitive of hominids, more primitive than *A. africanus*. In the dentition of A.L.444-2, however: 1) the canine is small in relation to the back teeth; 2) the buccolingual expansion clearly indicates advanced specialization; 3) the buccolingual diameter of P^4 is greater than the maximum known for *A. africanus*; and 4) the very large postcanine teeth reached a stage of molarization greater than in "*A. afarensis*", but within the upper range of *A. africanus*. The dentition of A.L.444-2, therefore, cannot be considered more primitive than in *A. africanus*.

Sexual dimorphism

In *Australopithecus* there is little sexual dimorphism in the size of the back teeth (Robinson 1956). By including A.L.444-2 in "*A. afarensis*", the maximum sexual difference in P^4 would be distinctly greater than in all *Australopithecus* species and closest to that of modern *Homo* (Table 9).

The maximum sexual difference in the post canine teeth (P^4-M^3) of *A. africanus* is 18.3 per cent. In "*A. afarensis*" it is 26.5 per cent without A.L.444-2. The difference between the male A.L.444-2 and the female "*A. afarensis*" A.L.199-1 is a surprising 35.8 per cent. In other words, by including A.L.444-2 in "*A. afarensis*" the sexual dimorphism in the back teeth would be as much as *twice* that of *A. africanus*.On the basis of sexual dimorphism, the back teeth of A.L.444-2 are much too big to belong to the same taxon as A.L.199-1.

Johanson notes that in A.L.444-2 a number of teeth are heavily worn, right down to the dentine, although the individual was only in its thirties at the time of death (McAuliffe 1994). This is inconsistent with the teeth of "*A. afarensis*" A.L.200-1a which, although also an adult, possesses teeth that are not worn flat. The heavily worn teeth of A.L.444-2 are, however, consistent with the moderately rapid rate of flat plane attrition in *A. africanus* (Tobias 1991).

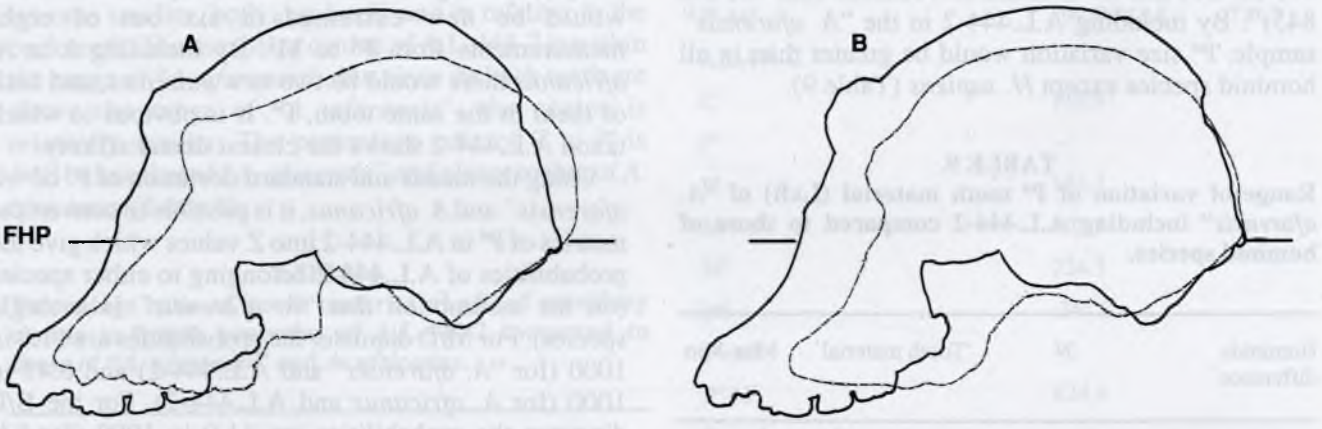


Figure 3: A) The skull A.L.444-2 (thick line) superimposed on composite reconstruction of "*A. afarensis*" (broken line). Drawn approximately to same calvarial length (left *norma lateralis*). Note total non-conformity of overall profile.
B) Male A.L.444-2 (thick line) superimposed on female *A. africanus*, Sts 5 (broken line). Drawn approximately to same relative scale. Note overall similarity of contour allowing for sexual dimorphism.

The composite reconstruction of the skull of "*A. afarensis*"

The new skull A.L.444-2 which supposedly belongs to "*A. afarensis*", does not look like White's composite reconstruction of the skull of "*A. afarensis*". Kimbel *et al.* (1994:449) get around this by saying it "is consistent with the major components" in the reconstruction. This is true insofar as the facial fragment A.L.333-1 is concerned, and that fragment may represent *A. africanus*.

A contour drawing of the skull of A.L.444-2 has been superimposed on the contour of the composite reconstruction of "*A. afarensis*" and on the contour of *A. africanus*, Sts 5, for the purpose of non-metric morphological comparison (Figure 3). The differences between A.L.444-2 and "*A. afarensis*" are striking. A.L.444-2 differs in proportion in the following ways:

1) there is a distinct forehead;
2) the vertex is relatively higher;
3) the occipital is flatter posteriorly (post-depositional deformation);
4) the nuchal plane is not concave, but pushed into the cranial cavity;
5) the face is much deeper and somewhat "dish-shaped";
6) there is greater alveolar prognathism.

When A.L.444-2 is superimposed on a presumed female *A. africanus*, Sts 5, there is overall morphological identity except for size, which can be attributed to a difference in sex. The zygomatic of A.L.444-2 is indeed consistent with the facial fragment A.L.333-1 of the composite in "*A. afarensis*" in its large, flaring zygomatics (greater than in *A. africanus*, Sts 5), broad region of the temporal process of the zygomatic, inferoanterior infraorbital region, and origin of the maxillary process of the zygomatic, all of which conforms with the specialized morphology of *A. africanus*. Unlike *Pan* and *Homo*, it manifestly does not represent the most generalized facial morphology of all hominids as claimed for "*A. afarensis*".

Since there was no complete skull of "*A. afarensis*", a composite reconstruction was made of 12 unassociated parts. Ferguson (1983) suggests that the reconstruction is a synthesis of hominid and pongid fossils. Shipman (1986) thought the reconstruction might belong to two different hominid species, the calvaria to a robust one, and the face to one that is gracile. It was then suggested that the calvaria did not belong to a hominid at all, but to a pongid (Ferguson 1992b), the face to *A. africanus* (Ferguson 1987), and

the jaws mostly from a pongid (Ferguson 1983). Either White's composite reconstruction of "*A. afarensis*" is wrong, or A.L.444-2 does not belong with "*A. afarensis*", or both.

Phylogeny

The skull of A.L.444-2 has been dated at 3 Myr, about 200 000 years younger than the earliest "*A. afarensis*" (Kimbel *et al.* 1994). It is thus synchronic with *A. africanus* from South Africa, dated at 3± 2.6 Myr (Vrba 1985). "*A. afarensis*" is supposedly ancestral to *A. africanus*, yet A.L.444-2 is coeval with *A. africanus*. Kimbel *et al.* (1994) fail to explain this discrepancy. The dating of A.L.444-2 is consistent with the dating of *A. africanus*, especially since an East African taxon, *A. africanus miodentatus* was described from the same location at 3.5 - 3 Myr (Ferguson 1987).

In view of the fact that A.L.444-2 is morphologically outside the range of variation for "*A. afarensis*" and is 200 000 years younger, it might be considered a temporal variant. Kimbel *et al.*(1994) state that the Hadar specimens range from 3.4 - 3 million years in age. They then claim that it constitutes "evidence for about 0.9 million years of stasis in the earliest known hominid species". If A.L.444-2 supposedly represents "*A. afarensis*" and the species was in stasis for almost a million years, it would have to be the same morphologically as earlier "*A. afarensis*", and it is not. A.L.444-2 had already reached the *A. africanus* level of development so it cannot be a temporal variant of "*A. afarensis*".

CONCLUSION

Until recently *A. africanus* was known mainly from female skulls. There is a large male cranium of *A. africanus*, Stw 505 from Member 4, Sterkfontein, but it has not yet been described (Tobias pers. comm.).

In the evolution of *Homo*, the gracile condition is the more advanced, and since the female is more gracile than the male, the female cranium is more advanced than that of the male (Wilfram, 1956). It is manifest that the robust features in a male, the stronger supraorbital ridge, the larger face and bigger canines are primitive features. The very large male skull, A.L.444-2, with more robust features than those of a gracile female *A. africanus*, were apparently mistaken as belonging to a more primitive species.

In this study the skull of A.L.444-2 has been compared morphologically with "*A. afarensis*" in order to determine if it indeed belongs with that taxon as claimed. Thirteen out of seventeen symplesiomorphic features on which the identification of A.L.444-2 as "*A. afarensis*" was based, are shared by *A. africanus*, and thus not diagnostic. The remaining four are not known from *A. africanus*, but neither are they new diagnostic characters for "*A. afarensis*". Before new characters can be added to an original diagnosis, it must be absolutely certain that they represent the same species. The diagnostic characters of "*A. afarensis*" were not based on a single holotype, but on unassociated fragments assumed to belong to the same species. In taxonomy this is a very risky thing to do, as the unassociated fragments might belong to more than one species. Such, in fact, is the case with the composite of "*A. afarensis*", in which the jaw A.L.200-1a belongs to a pongid (Ferguson 1983), the face A.L.333-1 to *A. africanus* (Ferguson 1987), and the partial calvaria A.L.333-45to a pongid (Ferguson 1992).

In a comparison of contours of the crania A.L.444-2 and the composite reconstruction of "*A. afarensis*", the proportions are different and there is no morphological identity. The skull A.L.444-2, however, is comparable to the presumed female *A. africanus*, Sts 5, apart from being larger and more robust. Several calvarial and dental features in A.L.444-2 are inconsistent with the preserved parts of the composite skull of "*A. afarensis*". Metrics and indices of A.L.444-2 are outside the range of variation for "*A. afarensis*".

The dentition of A.L.444-2 is not primitive as claimed for "*A. afarensis*". Measurements of the postcanine dentition (P^4-M^3), except for M^1, are outside the range of variation for "*A. afarensis*", but fall within the upper range of *A. africanus*. Six mesiodistal and buccolingual metrics exceed the maximum for "*A. afarensis*", and are above the mean for *A. africanus*. In "*A. afarensis*" the upper canine is about the same size as P^4 and relatively large compared to the back teeth. In A.L.444-2 , the upper canine is smaller than P^4, and relatively small compared to the back teeth, as in *A. africanus*. Unlike A.L.200-1a, there is no incurvature of M^3. The postcanine teeth indicate flat-plane attrition. Clearly the dentition of A.L.444-2 is not the most generalized yet documented for any unequivocal hominid; rather it should be considered as highly specialized.

Kimbel *et al.* (1994) recognize "*A. afarensis*" as a valid, single species. They then claim that A.L.444-2 belongs with "*A. afarensis*" and that it therefore confirms the unity of the species. An argument that includes the conclusion it hopes to prove as one of its premises is circular. The premise is that "*A. afarensis*" is a valid, single species. The argument could be considered fallacious.

A.L.444-2 had already reached the adaptive plane of *A. africanus* with certain metrics and indices beginning to fall within the range of a robust australopithecine, and thus cannot be conspecific with the more primitive "*A. afarensis*".

Since the morphological pattern of the mandible, cranium, and especially the dentition of A.L.444-2 is inconsistent with "*A. afarensis*", but conforms with *A. africanus*, it is suggested that A.L.444-2 be reassigned to the taxon *A. africanus*. Its apomorphic characters indicate it is early on the australopithecine lineage and the first nearly complete skull of a male *A. africanus* to be recorded from East Africa.

The skull A.L.444-2 has been dated at 3 Myr, within the time period ascribed to some specimens of *A. africanus*. This makes it highly improbable that "*A.*

afarensis" is ancestral to *A. africanus* and supports the determination that A.L.444-2 indeed belongs with *A. africanus*.

A.L.444-2 does *not* confirm the taxonomic unity of "*A. afarensis"* as claimed. There are three possibilities to explain the great variation in the hypodigm of "*A. afarensis":*

1) "*A. afarensis"* is an extremely variable unitary species;
2) "*A. afarensis"* is a composite "species" with *A. afarensis* and one or more other species included;
3) There is no "*A. afarensis"* at all, only other species.

The extreme morphological variation and apelike sexual dimorphism in "*A. afarensis"* are greater than in any species of the Hominidae, which suggests that more than one species is involved. "*A. afarensis"* cannot be one of a composite species unless it can be defined as a valid, new species after the other species are removed from the hypodigm. The true holotype of "*A. afarensis"* is the Garusi maxilla, not the lectotype LH-4 mandible, according to the International Rules of Zoological Nomenclature. The Garusi maxilla, included in the sample of "*A. afarensis"*, already has a name, *Praeanthropus africanus* (Weinert), 1950, which is valid, available and takes priority (Ferguson 1986). "*A. afarensis"* is, thus, an invalid replacement name for *P. africanus*. The mandible LH-4 and the Garusi maxilla are both from Laetoli and about the same geologic age. They are probably conspecific, but this cannot be demonstrated with any certainty as they are unassociated. If it can be shown that LH-4 is not conspecific with *P. africanus* then the name *afarensis* would be available and valid. It is, however, not an *Australopithecus,* but a pongid (Ferguson 1983).

An important point which has been overlooked is that all of the specimens from Hadar/Laetoli do not show the same degree of symplesiomorphic features. Some are apelike, some australopethecine, and some hominine. Due to their primitiveness and fragmentary nature they have been lumped together into a chimera and mistakenly named a single species, "*A. afarensis"*.

The cranial and dental morphology and metrics of A.L.444-2 once again confirm the existence of *A. africanus* at Hadar.

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