

Relationship of Squamosal Suture to Asterion in Pongids (*Pan*): Relevance to Early Hominid Brain Evolution

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KEY WORDS Australopithecine, Brodmann's areas, Endocasts, *Australopithecus afarensis*, Brain reorganization, Primary visual striate cortex, Brodmann area 17, Hadar 162-28

ABSTRACT Based on 244 measurements of the relationship of the squamosal suture to the landmark asterion in 49 chimpanzee skulls, it is shown that in the normal lateral view the squamosal suture is very rarely inferior to asterion. In hominid crania, the squamosal suture is always well superior to asterion. Even in *Pan*, that part of the squamosal suture most homologous with the remnant found on the Hadar AL 162-28 *Australopithecus afarensis* hominid cranial fragment is very rarely inferior to asterion. Such variability suggests that Falk's (Nature 313:45-47, 1985) orientation of the Hadar specimen is incorrect; she places asterion superior to the position of the squamosal suture if projected endocranially. The implication for the brain endocast is that, however the fragment is oriented, the posterior aspect of the intraparietal (IP) sulcus is in a very posterior position relative to any chimpanzee brain. The distance from the posterior aspect of IP to occipital pole is twice as great in chimpanzee brain casts than on the Hadar AL 162-28 endocast, even though the chimpanzee brain casts are smaller in overall size. This suggests that brain reorganization, at least as exemplified as a reduction in primary visual striate cortex (area 17 of Brodmann), occurred early in hominid evolution, prior to any major brain expansion. © 1992 Wiley-Liss, Inc.

INTRODUCTION

Fossil brain endocasts provide an important window on limited but significant aspects of the once living underlying cerebral mantle. Given the frequent poor quality of brain convolutional detail that imprints on the inner table of cranial bone, controversial interpretations of cerebral landmarks are common, as can be found in the arguments regarding the lunate sulcus and other sulcal features in the Taung *Australopithecus africanus* and the Hadar AL 162-28 *A. afarensis* endocast specimens. It is essential, therefore, given such poor preservation, that all clues be used to interpret the anatomical relationships provided by both ecto- and endocranial landmarks.

We focus on the Hadar cranial fragment AL 162-28, originally described by Kimbel et

al. (1982), since the orientation of this fragment is a major point of disagreement between Falk and Holloway (see below) as well as being a matter of important agreement regarding cerebral convolutions. Both writers agree upon the identification of a small groove, which is regarded as the intraparietal (IP) sulcus. The IP divides superior and inferior parietal lobules, and, in pongids, its posterior limit always abuts against the lunate sulcus or is exceedingly close to it (see Fig. 2 in Holloway, 1983). This is a pattern that is invariant in pongids. The lunate sulcus is the most anterior boundary of primary visual striate cortex, otherwise known as

Received July 7, 1991; accepted June 4, 1992.

area 17 of Brodmann (1909). If the IP is in a relatively posterior position, then the lunate sulcus must also be in such a position. A posterior position of the IP and/or lunate sulcus would mean that the cerebral cortex of the earliest hominids might be organized in a more human way than in any pongid yet known (see Holloway 1983, 1985, 1987, 1992, for quantitative details).

The IP sulcus would appear to be the only point on which Falk and Holloway agree, however. The major difference between us stems from the way the endocast (and thus the cranial fragment) has been oriented. In Holloway's (1983) paper, the endocast was oriented following Kimbel et al. (1982), in which the temporal squamosal remnant was situated superior to the remnant of asterion, both of which are clearly identifiable on the AL 162-28 cranial specimen. Their photograph on page 487 attempts to orient the fragment in a normal lateral view. Falk (1985) oriented the cranial fragment in such a manner as to place the asterionic landmark *superior* to the squamosal suture. When Holloway and Kimbel (1986) differed with her orientation, Falk (1986) claimed the following:

Neither the squamosal suture or asterion is reproduced on the endocast, and I do not think the calvaria of AL 162-28 is complete enough to allow speculation about where the locations and relative positions of both features would have been on the (whole) endocast. Even if Holloway and Kimbel's SS and A identifications . . . could be interpreted and projected onto the endocast as they suggest, given the overlap at the squamosal suture and the variation of its course in hominoids, there is ample room for forward rotation of their calvaria within the normal hominoid range" (p. 356).

The point raised by Falk regarding the lack of squamosal sutural or asterionic imprint on the endocast is not quite correct. They are very clear, ectocranially (Kimbel et al., 1982:456, 457, and Fig. 2B, 487). The asterionic notch can be seen on the endocast and was labeled on Holloway and Kimbel's (1986:536, Fig. 1b) diagram. Given the thinness of cortical bone in these regions, their endocranial position is essentially identical to their ectocranial locations. However, we do believe that her point concerning the variability of relationships between the

squamosal suture and asterion in hominoids is certainly worthy of further study. This paper provides such an examination of both *Pan* and early hominid crania. We intend to show that the squamosal suture (SS) in a large number of *Pan* crania rarely falls inferior to the anatomical landmark known as asterion (A). Moreover, such a morphological pattern does not exist in any known hominid. We believe that these relationships make the orientation originally provided by Kimbel et al. (1982:487) and adapted by Holloway (1983) and reargued by Holloway and Kimbel (1986) the most probable and anatomically correct orientation of the AL 162-28 cranial fragment. The implications for the underlying brain endocast are considerable.

MATERIALS AND METHODS

The material examined and measured in this study consisted of 49 crania of adult wild-caught *Pan*. (An additional 150 *Pan* crania from the Peabody Museum, Harvard University, were also examined for sutural relationships by orienting the skull visually in the Frankfurt Horizontal plane. These crania were not measured using dental floss and calipers but scored through visual examination.) Only those specimens in which A and SS were clearly discernible were used. Although some older specimens were eliminated given this constraint, examination of the dentition and complete fusion of the sphenoccipital suture indicated that sufficient numbers of fully adult specimens were used so that the sample was not skewed toward those that had just reached adulthood. Crania studied were taken from each of the putative taxa of *Pan* based on provenance (following Shea and Coolidge, 1988). The number studied from each species/subspecies is as follows: *P. t. troglodytes*, 16; *P. t. verus*, 9; *P. t. schweinfurthii*, 10; and *P. paniscus*, 14. Material was studied at several museums: American Museum of Natural History (AMNH); National Museum of Natural History (NMNH); Peabody Museum, Harvard University (PMNH); Cleveland Museum of Natural History (CNMH); and Kooninklijk Museum voor Midden Africa (KMMA/MRAC), Tervuren, Belgium.

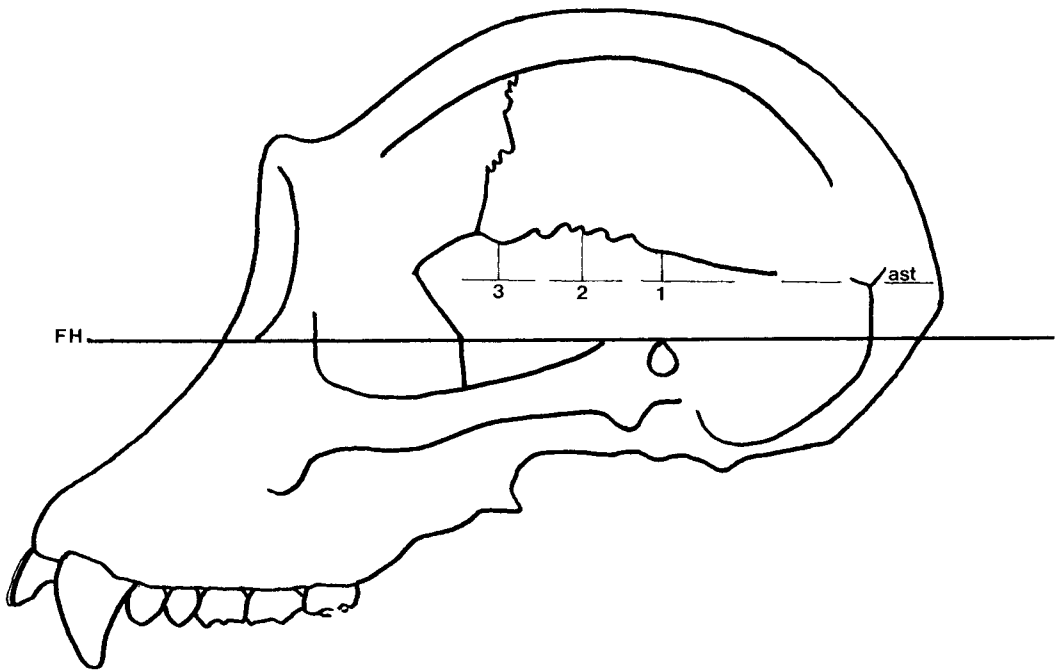


Fig. 1. Schematic diagram of a chimpanzee cranium, normal lateral view. FH, Frankfurt horizontal; ast, asterion. Measurements were taken 1) superior to porion, 2) at greatest height of squamous suture, 3) approaching the coronal suture. Locations 2 and 3 would be most similar to the high arching seen on the Hadar AL 162-28 cranial fragment.

Specimens were set laterally on a beanbag and oriented in the Frankfurt Horizontal (FH) (here synonymous with *norma lateralis*) with the left parietal surface exposed. Extra-fine dental floss was then used to set a horizontal line from asterion across the parietal and temporal surface. The distance was then measured between this line and the squamosal suture at points superior to (1) porion, (2) maximum height of suture, and (3) approximate (within 4 mm) to the coronal suture. The point relative to maximum height of the suture was usually towards its midpoint and was never taken where the suture veered dramatically in either direction. (Rather, this measurement reflects a conservative estimate of the course of the squamosal suture.) The identical procedure was used when measurements were taken on the right side. Measurements were repeated at least twice on each specimen using a Mitutoyo digital caliper and recorded in millimeters to an accuracy of 0.01 mm. The skull was reoriented prior to suc-

cessive measurement. When measures differed by 1.5–2.5 mm, the entire procedure was repeated, and the means of the measurements were used. Results were rounded to the nearest 0.25 mm for the purposes of analysis. It was very rare that measurements differed by more than 1 mm, and our use of 0.25 mm really results from numerical calculations rather than extreme measurement precision. (Fig. 1 illustrates these three points on the chimpanzee crania.)

In the case of the australopithecine (*Australopithecus africanus*, *A. afarensis*, *A. robustus*, and *Zinjanthropus boisei*) hominid crania (see below), the incomplete and unique nature of each specimen necessitated more flexibility. First, it is not possible to ascertain an FH precisely on endocasts. The usual method of orienting an endocast is to place a horizontal plane through occipital (OP) and frontal poles (FP) of the brain endocast (Connolly, 1950:121–129, and Hirschler, 1942, provide discussions of these landmarks). This is the most common

method of illustrating the lateral aspect of an endocast. In general, the FH plane is lower than the FP-OP plane, but they are almost parallel.¹ Second, some of the endocasts and crania of the fossil hominids are incomplete, and the orientations must be regarded as approximate to the FH, as they are oriented in a normal lateral view. A sliding caliper was used to *estimate* the maximal distance of the squamosal suture above (or below) the most likely location for the asterionic landmark. Where possible, each was oriented as in the chimpanzee specimens, i.e., in norma lateralis. Third, it should be remembered that the endocasts provide evidence for the location of the sutural line of the squamosal suture, while the crania show overlap of the temporal bone over the parietal. There is no way to control for these differences except to note them for each individual specimen. In any event, either the sutural imprint on the endocasts or the squamosal suture on the crania have an essentially similar relationship to either the ecto- or the endocranial location of asterion, the meeting place for the squamosal suture with the lambdoidal and occipitomastoid sutures. With overlap, the cranial measurements will be on average larger than the measures on the endocast surface. However, in neither modern forms nor fossil hominids will the slight difference between ecto- and endocranial sutural landmarks seriously alter the relationship of the squamosal suture to asterion. For example, OH 5 shows a difference of roughly 5–10 mm between endo- and ectocranial sutural marks, and this is the maximum found in any of the early hominids so far. The following hominid cranial/endocast fragments were measured: MLD 37/38, MLD 1; STS 5, STS 60; SK 1585, SK 48; Taung; OMO 338s; OH 5; KNM-ER 406, KNM-ER 732; Hadar AL 333-4. (MLD 1, STS 60, SK 1585, and Taung are endocasts.)

Univariate statistics (mean, mode, s.d., range) were calculated for all measurements within each taxon and for the *Pan* taxon as a whole. The Student *t* test was used to see if there were left-right side differences, and Pearson correlation coefficients were calculated for the three measurements. Analysis of variance using taxon as a covariate and side as a main effect was also performed to see if either side or taxon significantly influenced measurements.

RESULTS

Table 1 provides the mean, standard deviation, range, and mode for each of the three measurements for the taxa of *Pan*. Table 2 provides the measurements and/or estimates for each of the fossil hominids. Analysis of variance shows that the right side is usually higher than the left in all groups and that there is also significant between-group variation (Table 3). We do not know the explanation for this asymmetry.

Table 4 shows measurements taken on 18 *Pan* brains or endocranial casts between the landmarks of occipital pole (OP) and the posterior or caudal end of the intraparietal sulcus (IP). These results reveal that, despite their smaller brain capacities, the *Pan* brains show an OP-IP distance roughly twice as great as in the Hadar AL 162-28 brain endocast.

DISCUSSION

A number of interesting points emerge from this study. First, as Falk (1986) suggested, there is indeed variability of the relationship between the squamosal suture and the asterionic landmark. However, the only instances in which the squamosal suture falls at the same level or inferior to asterion is at measure 1, just superior to porion. Of the seven cases from a total of 244 measurements (using both sides), four appear at measurement 1 above porion. Not a single case occurs in which the suture is inferior to asterion for either measurement 2 or 3, which is closest to the inferior margin of the coronal suture. Of 150 *P. t. verus* crania observed but not measured at Harvard, three crania showed asterion to be slightly lower than point 2 or 3. Measurements 2 and 3 are thus overwhelmingly more superior

¹R.L.H. has examined roughly ten radiographs of pongid crania and will report the exact measurements in a later paper. For the present, it can be said that the FH and FP-OP planes are nearly parallel, differing within 5–10°. We emphasize that our comments regarding the parallelism between these two planes refers to pongids and early hominids only; with increased brain size and craniobasal flexion, the two planes depart significantly from a parallel condition in modern humans.

TABLE 1. Statistical results for measurements 1–3 for each *Pan* species/subspecies. Both sides¹

	Measure 1	Measure 2	Measure 3
<i>Pan t. verus</i> (N)	18	18	18
Mean	6.89	9.90	9.50
Mode	8.50	11.25	4.5
Range	0–13.25	2.25–15	2.25–15
s.d.	3.77	3.50	3.74
<i>Pan t. schweinfurthii</i> (N)	20	20	18
Mean	5.59	9.17	8.28
Mode	5.5	12.0	11.25
Range	–4.5–11.5	0.5–16	0–17.5
s.d.	4.49	4.23	4.48
<i>Pan t. troglodytes</i> (N)	26	26	26
Mean	5.46	8.10	8.80
Mode	8.5	4.25	3.75
Range	–1.25–12.5	0.25–16	1–16
s.d.	3.19	3.81	4.33
<i>Pan paniscus</i> (N)	18	18	18
Mean	2.92	4.57	4.97
Mode	1.00	3.75	5.5
Range	–1.75–7	2.5–8.5	1.75–10.25
s.d.	2.31	1.66	2.12
Combined, all <i>Pan</i> (N)	82	82	80
Mean	5.25	7.98	7.98
Mode	8.5	4.25	4.0
Range	–4.5–13.25	0.25–16	0–17.5
s.d.	3.72	3.95	4.13

¹ All measurements are in mm. Ns refer to the number of measurements taken for both left and right sides. Measurements 1, 2, and 3 correspond to those shown in Figure 1.

TABLE 2. Measurements and/or estimates for maximum height of squamosal suture above asterion (in mm)¹

AL 333-45 (left) C	35 at porion; 30 toward coronal s.
Omo 338s (left) C	15–20 minimal, at 35 ant. to asterion
STS 60 (left) E	7-12 (minimal), 15–20 ant. of porion
STS 5 (left, right) C	35 superior to porion
Taung (right) E	clearly higher (est. 15 on temp. flake)
MLD 37/38 (left, right) C	32 sup. porion; 25–28 sup. porion
MLD 1 (right) E	clearly higher, but unmeasurable ²
SK 1585 (right) E	10 min., 15 mm ant. to porion
SK 48 (right) C	crushed, but higher above porion ³
KNM-ER 406 (right) C	35 toward coronal, 40 sup. porion
KNM-ER 732 (right) C	Est. min. of 20–25.
OH 5 (left, right) C, E	both, 30–35 sup. porion; 28 toward coronal suture

¹ Suggested value for AL 162-28, when correctly oriented: 20–25 mm superior to asterion roughly at a coronal plane through the poria. Where possible, cranial (C) portions were oriented in the Frankfurt Horizontal or norma lateralis. Endocasts (E) were oriented in an OP-FP plane where possible. The two planes are very similar, and in the central part of the crania or endocast, the relationships between squamous suture and asterion would not appreciably differ.

² MLD 1 is too fragmentary for actual measurement, but in that asterion is there, any orientation that elevated it above the squamosal suture would put the cerebellar lobes posterior to the cerebral ones, which would be a mistake in this case.

³ The SK 48 cranium is very crushed, but the temporal squamous portion clearly extends substantially above asterion.

than measurement 1, and it would be these latter two measurements which are the most similar in their position to the squamosal remnant on the *A. afarensis* AL 162-28 specimen. In sum, the limited variability of the relationship of the squamosal suture to asterion in *Pan* suggests that the orientation favored by Falk would be an extremely rare occurrence within a hominoid such as *Pan*.

The hominid pattern is very different. Table 2 shows that, for early hominids, there is

a greater degree of arching of the squamosal suture than in *Pan*. The estimates by and large far exceed the average or modal *Pan* values. Not a single hominid encountered thus far shows a disposition of the squamosal suture to be inferior to the asterionic landmark. SK 1585 is *Pan*-like in its flattish morphology of the squamosal suture, but the maximal height is still 5–7 mm superior to asterion. In general, the highest part of the squamous sutural arch on hominids is located well anterior to asterion and in partic-

TABLE 3A. Analysis of variance: Results for side(s) and taxonomic group (G)¹

Measurement	F ratio	Signif.
1	7.967 (G)	0.0060
	8.330 (S)	0.0050
2	17.778 (G)	0.0001
	8.246 (S)	0.0052
3	7.108 (G)	0.0093
	0.096 (S)	0.0035

¹The F ratios are the results of dividing between-group variance by within-group variance. In this analysis, "taxonomic group" was allowed to covary, while "side" was treated as a factor or main effect. The results show that the right side is significantly higher than the left over pooled values and that there is also a taxonomic effect that is significant, possibly related to cranial capacity (cf. Table 1). A Student t test applied to aggregate data for left and right sides showed significantly higher values for the right side, just as the ANOVA analysis did.

TABLE 3B. Student t test for side differences¹

Measurement	Left (mean)	Right (mean)	t Value ²	P
1	4.14	6.63	-3.23	.0017
2	6.77	9.47	-3.26	.0016
3	6.66	9.59	-3.36	.0012

¹See footnote to Table 3A.

²The negative t values simply indicate that the right-side values are larger and are being subtracted from the left-side values.

TABLE 4. Arc measurements for OP-IP distances on Pan brains and the Hadar hominid AL 162-28¹

Specimen	Volume (mL)	Distance (OP-IP) ¹
<i>Australopithecus afarensis</i>		
AL 162-28	375-400	15-16
<i>Pan troglodytes</i> (based on 18 <i>Pan</i> brains, not including infant)		
Range	200-400	24.5-35.5
Mean	271	31.2
S.D.	20.7	3.08
Infant value	140	25.5

¹No. of s.d.'s that AL 162-28 specimen's IP-OP distance is from the *Pan* average (without infant): 5.1. Distance (mm) from occipital pole (OP) to the caudal or posterior end of the intraparietal sulcus (IP). Reproduced from Holloway, in press, with permission of the publisher.

ular to porion. These general relationships hold whether the crania/endocasts are oriented in the FH plane, the OP-FP plane, or an approximation to norma lateralis. We believe these findings fully vindicate Kimbel et al.'s (1982) orientation of the Hadar AL 162-28 cranial fragment and the subsequent positioning of the endocast by Holloway (1983) and Holloway and Kimbel (1986). Furthermore, we believe that these results leave Falk's (1985, 1986) orientation, the ensuing endocranial positioning, and most significantly her interpretation of brain evolution open to doubt.

First, Falk's (1985) orientation was nearly 40° different from that of Kimbel et al. (1982), which placed the squamosal suture inferior to asterion. Falk's orientation brought the cerebellar lobes of the endocast into a more posterior projecting position, relative to the occipital pole (OP) of the occipital lobe. This morphological pattern does occur in *Pan*, but very rarely. Of the almost 80 *Pan* (both *troglodytes* and *paniscus*) brain endocasts in the collection of RLH, only two or three cases show such a morphology when the endocasts are oriented in an OP-FP plane. There are no fossil hominid cases where such a pattern occurs. This primitive feature, which is not shared by pongids and hominids, thus vanishes when the cranial fragment is correctly aligned.

Second, Falk's (1986) argument regarding the orientation of the endocast introduced two tiny dimples, which she labeled as superior temporal sulcus (TS) and its superior parallel branch (P), arguing that the endocast could not be oriented any other way given the usual orientation of these sulci. These sulci are impossible to identify in such an exact matter. They could alternatively be the sublunatus or postlunatus sulci (Shanta and Manocha, 1969). We think it is risky to attempt to orient a large cranial fragment using minor or tertiary cerebral convolutions that are highly variable, particularly when these sulci are controversial and when there are good solid ectocranial landmarks such as the squamosal suture and asterion.

Finally, in support for her pongid-like interpretation of the Hadar AL 162-28 fragment, Falk criticizes Holloway and Kimbel's (1986) statistics. Falk (1986:537) states:

If I am correct in my observations, then Holloway and Kimbel's statistics on distances between points on the endocast are not useful since all of them would depend on an incorrectly identified occipital pole (OP) (if one is used which is consistent with Holloway and Kimbel's orientation of the endocast). The OP I have identified . . . does not project as far caudally in this specimen as it does in most hominoids. This alone would account for shortened distances. Furthermore, absolute distances should not be used to refute a chimpanzee-like sulcal pattern; ratios would be better.

We believe that the evidence indicates otherwise. The OP is the most projecting caudal point on the occipital lobe *however*

the endocast or brain is oriented (within reason, of course). Obviously, the point will differ relative to a baseline depending on the orientation of the endocast, but there will be only one region on the occipital lobe of the endocast that has the requisite curvature corresponding to the cusp of the occipital lobe curvature and its approximation to the lateral calcarine sulcus. We both correctly identify OP. Figure 1 in Holloway 1983 shows the location of OP very clearly, a position with which Falk has not yet disagreed (Connolly, 1950, and Hirschler, 1942, discuss the conventions for identifying these landmarks). In that sense, the OP was the same landmark used by both Holloway (1983) and Falk (1985). The "statistics" dismissed by Falk show the following: the distance between OP and the lunate sulcus (the posterior limit of intraparietal sulcus IP) is approximately one-half that separating these structures in *Pan* (at that time based on ten chimpanzee brains), despite the fact that the brain volumes were less than the 375 ml estimate for Hadar AL 162-28. This table was published by Holloway (1985:57), and the sample was enlarged for a recent presentation (Holloway, in press). Table 4, adapted from Holloway (in press), shows that for 18 *Pan* brains and brain casts the arc measurements average 31.2 mm from IP to OP, a figure roughly double that of AL 162-28 (16 mm). The average *Pan* brain size is smaller than the lower estimate for AL 162-28 (e.g., 271 vs. 375 ml). An infant chimpanzee with a brain volume of 140 ml has an IP-OP distance of 25.5 mm, still well above that of a substantially larger brained adult AL 162-28 hominid. The AL 162-28 specimen's IP is 5.1 s.d.s from the *Pan* average. We await Falk's own measurements of this distance according to her orientation.

There is no argument about our respective identification of the OP, nor that of IP, and the suggested ratios are not available in that the frontal portion of the brain endocast is missing. The important "ratio" to remember here is that, with the same brain size or a smaller one, all chimpanzees have roughly twice the distance between IP and OP as the Hadar AL 162-28 specimen. Clearly then, however one orients it, the posterior part of IP on the Hadar AL 162-28 specimen is in a very posterior position relative to the aver-

age (and all cases studied here) *Pan* brain. This indicates that the caudal end of IP is *not* in a typical *Pan* position, suggesting cortical reorganization by the time of the Hadar hominids.

The implications of these results for the issue of brain evolution are very important. If IP has been correctly identified by both Falk (1985) and Holloway (1983), the Hadar AL 162-28 brain endocast is the earliest hominid fossil showing cerebral reorganization toward a human pattern, meaning a relative reduction of primary visual striate cortex (area 17 of Brodmann) with an attending relative increase in posterior parietal cerebral cortex, presumably peri- and parastriate areas 18 and 19 of Brodmann (1909). This suggests, indirectly, a relative increase in posterior parietal lobule, involving both the angular gyrus (area 39 of Brodmann) and the supramarginal gyrus (area 40 of Brodmann). Posterior parietal cortex is important in the mediation of perception of spatial relationships among objects, and the analysis and integration of sensory information (i.e., cross-modal matching). Elsewhere (Holloway, in press), I have attempted to link these changes suggesting reorganization of the early hominid brain to multimodal processing, possibly involved in social communication, and an increased capacity for spatiovisual integration associated with adaptations involving bipedal locomotion and opportunistic feeding within patchy environments. In the sense that cerebral reorganization might have distinguished early hominids from true pongids, which retained a primitively located lunate sulcus, the Hadar AL 162-28 endocast could well be the mother of all hominid brains, since its cerebral organization suggests a more derived hominid pattern of relative increase of inferior parietal association cortex through the reduction of primary visual cortex.

ACKNOWLEDGMENTS

R.L.H. is grateful for support from the NSF, grant BNS-84-18921. A great debt is owed to many individuals and institutions for their gracious assistance and access to specimens: Dr. G. Musser, J. Augustin, W. Fuchs, American Museum of Natural History; Dr. T. van den Audenaerde, Dr. W. van

Neer, Koninklijk Museum voor Midden-Afrika; Dr. R. Thorington, Dr. C. Wozencraft, L. Gordon, National Museum of Natural History, Smithsonian Institution; Dr. B. Latimer, L. Jellema, Cleveland Museum of Natural History; M. Rutzmoser, Museum of Comparative Zoology, Harvard University, Dr. D. Pilbeam and Dr. J. Barry, Peabody Museum and Dept. of Anthropology, Harvard University. Critical comments by Dr. William Kimbel were very useful and are greatly appreciated. Critical commentaries by Dr. Dean Falk and an anonymous referee were useful in editing this paper. We are especially grateful to Dr. Matt Cartmill for his helpful editorial suggestions.

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