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TAXONOMIC STATUS OF THE PARTIAL CALVARIA A.L. 333-45 FROM THE LATE PLIOCENE OF HADAR, ETHIOPIA

by

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ABSTRACT

The taxonomic status of a partial calvaria, A.L. 333-45, from the late Pliocene of Hadar, in Ethiopia, classified as a hominid and paratype of "*Australopithcus afarensis*" Johanson, White and Coppens 1978 is reassessed. Its total morphological pattern and adaptive affinities agree with the Pongidae, and do not exhibit a single unequivocal hominid character. The evidence in fact suggests that A.L. 333-45 represents a relatively generalized ape, the only pongid calvaria known from the late Pliocene of Africa: and may be the first skull found of *Praeanthropus africanus* (Weinert), 1950. Moreover, this indicates that the fossils assigned to "*Australopithecus afarensis*" do not represent a single taxon: and that the reconstruction of the skull of a male "*A. afarensis*" seems to be a composite of pongid and hominid fossils.

INTRODUCTION

A partial calvaria, A.L. 333-45, from the Late Pliocene of Hadar, in Ethiopia, and assumed to be a hominid, is a paratype of "*Australopithecus afarensis*". Since there is no complete cranium in the collections from Hadar, a composite skull was reconstructed from 13 unrelated parts, including A.L. 333-45, the only and complete calvaria of a presumed male (Kimbel, White and Johanson, 1984).

Johanson and White claim that the Laetoli-Hadar specimens are distinct from apes and from any of the later hominids (Johanson and Edey 1981). "The small A.L. 162-28 cranium emerges as unique among hominids suggesting a common chimpanzee morphological pattern in *A. afarensis*" (Kimbel *et al.* 1984 p.369), yet it supposedly belongs to a "fully bipedal" hominid (Johanson and Edey 1981 p.274).

Washburn described "*A. afarensis*" as having "human bodies topped with heads of apes" (Johanson and Edey 1981p.353). Their heads, which are "more ape-shaped than human-shaped" (Johanson and Edey 1981p.275), exhibit eight features of the calvaria not found in hominids, and share only one derived feature with the robust australopithecines (Kimbel *et al.* 1984). Although Johanson and White observed that A.L. 333-45 fits neither *Homo* nor *Australopithecus* (Johanson and Edey 1981), it was classified as an unequivocal hominid and an *Australopithecus*. Olson (1981, 1985) claims that A.L. 333-45 has advanced basicranial features and represents a primitive robust australopithecine. He transferred it to the genus "*Paranthropus*", and called it "*Paranthropus africanus*", a new combination for *Praeanthropus africanus* (Olson 1981 p.118; Weinert 1950).

Kimbel *et al.* (1984, 1985) countered Olson's claim. They observed that African ape crania match the basal morphology of the A.L. 333-45 mastoid region, and that the overall morphology of this region is strikingly primitive.

In 1983, Ferguson suggested an alternative view, that A.L. 333-45 represents a generalized ape, and that *Praeanthropus africanus*, the Garusi maxilla from Laetoli, is an ape (Ferguson 1986). Kimbel *et al.* (1984) acknowledge that an apelike morphological pattern is indicated in "*A. afarensis*" crania, but nevertheless continue to regard A.L. 333-45 as hominid.

This study reassesses the morphological pattern of A.L. 333-45 in order to determine if the calvaria is indeed an unequivocal hominid, or rather, a relatively generalized pongid.

MATERIALS AND METHODS

The material examined consists of a cast of A.L. 333-45, a partial calvaria that lacks the frontal, most of the right parietal, and the basal portion of the occipital bone, and has only minor plastic deformation. It was described anatomically in detail by Kimbel *et al.* (1982) and reconstructed, except for the upwardly crushed left anterior part of the nuchal plane (Kimbel *et al.*1984). It is unassociated with any fossil dentition. Orientation of the nuchal plane in relation to the Frankfurt Horizontal (F.H.) is after Kimbel *et al.* (1984).

The non-correctable artificial asymmetry of the basicranial region is restored photographically by using a mirror image of the right part, which is undistorted and more complete, and a mirror image of the left occipital condyle which is slightly displaced laterally.

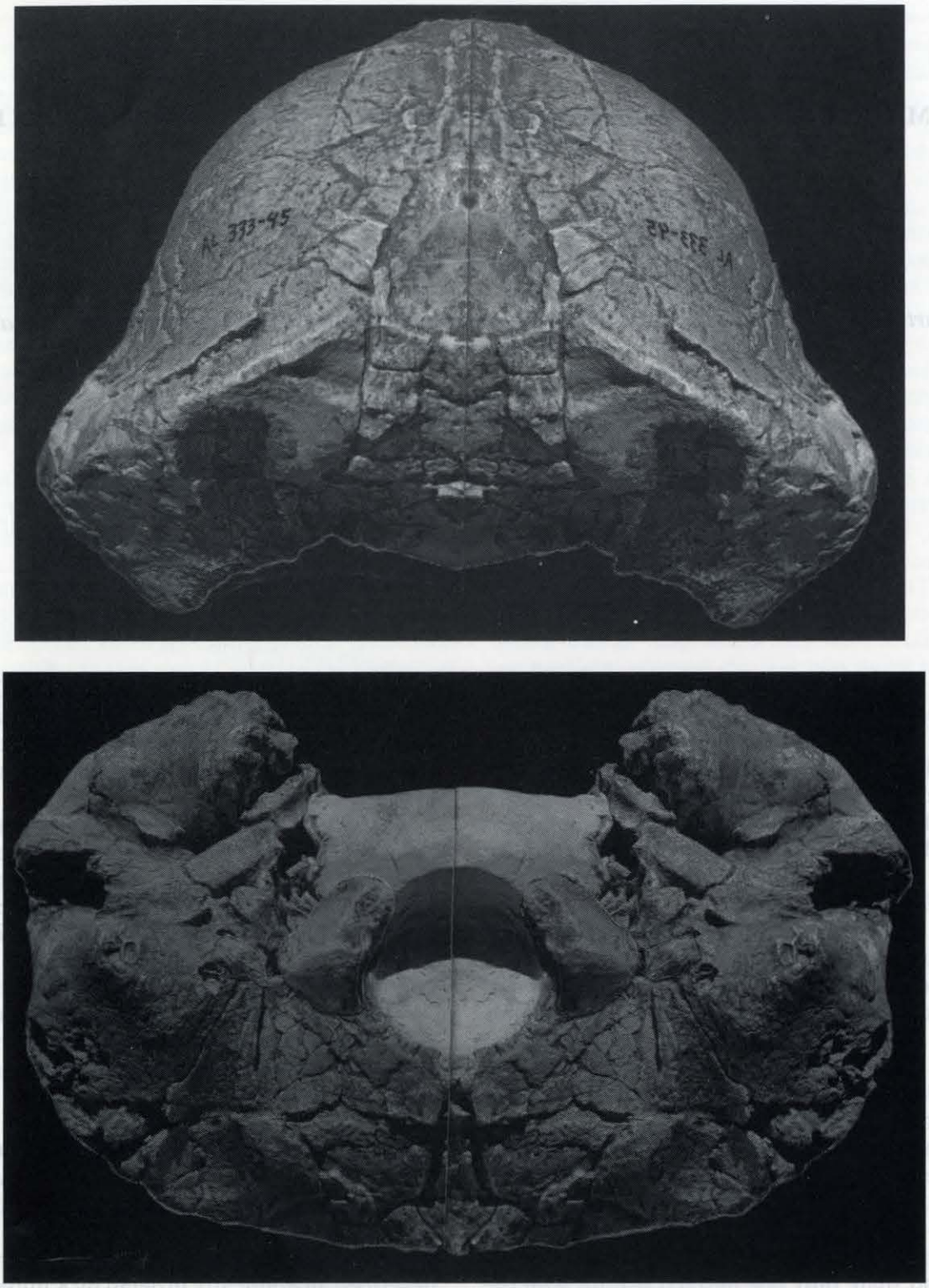


Figure 1. Restoration of the calvaria A.L.333-45. Above, norma occipitalis. Below, norma basalis.

Also examined were casts of *H. erectus*, *A. africanus* Sts 5, *A. boisei* OH 5, *A. walkeri* KNM-WT 17000, (Ferguson 1989) and the occipital fragment "*A. afarensis*" A.L. 162-28, as well as modern skulls of *H. sapiens* (N=20), *Pan troglodytes* (N=10) and *Gorilla gorilla* (N=7). The data base includes the *A. africanus* occipital bone (MLD 1) from Makapansgat and skull I from Sterkfontein, and *A. robustus* skulls SK 48, SK 49 from Swartkrans and the Kromdraai skull (Broom 1936, 1938; Robinson 1954).

The cranial morphology of A.L. 333-45 is compared with criteria by Le Gros Clark (1964) and Tobias (1967) for distinguishing the crania of the Pongidae from those of the Hominidae.

Drawings of the ventral view of A.L. 333-45 are superimposed on those of the gorilla and *Australopithecus* as a new way of determining the development of the occipital torus and comparing the suboccipital features.

RESULTS AND DISCUSSIONS

The morphology of A.L. 333-45 is compared first with the differential diagnosis for the calvaria of the Pongidae and Hominidae (after Le Gros Clark 1964). Numbers 6 under Pongidae and 5 under Hominidae were added by the author.

Pongidae	**Hominidae**
1. Strong muscular ridges	1. Weak muscular ridges*
2. Nuchal area becoming extensive with relatively high position of inion	2. Restriction of nuchal area of occiptal squama, associated with low position of inion*
3. Occipital condyles retain backward position well behind level of auditory apertures	3. Relative displacement forward of occipital condyles
4. Only a limited degree of flexion of basicranial axis associated with maintenance of low cranial height	4. Increasing flexion of basicranial axis associated with increasing cranial height
5. Cranial capacity shows no marked tendency to expansion	5. *Australopithecus* cranial capacity shows a relative or differential expansion. *Homo* shows a relative differential or absolute expansion
6. Inconsistent and late ontogenetic development of flattened mastoid process	6. Consistent, early ontogenetic development of pyramidal mastoid process

* Except *Homo erectus*

A.L. 333-45 has the following characteristics:

1. There is a " strongly apelike arrangement of muscle on the back of the skull " (Johanson and Edey 1981p.259). The nuchal plane exhibits "deeply excavated depressions for the nuchal masculature" (Kimbel *et al.* 1982p.471).
2. The nuchal area is extensive with a relatively high position of inion, which is distinctly above the Frankfurt Horizontal Plane (F.H.P.).
3. The position of the occipital condyles is more posteriorly located than in *A. boisei* Leakey 1959 O.H. 5, and slightly behind the level of the auditory apertures.
4. In view of the low cranial height, posteriorly positioned foramen magnum, horizontal tympanics, and low petro-median angle, it is expected that the associated flexion of the basicranial axis would be limited in degree. However, flexion in *A. walkeri* KNM-WT 17000 is also weak (Walker *et al.* 1986).
5. The cranial capacity, estimated at 500 cc by Holloway (Johanson *et al.* 1982), shows no expansion compared to *A. africanus*, by the lack of

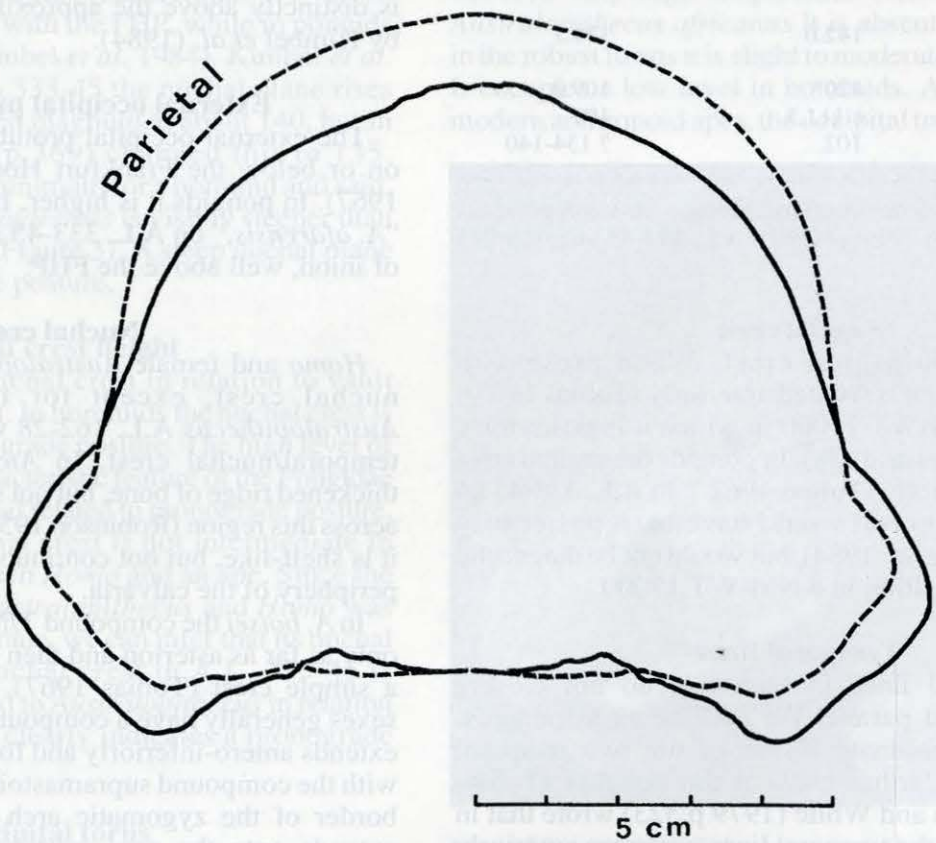


Fig.2. Norma occipitalis of the calvaria A.L. 333-45 (solid line) superimposed on that of *A. africanus* (broken line). Note lack of parietal expansion in A.L. 333-45.

parietal expansion in the coronal plane (Figure 2), and the occipital bone has not rotated downward as seen by the higher position of lambda and inion in relation to the F.H.P. (Kimbel *et al.* 1984, Fig. 14).

6. The flattened mastoid morphology is the "most similar to female *gorillas*" (Kimbel *et al.* 1985 p.122), and is attributed to late ontogenetic development.

In addition to the criteria of Le Gros Clark, many other features are compared, even though several are not diagnostic.

Cranial breadth

In *Australopithecus* the maximum bimastoid breadth is greater than the maximum breadth across the supramastoid crests. In *H. erectus* and pongids the breadth across the supramastoid crests is greater than the bimastoid breadth (except for some gorillas in which the bimastoid breadth is also greater). The maximum breadth in A.L.333-45 is distinctly less than the maximum breadth across the supramastoid crests, unlike *Australopithecus*; it is therefore pongid-like.

TABLE 1

Selected metrics of maximum cranial breadth

Hominoid	Bimastoid	Supramastoid
A.L. 333-45	100 ± 2.0*	126.5 ± 2.0*
A. boisei		
O.H.	142.0	139.5
A. africanus		
MLD/37/38	120*	109.0
Sts 5	c.111.5	107
H.e. erectus	102	? 134-140

* Measured on reconstruction. Metrics *Australopithecus* and *H. erectus* after Tobias (1967): A.L. 333-45 after Kimbel *et al.*, (1982).

Sagittal crest

Homo has no sagital crest. When present in *Australopithecus* it is located anteriorly (Tobias 1967), except for KNM-WT 17000 in which it is posteriorly located (Walker *et al.* 1988). In pongids the sagittal crest is located posteriorly (Tobias 1967.). In A.L. 333-45 an inferred sagittal crest would have been posteriorly located (Kimbel *et al.* 1984), but would not be diagnostic in view of its position in KNM-WT 17000.

Temporal lines

The temporal lines in hominids do not closely approximate and parallel the midline as in pongids. The region of intimate fusion of the two temporal crests is much farther back in the pongids (Tobias 1967). Johanson and White (1979 p.323) wrote that in "*A. afarensis*" " the temporal lines converge anteriorly and closely approximate the midline." This was corrected by Kimbel *et al.*, (1984 p.365) who said, "the temporal lines on the male A.L. 333-45 cranium [sic] more closely approximate and parallel the midline further back on the cranial vault than in any other hominid cranium known," (13.0 posterior to lambda).

The divergence of the temporal lines relative to lambda is not below that in A.L. 333-45, unlike that in *Australopithecus*, except for KNM-WT 17000 (Walker *et al.* 1986), and is thus not diagnostic.

Occipital measurements

Kimbel *et al.* (1984) state that the high occipital scale ratio in males and some females of "*A. afarensis*" is not found in other hominids. The only occipital measurement given by Kimbel *et al.* (1984), that falls outside the range of variation in hominids is the lambda-inion chord. This chord is shorter in apes (*Pan*) than it is in hominids. In A.L. 162-28 the lambda-inion chord is clearly shorter than in hominids, but in A.L. 333-45 and A.L. 288-1 it is virtually the same as the minimum for hominids. The lambda-inion chord A.L. 333-45, however, is relatively small compared to its larger cranial capacity. (Table 2).

Inion

Inion is low in *Homo*, except for *H. erectus* OH 9, in which it is above the Frankfurt Horizontal Plane. In *Australopithecus* inion is low and generally close to the FHP (Tobias 1967), whereas in pongids it is higher, above the FHP. As already noted, in A.L.333-45 inion is distinctly above the approximate FHP, as oriented by Kimbel *et al.* (1984).

External occipital protuberance

The external occipital protuberance in hominids is on or below the Frankfurt Horizontal Plane (Tobias 1967). In pongids it is higher. In the reconstruction of "*A. afarensis*," on A.L. 333-45 it is located at the level of inion, well above the FHP.

Nuchal crest

Homo and female *Australopithecus* have a simple nuchal crest, except for the putative female *Australopithecus* A.L. 162-28 which has a compound temporal/nuchal crest. In *Australopithecus* it is a thickened ridge of bone, but not shelf-like or continuous across this region (Robinson 1954). In KNM-WT 17000 it is shelf-like, but not continuously salient around the periphery of the calvaria.

In *A. boisei* the compound T/N crest extends laterally only as far as asterion and then continues anteriorly as a simple crest (Tobias 1967). Modern apes of both sexes generally have a compound T/N crest. This crest extends antero-inferiorly and forms a continuous ridge with the compound supramastoid crest and the superior border of the zygomatic arch (Olson 1981). It also extends onto the pars mastoidea. In A.L. 333-45 a continuous salient shelf defines the periphery of the calvaria from the compound T/N crests posteriorly to

TABLE 2
Hominid and pongid cranial measurements and indices

	Hominids* (n=23)	A.L. 288-1	A.L.333-45	A.L.162-28	*Pan troglodytes* mean (n=10)
Lamba-inion chord (la-i)	32.0 ± 1.0 - 70.0**	30.7 ± 1.0	31.6	25.1	21.2
Inion-opisthion chord (i-o)	26.0 - 58.0	27.2	38.0 ± 1.0	-	41.6
Index of occipital scale chords (io/la-ix100)	61.9 -120.7	88.6	120.3	>100	192.6
Occipital sagittal chord (la-o)	56.7 - 85.9	51.2 ± 1.0	60.5	-	56.8
Occipital sagittal arc	68.0 -118.2	58.8 ± 1.0	72.0	-	67.6
Occipital sagittal index (chord/arch x 100)	80.0 - 87.6	87.1	84.0	-	84.0
Biasterion chord (ast-ast)	72.5 -125.8	-	94.5 ± 2.0	79.2	79.2

Data after Kimbel *et al.*, 1984.

* *A. africanus*. (n=4), KNM-ER 1805, *A. boisei* (n=4), KNM-ER 1813, *H. habilis* (n=3), *H. erectus* (=*Sinanthropus*) X (n=4), Solo X (n=6)

**After Tobias, 1967

the roots of the zygomatic process anteriorly (Kimbel *et al.* 1982), and extends onto the pars mastoidea (Kimbel *et al.* 1985) (Figure 6).

Nuchal plane angle

The nuchal plane of hominids is not as steeply inclined as it is in pongids. In hominids it faces downward rather than backward as in pongids (Zuckerman 1954a). In hominids it is 139-160, with the FHP, while in pongids (*Pan*) it is 103-138 (Kimbel *et al.* 1984). Kimbel *et al.* (1982) said that in A.L.333-45 the nuchal plane rises steeply from the foramen magnum at about 140, but in 1984, Kimbel *et al.* (p.369) changed this to 135, distinctly less than the minimum for a hominid and said, "the nuchal plane in *A. afarensis* is visibly steeper than in other hominid taxa. (Figure 3). A steep nuchal plane is related to pronograde posture.

Nuchal crest height

The height of the nuchal crest in relation to vault height is also significant. In hominids the nuchal crest is low and related to orthograde posture. The high level of the nuchal crest is a characteristic feature of the Pongidae (Le Gros Clark 1958), and related to pronograde posture. The height of the nuchal crest is not intermediate in *Australopithecus* between *Homo* and an ape. Since the common ancestor of *Australopithecus* and *Homo* was almost certainly orthograde, we can infer that its nuchal crest was low. The nuchal crest in A.L. 333-45 is relatively high compared to *Australopithecus* in relation to the vault height and clearly indicates a pronograde posture (Figure 4).

Occipital torus

At the posterior of the occipital bone on each side of the nuchal crest is a smooth, rounded protuberance or raised portion which projects posteriorly, called the occipital torus (Poirier 1973). In *H. habilis* it is of moderate relief (Day *et al.* 1975). In *H. erectus*, particularly Sangiran IV, it is massive (Le Gros Clark 1964) and enormously thick (Tobias 1967). In *H. sapiens neanderthalensis* it is strong (Le Gros Clark 1972). In some modern populations, occipital tori occur in very high frequencies (Kennedy 1991). In *Australopithecus africanus* it is absent or weak, while in the robust forms it is slight to moderate (Tobias 1967). It occupies a low level in hominids. Among the large modern anthropoid apes, the occipital torus forms a crest



Figure 3 Restoration of the calvaria A.L. 333-45. Left norma lateralis. Note that the steep nuchal plane faces backward more than downward.

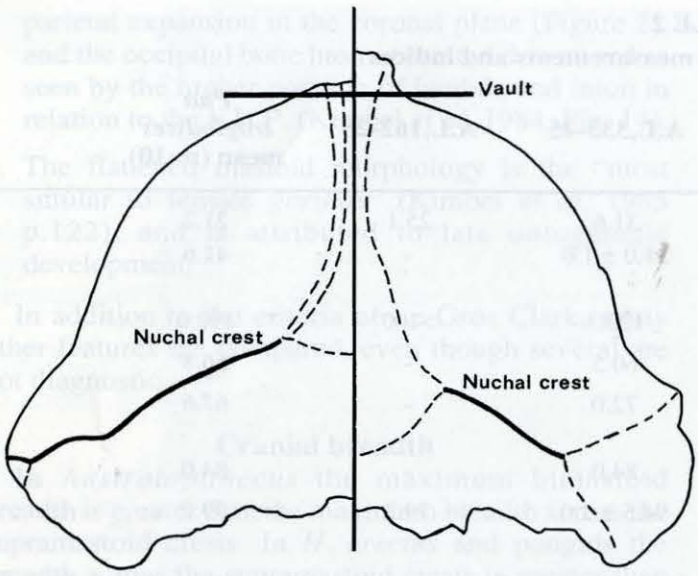


Figure 4 Norma occipitalis of the calvaria A.L. 333-45 (left half) and *A. boisei* O.H. 5 (right half) showing height of compound T/N crest in relation to the vault. Both specimens drawn to the same height. The nuchal crest and occipital torus of A.L. 333-45 are clearly relatively higher and ape-like. Simple crest (broken line), compound crest (solid line).

that reaches high up on the skull (Zuckerman 1954a). Schultz (1965 p.173) notes that "the mechanically disadvantageous location of the occipital joint of adult apes requires such powerful nuchal muscles that their area of cranial attachment has usually to be enlarged with the addition of occipital crests." In A.L. 333-45 the area for nuchal muscles has been expanded by a relatively high compound T/N crest continuous with a salient occipital torus (Figure 5.)

Nuchal area

As already noted by Le Gros Clark (1972) the nuchal area in pongids is extended, whereas in hominids it is restricted and a "particularly distinctive character of the hominid skull" (Le Gros Clark 1959 p.167). The nuchal area in *H. erectus* is expanded compared to *H. habilis* (Kimbel *et al.* 1984), but its simple nuchal crest is not shelf-like nor is its occipital torus a crest. In A.L. 288-1 the nuchal area is not expanded and there is no indication of an occipital torus. Its postcranial skeleton is clearly orthograde. In apes the mastoid process has a flat posterior surface which represents a lateral extension of the nuchal plane (Schultz 1950). A.L. 333-45 has a relatively high compound T/N crest continuous with an expanded occipital torus and flat posterior surface of the mastoid process, indicating a lateral extension of the nuchal plane as in apes.

Foramen magnum

The relative position of the foramen magnum on the base of the cranium is related to posture. In hominids it is more forwardly placed than in pongids and related to upright posture and bipedalism. The foramen magnum of australopithecines is situated well forward (Tobias 1967), intermediate between ape and man (Tobias 1983a). The opisthion is missing in A.L. 333-45, but the ectobasion is preserved and indicates that the foramen magnum is not as posterior as in modern apes, but more posteriorly located than in *A. boisei* O.H. 5 (Figure 5).

Digastric fossa

The digastric fossa (incisura mastoidea) in hominids (mastoid notch in *Homo*), is short, narrow and oval, and varies from shallow and ill-defined to deep and ridged in *H. sapiens* (De Villiers 1968). In *A. africanus*, "both STS 5 and MLD 37/38 have narrow and deep mastoid notches" (Olson 1985 p.108). Kennedy (1991) says MLD 37/38 "reveals a short and wide mastoid notch." In pongids it is *long*, broadly triangular, oval or V-shaped according to Olsen (1981), and shallow. The digastric fossa in A.L. 333-45 is long, "shallow, triangular and mediolaterally concave" (Kimbel *et al.*, 1985 p.130). The mastoid notch is not a "reliable taxonomic character" (Kennedy 1991) among hominids, but valid between hominids and pongids.

Venous sinus drainage pattern

Kimbel *et al.* (1984) list only one derived feature that A.L. 333-45 shares with the robust australopithecines - the venous sinus drainage pattern. Falk

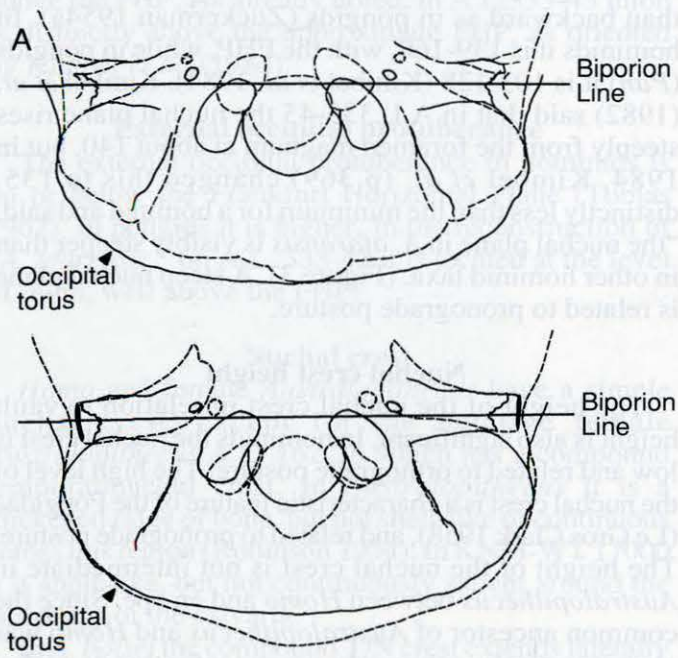


Figure 5 Norma basalis of the occipitomastoid region of A) A.L. 333-45 (solid line) superimposed on that of a female gorilla (broken line), and B) A.L. 333-45 (solid line) superimposed on *A. boisei* O.H. 5 (broken line). Note that occipital tori and mastoid process of A.L. 333-45 and gorilla are nearly identical, unlike O.H. 5, and that the occipital condyles and foramen magnum of A.L. 333-45 are more posteriorly located than in O.H. 5.

and Conroy (1983) suggest that the high frequency of this feature in robust *Australopithecus* has phylogenetic and systematic significance. They say that this feature in A.L. 333-45 is either ancestral to the robust australopithecines, or is shared with a common ancestor. Kimbel *et al.* (1984 p.377) regard the use of this feature for phylogenetic reconstruction as "doubtful owing to the marked temporal and spatial fluctuations in the frequencies of different venous drainage patterns in the *Homo* lineage". In pongids it is undocumented.

Asterionic notch

The asterionic notch is characteristic of pongids and is unknown in hominids. Its presence in the hominid KNM-WT 17000 is "probable" (Leakey and Walker 1988 p.520). The calvaria A.L. 333-45 shares this primitive sutural arrangement with apes (Kimbel *et al.* 1984).

Supramastoid crest

In hominids the posterior part of the temporal ridge from the border of the zygoma arches backward and upward and is called the supramastoid crest. It coincides with the root of the inferior temporal line above the mastoid. In *H. sapiens* it may be slight, moderate or marked (De Villiers 1968). In *A. boisei* O.H. 5 the lateral part of the superior nuchal line continues from the compound T/N crest as a simple nuchal crest onto the inferior surface of the mastoid process (Tobias 1967). It does not join the supramastoid crest, whereas in almost all adult modern great apes the inferior temporal and superior nuchal lines form a robust compound supramastoid crest, the most prominent feature in an occipital view (Olson 1981). In A.L. 333-45 the inferior temporal and superior nuchal lines continue antero-inferiorly as a robust, compound supramastoid crest (Figure 6).

In australopithecines the simple supramastoid crest does not bulge as much laterally as the pars mastoidea (Tobias 1967). In apes the compound supramastoid crest is prominent and is usually, although not always, lateral to the pars mastoidea. The compound supramastoid crest in A.L. 333-45 is prominent and projects slightly more laterally than the *pars mastoidea*, as in A.L. 333-112. The " supramastoid crest of the A.L. 333-45 skull retains the primitive projecting condition found in the great apes" (Olson 1981 p.115).

Supramastoid sulcus

In hominids, between the supramastoid crest and the mastoid crest lies a supramastoid sulcus. Kimbel *et al.*(1985) note that in A.L. 333-45 the supramastoid crest and mastoid crest merge, with no sulcus between them. The supramastoid region of A.L. 333-45 does not share the characteristic occipital profile of *Australopithecus* (Figure 7).

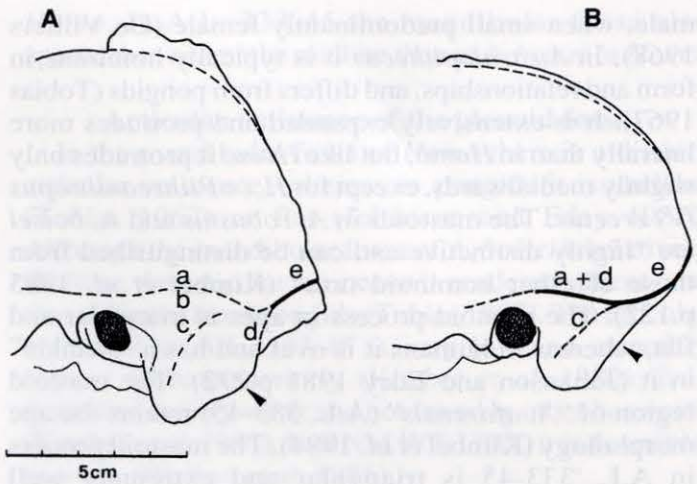


Figure 6 Left norma lateralis of A) *A. boisei* O.H. 5 and B) A.L. 333-45, depicting the occipitomastoid region. Simple crest (broken line), compound crest (solid line). Structures indicated: a) supramastoid crest, b) supramastoid sulcus, c) mastoid crest, d) superior nuchal crest, e) temporal/ nuchal crest. Arrow points to posterolateral face of the mastoid

Mastoid process

In hominids the mastoid process is variably large, medium or small, prominent, pyramidal or cone shaped, and protrudes both laterally and inferiorly. In *H. sapiens* it is mostly medium in size, when large predominantly

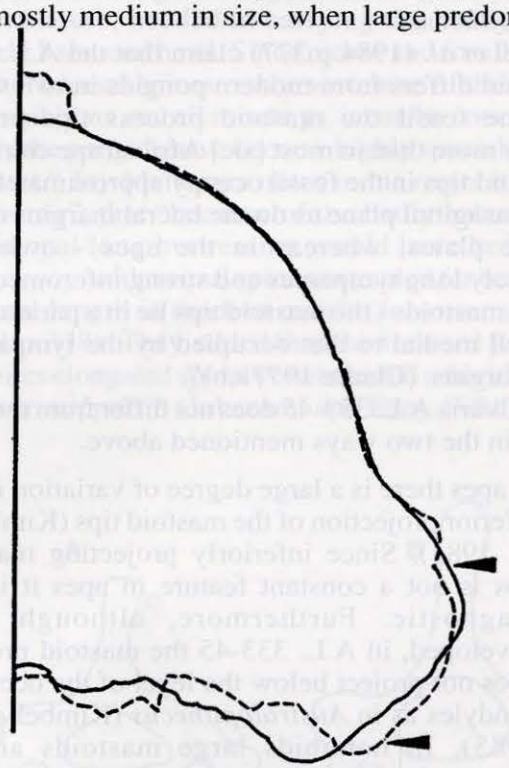


Figure 7 Norma occipitalis of the contour of right half of the calvaria A.L. 333-45 (solid line) superimposed on that of *A. boisei* O.H. 5 (broken line). Note that the supramastoid sulcus is absent in A.L. 333-45, and that the masoid process in O.H. 5 bulges laterally whereas in A.L. 333-45 it is inflected.

male, when small predominantly female (De Villiers 1968). In *Australopithecus* it is typically hominine in form and relationships, and differs from pongids (Tobias 1967). It is extensively expanded and protrudes more laterally than in *Homo*, but like *Homo* it protrudes only slightly medialwards, except for *H. (=Pithecanthropus IV) erectus*. The mastoids in *A. robustus* and *A. boisei* are "highly distinctive and can be distinguished from those of other hominoid taxa" (Kimbel *et al.* 1985 p.122). The mastoid process in apes is triangular and flat, whereas in humans it is oval and has a "wrinkle" in it (Johanson and Edey 1981 p.272). The mastoid region of "*A. afarensis*" (A.L. 333-45) retains the ape morphology (Kimbel *et al.* 1984). The mastoid process in A.L. 333-45 is triangular and extremely well developed. It exhibits a posterolateral face that is flat mediolaterally and slightly concave inferosuperiorly (Kimbel *et al.* 1982 p.122). It has a strong inferomedial inflection not found in hominids (Kimbel *et al.* 1984). "The inferior and lateral projection is not remarkable compared to that of African great apes" and the inflation "does not differ significantly from the condition found to characterize many extant apes, particularly the female gorilla" (Kimbel *et al.* 1985 p.122). The mastoid process in the temporal fragment of "*A afarensis*" A.L. 166-9, however is not flattened but is globular despite the eroded external surface (Taieb *et al.* 1974) as in *Australopithecus*.

Kimbel *et al.* (1984 p.377) claim that the A.L. 333-45 mastoid differs from modern pongids in two ways: 1. "in the fossil the mastoid process tips project inferiorly more than in most [sic] African ape crania; 2. the mastoid tips in the fossil occupy approximately the same parasagittal plane as do the lateral margins of the tympanic plates, whereas in the apes - owing to transversely long tympanics and strong inferomedially inflected mastoids - the mastoid tips lie in a parasagittal plane well medial to that occupied by the tympanic's lateral margins (Clarke 1977a,b)".

The calvaria A.L. 333-45 does not differ from modern pongids in the two ways mentioned above.

1. In apes there is a large degree of variation in the inferior projection of the mastoid tips (Kimbel *et al.* 1984). Since inferiorly projecting mastoid tips is not a constant feature in apes it is not diagnostic. Furthermore, although well developed, in A.L. 333-45 the mastoid process does not project below the level of the occipital condyles as in *Australopithecus* (Kimbel *et al.*, 1985). In hominids large mastoids are an advanced, rather than a primitive feature and hence the "extremely well developed" (Kimbel *et al.* 1982: p.470) mastoids in A.L. 333-45 at such an early date of 3.5 m.y. would be the reverse of the anticipated human evolutionary trend from small mastoids to large (non-projecting mastoid tips notwithstanding).
2. In hominids the tip of the mastoid process is in the same parasagittal plane as the lateral margin of the external auditory meatus. In pongids the tip is medial to the opening of the external auditory meatus (Olson 1981). The mastoid process tip of A.L. 333-84 is about 5.0 mm medial to the lateral tympanic margin, but in A.L. 333-45 the mastoid process tips occupy the same sagittal plane as the auditory apertures (Kimbel et al. 1982). In A.L. 333-45 "most of the anterior lateral portion of the right tympanic (and part of the left) is missing and the entire lateral edge is abraded" (Kimbel *et al.*, 1982 p.470). If the lateral margin of the tympanic plate were intact, the mastoid process would lie medial to it as it does in A.L. 333-48.

Kimbel *et al.* (1985) demonstrated that the mastoid and supramastoid morphology of *A. robustus* and *A. boisei* diverge sharply from A.L. 333-45 and extant African apes.

Postglenoid Process

Postglenoid process in hominids is small or moderate and recessed medially on the same sagittal plane as the tip of the mastoid process. In pongids it is large and inflated (Tobias 1967), and extends laterally, which is the primitive condition. The postglenoid process of A.L. 333-45 is large, extends laterally, and is the most external part of the cranium (Kimbel *et al.* 1982). It is lateral to the sagittal plane of the tip of the mastoid process.

In pongids, the outer part of the tympanic is situated mainly behind the postglenoid process, whereas in hominids it is situated mainly below the postglenoid process, (Broom 1938). The tip of the postglenoid process in the hominid KNM WT 17000 is " completely anterior to the anterior [sic] edge of the external acoustic meatus" (Leakey and Walker 1989 p.9). "In the apes and *A. afarensis* [A.L.333-45] the postglenoid process lies anterior [to] the tympanic plate . . ." (Kimbel *et al.* 1984 p.376) (Figure 8).

Tympanic plates

When viewed basally, the tympanic plate in hominids is squeezed into more of a ridge than a tube, while in apes it resembles a tube (Johanson and Edey 1981). In A.L. 333-45 there is no marked tendency for the auditory meatus to constrict medially and the tympanic plates are tubular (Johanson and Edey 1981), "strongly resembling the pongid condition" (Johanson and White 1979 p.323).

The conformation of the tympanic plate is nearly horizontal in many pongid crania (Tobias 1967). In A.L. 333-45 the tympanic plate tends to be horizontally oriented (Johanson *et al.* 1982).

Styloid process

The styloid process of modern *Homo* does not occur in *H. erectus pekinesis*, australopithecines or pongids

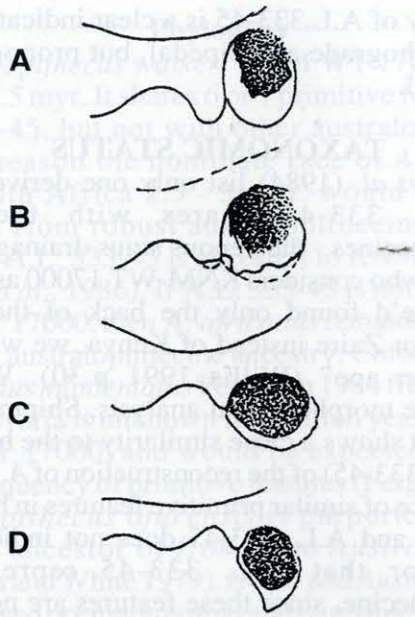


Figure 8 Postglenoid process in relation to the external acoustic meatus in A) *Gorilla*, B) A.L.333-45, C) *A. robustus*, D) *H. sapiens* (after Broom, except A.L. 333-45). In A.L.333-45 the outer part of the tympanic is situated mainly behind the postglenoid process, as in *Gorilla*.

(Tobias 1967). Clarke (1990) records the presence of styloid process in *H. erectus leakeyi* Heberer, 1963 SK 847, which he raises to specific rank, *Homo leakeyi*. Kimbel *et al.* (1982) describe the broken stub of an ossified styloid process in A.L. 333-45, but no styloid process is present in A.L. 166-9 (Taieb *et al.* 1974). The presence or absence of the styloid process is indeterminate as it may not always fossilize.

Pneumatization of the temporal squama

The mean thickness of the temporal squama measured just above the supraglenoid gutter in the robust australopithecines is 5.5, range 4.5 - 6.0 (n=6), in *Pan troglodytes* it is 11.3, range 10.5 - 12.5 (n=3) and in "*A. afaren*sis" it is 9.8, range 9.1 - 10.5 (n=4) (Kimbel *et al.* 1984). The pattern of pneumatization in "*A. afarensis*" was thought to occur only in the extant apes among hominoids (Kimbel *et al.* 1984), but was found in KNM-WT 17000 to be 11.5, (Walker *et al.* 1986) twice as thick as in *A. boisei*, and within the range of apes.

Petro-median angle

Appreciable flexion and anteroposterior reduction of the cranial base is reflected in the high angle between the petrous angle and the median plane (Tobias 1967). The angle in hominids is 32-47.4°, while in modern pongids it is 10 -30° . In A.L. 333-45° the "right petrous angles forward about 30° to the midsagittal line" (Kimbel *et al.* 1982) below the minimum for hominids.

Mandibular (glenoid) fossa

The mandibular fossa approaches nearer the midline in the gorilla than in *A. boisei* (Tobias 1967), or in *Homo*. In A.L. 333-45 the mandibular fossa also approaches nearer the midline than in *A. boisei* or *Homo*.

Articular eminence of the glenoid fossa

In the mandibular fossa of *Homo* there is a distinct articular eminence, whereas in pongids it is shallow (Tobias 1967) or flat (Johanson and Edey 1981). Although the mandibular fossa of *A. boisei* is relatively shallow, the articular eminence is rendered salient, and thus different from pongids (Tobias 1967). The articular eminence in A.L. 333-45 is very low and smoothly convex anteroposteriorly (Kimbel *et al.* 1982). It is described as very weak and not found in other hominids (Kimbel *et al.* 1984). In KNM WT 17000 it is described as weak (Walker *et al.* 1986).

POSTURE AND LOCOMOTION

A lineage is characterized by the main trends of its evolutionary development (Le Gros Clark 1959). The Pongidae are adapted to pronograde posture and quadrupedal locomotion. The Hominidae are adapted to orthograde posture and bipedal locomotion. The skull in apes is supported by a cantilever-like neck, whereas in hominids it is well balanced from below.

Schultz (1968 p.154) wrote that "the dorsal spines of the cervical vertebrae of all great apes have acquired an exceptional length to support their powerful nuchal musculature, needed in carrying the heavy and very poorly balanced head. Since recent and fossil man have as short dorsal spines on the vertebrae of their necks as have gibbons and all monkeys, it can be concluded that "only the pongids have become highly specialized in this respect." Jay Matternes notes in his restoration of "*A. afarensis*", that "because of the badly balanced head, additional long buttressing would have been necessary. . . . . with neural spines extended far beyond their normal length in modern man". (Johanson and Edey, 1981 p.378). They added that the forward jutting face requires elongated spinal vertebrae and a thickly muscled neck to support it (Johanson and Edey 1981).

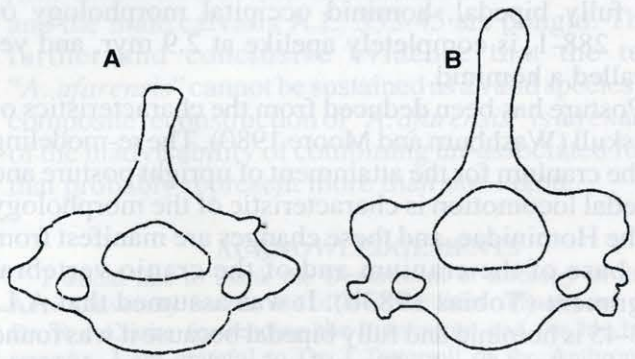


Figure 9 Cervical vertebrae of hominoids (superior view).
A) *Homo sapiens*, 7th cervical vertebra.
B) A.L. 333-106, 6th or 7th cervical vertebra (after Lovejoy *et al.*, 1982). Drawn to the same breadth. Note the very long spinous process of A.L. 333-106.

Although the long cervical spines have been called an adaptation to balancing the head, the major muscles which arise from these spines are for the arms and not to balance the head (Washburn and Moore 1980). Regardless of their function, the long cervical spines are diagnostic of the great apes. It may be significant, therefore that a 6th or 7th cervical vertebra A.L. 333-106 was found at the same site as A.L. 333-45 with a very "long spinous process that is quite distinct" (Johanson and White 1979 p.324) (Figure 9).

According to Bierget (1963) "the kind of locomotion of fossil primates can be determined only from the condition of the post-cranial skeleton". He thus claims that the alterations in the topography of the skull of a hominid in contrast with that of a pongid are not criteria for upright locomotion. The features he refers to are increased kyphosis, which causes increasingly horizontal orientation of the nuchal plane, anterior shifting of the foramen magnum and the more oral position of the occipital condyles. These acknowledged alterations in the topography of the hominid skull, plus the low nuchal height, reduced occipital torus and nuchal area, and weak nuchal masculature are indeed characters correlated with upright locomotion.

The differences in the nuchal and suboccipital regions that distinguish the great apes and hominids are correlated with adaptation to posture (Robinson 1958; Le Gros Clark 1964; Poirier 1973; Tobias 1983). Lovejoy said that animals have to give up one form of adaptation for another (Johanson and Shreeve 1989). Hominids would have lost an apelike occipitomastoid morphology when they adapted to bipedal locomotion. Tobias (1983a p.172) wrote that "all the fossil evidence goes to indicate that elements of this bipedalism complex [including the cranium] were developed early in the history of hominization". This is thought to have occurred between 5 - 7 myr. "The evolution of upright posture was the single most important factor in shaping the derived morphology of the hominid occipitomastoid region" (Olson 1985 p.106). It is inconsistent, therefore, that the occipitomastoid morphology of A.L. 162-28, which is synchronic with the fully bipedal, hominid occipital morphology of A.L. 288-1, is completely apelike at 2.9 myr, and yet is called a hominid.

Posture has been deduced from the characteristics of the skull (Washburn and Moore 1980). The re-modeling of the cranium for the attainment of upright posture and bipedal locomotion is characteristic of the morphology of the Hominidae, and these changes are manifest from the base of the cranium and of the cranio vertebral alignment (Tobias 1983b). It was assumed that A.L. 333-45 is hominid and fully bipedal because it was found near hominid fossils. Classification, however, is based on morphology and not proximity. By including A.L. 333-45 together with undisputed hominid fossils, the significance of its adaptive affinities had been obscured and ignored. The unequivocal apelike occipitomastoid morphology of A.L.333-45 is a clear indication that it was not orthograde and bipedal, but pronograde and quadrupedal.

TAXONOMIC STATUS

Kimbel *et al.* (1984) list only one derived feature that A.L. 333-45 shares with the robust australopithecines - the venous sinus drainage pattern.

Walker, who considers KNM-WT 17000 as *A. boisei*, said, "if we'd found only the back of the skull in Cameroon or Zaire instead of Kenya, we would have called it an ape" (Willis 1991 p.30). Without a comparative morphological analysis, Shipman (1986) states that it shows a close similarity to the back of the skull (A.L. 333-45) of the reconstruction of *A. afarensis*. The presence of similar primitive features in both KNM WT 17000 and A.L. 333-45 does not indicate close affinity, or that A.L. 333-45 represents an australopithecine, since these features are not derived characters of the Australopithecinae, but are either homonoid features shared by pongids and early *Australopithecus*, or due to parallel evolution.

Le Gros Clark (1958 p.66) wrote that "in its general proportion, indeed, the australopithecine skull has a superficial appearance not unlike that of a large ape, but in details of its construction it presents many differences". The calvaria KNM WT 17000 shows the following hominid characters not seen in A.L. 333-45:

1. greater posterior extension of the occipital in relation to brain size
2. greatest breadth bimastoid
3. occipital torus slight or moderate
4. inclination of nuchal plane less steep and restricted
5. mastoid crest lateral to supramastoid crest
6. supramastoid sulcus probably present (damaged)
7. mastoid posterior surface almost, but not flat
8. medial inflection of the mastoids reduced
9. relatively small postglenoid process, not opposite outer tympanic plate
10. coronally placed petrous temporalis

Olson (1985) regards the basicranial morphology of A.L. 333-45 as advanced and highly specialized, while Kimbel *et al.* (1985) say that the occipitomastoid region of A.L. 333-45 is strikingly primitive and resembles that of an ape.

Slowly changing characters are used to characterize the higher categories (Mayr, 1953). The basicranial morphology of hominoids has changed slowly and is thus useful for classification. Olson's (1985) analysis of the cranial morphology of A.L.333-45, in which he claims 3 apomorphic features identify it as a "*Paranthropus*", was shown by Kimbel *et al.*, (1985) to be instead extremely primitive and apelike. The most reasonable classification of A.L.333-45 would be as a member of the Pongidae.

Phylogeny

Australopithecus walkeri KNM WT 17000 is dated at about 2.5 myr. It shares 6 or 7 primitive features with A.L. 333-45, but not with other australopithecines. For this reason the nominate race of *A. africanus* from South Africa 2.5 - 3 myr, would seem to be excluded from robust australopithecine ancestry, assuming A.L. 333-45 is ancestral to KNM WT 17000 (Walker *et al.*, 1986). If A.L. 333-45 is not ancestral to KNM WT 17000, then *A. africanus* remains a candidate for robust australopithecine ancestry. Chronologically, *A. africanus miodentatus* Ferguson 1984 from Ethiopia, whose calvaria is unknown is a million years older than KNM WT 17000, and would be expected to retain a higher frequency of primitive features (Ferguson 1987). *Australopithecus afarensis* is purported to be the common ancestor of *Homo* and *Australopithecus* (Johanson and White 1979). *Homo* and *Australopithecus* share derived occipitomastoid and tympanic morphology not found in A.L. 333-45. The calvaria A.L. 333-45 cannot, therefore, belong to a taxon that was the common ancestor of *Homo* and *Australopithecus*.

SUMMARY AND CONCLUSION

In 1985, Pilbeam wrote that "*Australopithecus afarensis*" resembles *Pan* and *Gorilla* in a few cranial characters. Reassessment of the morphology of the calvaria A.L. 333-45 reveals that it conforms with the Pongidae in its total morphological pattern and differs from the Hominidae in the following characters (even without those related to a steep, nuchal plane).

1. maximum breadth across supramastoid crests greater than maximum bimastoid breadth
2. lambda-inion chord short in relation to cranial capacity
3. strong muscular ridges, particularly in occipital region
4. nuchal crest high in relation to occipital height
5. compound T/N crest shelf-like and extends onto pars mastoidea
6. occipital torus pronounced
7. nuchal area extensive
8. nuchal plane steep relative to FHP
9. foramen magnum (ectobasion) posteriorly located
10. incisura mstoidea long
11. asterionic notch present
12. inferior temporal and superior nuchal lines form compound supramastoid crest
13. supramastoid crest and mastoid crest merge
14. supramastoid crest lateral to pars mastoidea
15. supramastoid sulcus absent
16. mastoid process triangular, posterolateral face flat mediolaterally, slightly concave inferosuperiorly
17. mastoid process inferomedial inflection strong
18. tip of mastoid process medial to opening of external auditory process
19. tympanics tubular in basal view
20. tympanic plate horizontally oriented
21. postglenoid process large, projects laterally
22. postglenoid process anterior to the outer part of tympanic
23. mandibular (glenoid) fossa closely approaches midline
24. petro-median angle low

The calvaria A.L. 333-45 was assumed to belong to a hominid because it came from the same site as hominid fossils. It is sympatric and synchronic with A.L. 333-1, an unmistakable specialized gracile *Australopithecus*. However, A.L. 333-45 is unassociated anatomically with any hominid fossils and I found not a single unequivocal hominid character. Its extremely well developed mastoids are inconsistent with the hominid evolutionary trend from small to large mastoids. Although some of the features are less specialized than in a modern ape, it would be incredibly primitive for a hominid - but not for a pongid.

The hominoid A.L. 333-45 was assumed to be upright and fully bipedal on the basis of its proximity to unassociated hominid specimens. No morphological evidence has been given to support A.L. 333-45 as a hominid. The adaptive affinities of the occipitomastoid morphology of the Pongidae are related to pronograde posture and quadrupedal locomotion. Since the apelike occipitomastoid morphology of A.L. 333-45 is undisputed, its adaptive affinities are related to pronograde posture and quadrupedal locomotion. To conclude that it is a hominid is a *non sequitur*. The calvaria A.L. 333-45 cannot, therefore, belong to a hominid - but belongs to an ape.

I believe A.L. 333-45 is the only known pongid calvaria from the late Pliocene of Africa, and may represent the first known skull of *Praeanthropus africanus*.

The reconstruction of a male "*A. afarensis*" skull is a chimera, a composite of hominid and pongid fossils. The facial fragment A.L. 333-1 is that of a gracile *Australopithecus*, while the female maxillae A.L.200-la and the male calvaria A.L. 333-45 are pongid. This is further and conclusive evidence that the taxon "*A. afarensis*" cannot be sustained as a valid species. The composite reconstruction of "*A. afarensis*" is an example of the inadvisability of combining un-associated fossils that probably represent more than one taxon.

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