

# Revisiting the South African Taung Australopithecine Endocast: The Position of the Lunate Sulcus As Determined by the Stereoplotting Technique

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**ABSTRACT** Falk's (1980a) claims regarding the pongid-like disposition of convolutional patterns on the South African australopithecine endocasts are critically examined. Using a stereoplotter apparatus and a small sample of chimpanzee brain casts, the angular coordinates of the lunate sulcus are recorded, and placed as such on the Taung and SK 1585 endocasts. The resulting location of such pongid-oriented lunate sulci violates the gross morphology of the australopithecine endocasts. Relative brain:body weight ratios for *Australopithecus* are shown to be advanced over any of the pongids. In addition, evidence is provided from LeGros Clark's (1947) paper that controverts certain of Falk's claims regarding his methods. It is concluded that the secondary sulci and gyri on the now available australopithecine endocasts are not clear enough to warrant unambiguous demonstration; with regard to the lunate sulcus, the Taung endocast *does not* show a pongid pattern.

In a welcome addition to the growing literature on hominid brain endocasts, Falk (1980a) has reinterpreted the sulcal and gyral patterns of the South African gracile australopithecines and their significance toward a fuller understanding of hominid brain evolution. After direct observation and palpation of all six available endocasts (5 gracile, 1 robust), Falk has concluded that previous interpretations regarding their hominid rather than pongid status are incorrect (e.g., Dart, 1925, 1926; Broom and Schepers, 1946; Broom et al., 1950; LeGros Clark, 1947; Holloway, 1966, 1970, 1972a, 1972b, 1973, 1974, 1975, 1976a, 1978).

It is a well appreciated fact that direct visual observations of convolutional relief patterns on endocasts are difficult to substantiate (e.g., LeGros Clark et al., 1936; Hirschler, 1942; Symington, 1916; Connolly, 1950; von Bonin, 1963; Holloway, 1978, to mention but a few). More often than not, interpretations depend on skills and perceptions that are always open to doubt and reinterpretation. Palpation,<sup>1</sup> as a technique for substantiating the presence or absence of convolutions, has a chequered history (i.e., Gall, Spurzheim, and other phrenolo-

gists), but has never been validated. Wholly objective and precise methods for deciding which sulcus or gyrus is which, simply have not been developed, and we are left in the unfortunate "limbo" of having one observer saying "X" and the next saying "Y." Since there are so few practicing "phrenologists"<sup>2</sup> available, the matters of depiction and interpretation remain open and somewhat confusing.

The Taung endocast is probably the most infamous example of all, with a long controversial history, and now, some 55 years after its discovery (Dart 1925), it is to be demoted once again to a pongid-like status.

This paper will attempt to bring greater objectivity to such studies, at least with respect

<sup>1</sup>I think Falk places undue stress on palpation as a technique which is somehow more valuable in her study than those of others who have not mentioned it. The fingertips are no less easily deceived than the eyes, since it is the brain and its conceptual contents that either interpret the sensations or the preconceptions.

<sup>2</sup>I have used this term even though it has negative connotations. "Paleoneurologists" would be better, but given the stress on palpation and surface features, this term has a certain embarrassing appropriateness.

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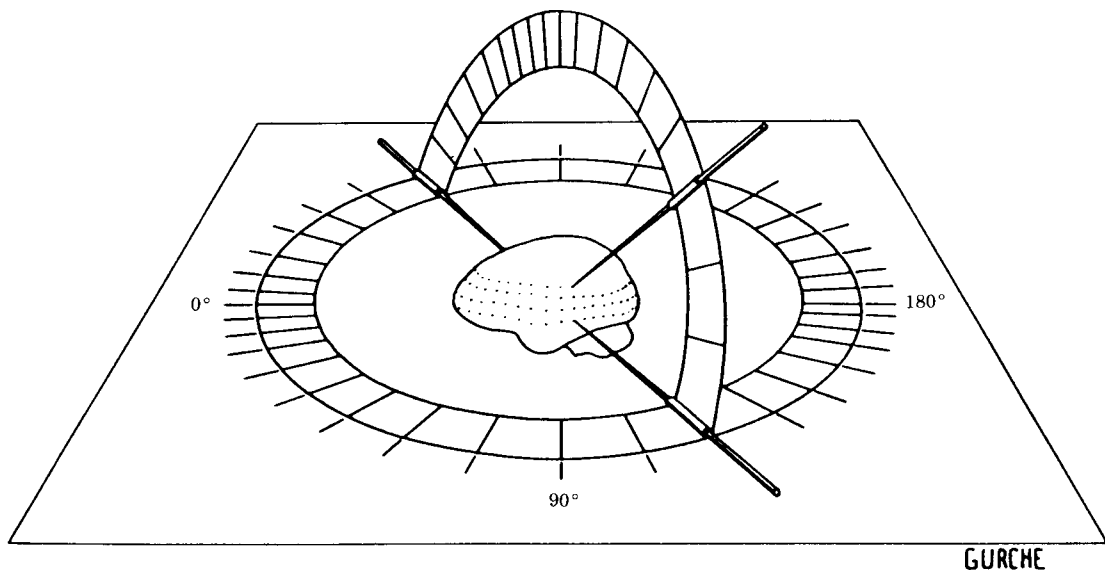


Fig. 1. Schematic drawing of the stereoplottting apparatus used to locate the coordinates of the lunate sulcus on five Chimpanzee brain casts. The averaged values were then

placed onto the Taung and SK1585 endocasts once they were similarly positioned in the apparatus.

to the position of the lunate sulcus, upon which Falk has placed her major emphasis. Though any positive proof of the exact location of the lunate sulcus is not possible on the basis of the Taung endocast, it can be shown where it is *not* located. While it is appreciated that the reader might find the above statement somewhat odd in that an emphasis is being placed on a negative rather than a positive position of a morphological feature, the emphasis is necessary, given the peculiar combination of its published history, its significance, and the nature of the endocast itself.

In concentrating on the position of the lunate sulcus a newer technique will be used to show that Falk's interpretation is incorrect. This is not to be construed purely as a rebuttal to Falk's efforts to provide a fresh, and unique assessment of the australopithecine endocasts, although it will be clear that this author does not agree with many statements and conclusions that Falk provides in her paper. Thus, in addition to applying some different techniques to the problem of the Taung lunate sulcus, other comments and observations regarding LeGros Clark's (1947) paper, relative brain size, the frontal lobe, and indices and reorganization, will be provided. As it is the firm con-

viction of this author that the available australopithecine endocasts are not *sufficiently* preserved to permit truly accurate and unassailable gyral and sulcal identifications, I will not attempt to provide an alternative convolutional map.

#### MATERIALS AND METHODS

##### *Stereoplottting the lunate*

In the course of several years of study on the dorsal surface of some 92 hominoid endocasts, the utilization of the Oyen and Walker (1977) stereoplotter has been a useful methodological advance in quantifying the radial distances from the surface to an homologous center point located within the once-living brain (see Fig. 1).

Aside from these measurements (see Holloway 1976a,b, 1978, 1979, 1980, 1981, for details), which can be treated in numerous statistical ways, the stereoplotter apparatus also permits accurate determinations of various surface landmarks in a polar-coordinate notation, i.e., two angles and a radial distance,  $r$ . One aspect of the studies in progress using the stereoplotter is that gyral and sulcal landmarks have a relatively stable location in coordinates, although the shapes are variable.

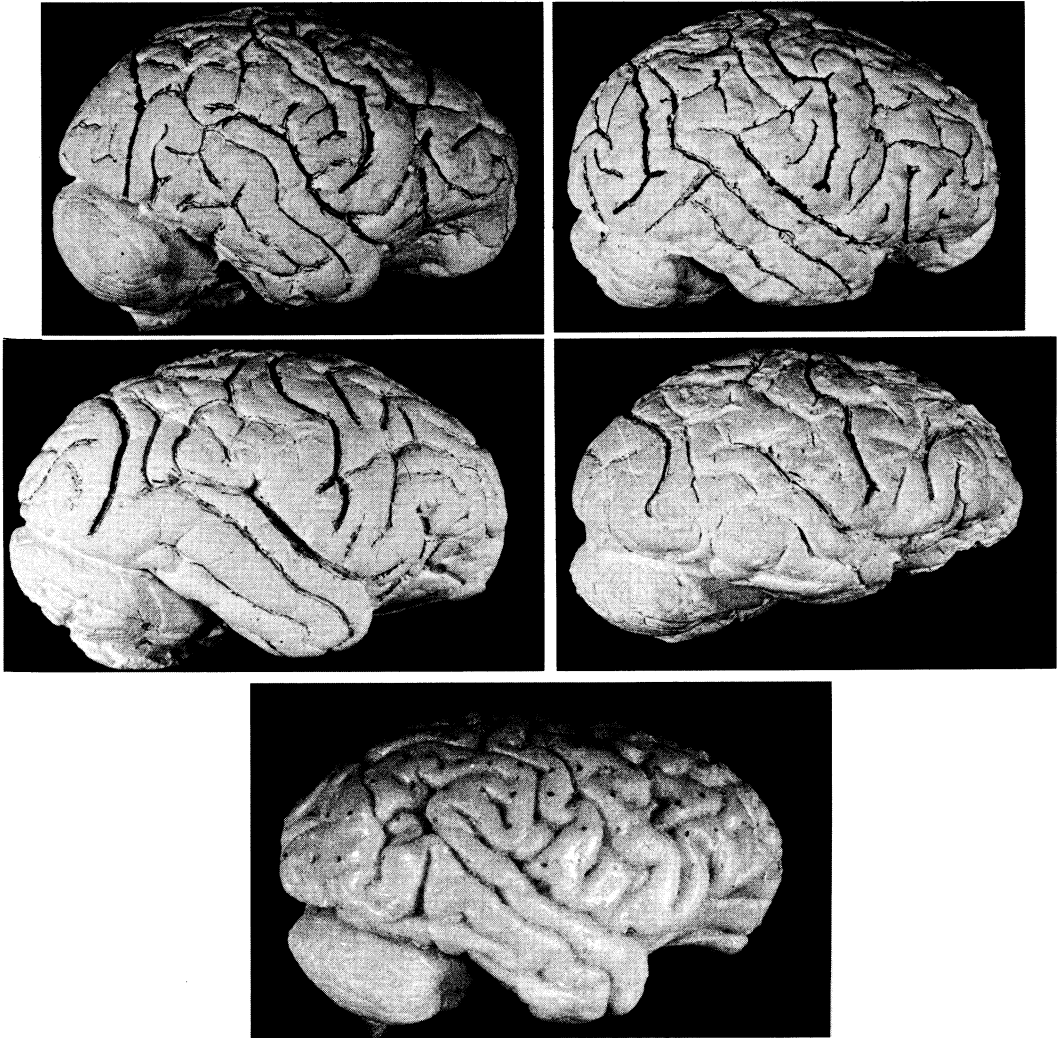


Fig. 2. Composite photograph of the right lateral side of four Chimpanzee brain casts. The fifth, the largest, is actually the left hemisphere, but has been reversed here. The lun-

ate, superior temporal, Sylvian, and central sulci have been emphasized with pencil.

Thus far, the actual brains of five chimpanzees<sup>3</sup> (*Pan troglodytes*) have been obtained through the courtesy of Dr. Alan Walker and Dr. David Bodian. Dr. Yves Coppens and Dr. Wally Welker, have provided casts of fully adult *Pan*. Three chimpanzee brains were received hardened in fixing solution, and all meningeal tissue (dura, arachnoid, and pia mater) were later removed. Next, the right and left hemispheres were cast using dental Xantopren blue, which is ideally suited for such work. Retainers are not required; little if any heat is

generated; the flow characteristics are superb; the molds are ready for removal within five

<sup>3</sup>I hope that critics will not find the number *five* unpalatable. Prior to this study, I could not find a single chimpanzee brain cast (aside from Prof. Welker's) in any of the following institutions: American Museum of Natural History, Cleveland Museum of Natural History, The British Museum of Natural History, London University, Oxford, Cambridge, The Smithsonian, Harvard, Yale, Chicago, the University of Pennsylvania, or the Carnegie in Pittsburgh. And before critics complain of small sample sizes, I hope they will first examine all of the published diagrams, photographs, and line drawings of chimpanzee brains that exist in the literature from the late 19th century on. They will discover that for *Pan*, a lunate is a lunate and that it is always in just about the same place, displaying an annoying (or pleasing) regularity.

minutes; there are no adhesion problems; and the finished mold is very tough but flexible. There is no detectable shrinkage.

Plaster or plastic casts of the hemispheres were made directly from the Xantopren molds, and all available sulcal and gyral patterns were readily captured (see Fig. 2).

The frontal and occipital poles of each brain cast were marked, and each brain cast was aligned within the stereoplotter such that the center of the cast was equally distant from both poles; the midsagittal plane aligned along the 0°–180° axis of the stereoplotter table; and the horizontal plane passing through the two poles and center point.<sup>4</sup>

For the purposes of this study, only the lunate sulcus was charted, i.e., its angular coordinates determined. Radial distances were not taken as they are irrelevant to the issues to be discussed herein.

Once the coordinates were established and averaged for each 10° angle above the horizontal plane, the Taung and SK 1585 endocasts were *similarly* oriented in the apparatus. The average *Pan* values were then marked onto the hominid endocasts (see Fig. 3).

The resulting *Pan*-based location of the lunate on the Taung and SK 1585 endocasts were next evaluated as to whether any of the existing endocranial morphology of the endocasts were indeed compatible or congruent with such a pongid location.<sup>6</sup>

#### *Morphological observations*

In addition to the stereoplotting methods discussed above, 42 endocasts of *Pan paniscus*, 36 of *Pan troglodytes*, 40 of *Gorilla gorilla*, and 20 *Pongo pygmaeus* were examined visually for evidence of convolutional imprints in the parieto-occipital zone to ascertain whether the lunate (in particular) sulcus could be identified.<sup>7</sup>

It is apparent that a strict adherence to the average values in Table 1 is not the best approach, since the values of 53°, 50°, and 41° (i.e., 10°, 20°, and 30°, respectively above the horizontal plane) produce a somewhat pronounced rostrally-directed curve that is not evident on any of the actual *Pan* brains. In almost all cases, the lower margin of the lunate approximates the sigmoid sinus, and the angle to 30° above the horizontal at the superior margin of the lunate sulcus also appears relatively invariant. A more reasonable approach is to accept these two locations as empirically supportable, and correct them with a relatively smooth, but curved line, that better approxi-

mates the actual disposition of the lunate sulcus in pongids.

These results should be regarded as tentative only, since the present apparatus (stereoplotter) is not sufficiently accurate to but the nearest 2°. Table 1 indicates more variability than originally anticipated, particularly the chimpanzee cast number 3. As Figure 2 indicates, there is a very high degree of variation in overall size, undoubtedly due in part to shrinkage of the brains during fixation and age. Nevertheless, these figures do provide some objective indications of where to expect the lunate sulcus to be located if it were in a typical *Pan* position.

#### RESULTS

Figures 4 and 5 show the position of the average coordinates when plotted back onto the Taung endocast; these also include Falk's proposed position for the superior end of the lunate sulcus on the Taung specimen. Falk's placement is approximately 10 mm rostral from the normal pongid pattern, and is thus actually in a more cercopithecoid than pongid position. The dotted lines transect the *convexities* of roughly four gyri and do not align with any *concavities* that could be regarded as sulcal in nature. In other words, transferring a pongid lunate sulcus pattern onto the Taung endocast violates the existing morphological details visible on the Taung endocast. The dotted line on the SK 1585 robust endocast also traverses a convex surface in its entirety.

#### *Morphological observations*

All of the chimpanzee brain casts show strong gyral relief in the region of the occipital pole, which are a part of the lateral calcarine

<sup>4</sup>It should be appreciated that frontal and occipital poles in hominid brains are fully homologous both structurally and functionally. If a line is drawn on the medial surface connecting these two landmarks (either on the actual brains, diagrams to scale, or photographs), and divided into half, the midpoint is always in the thalamic zone just anterior to the posterior commissure.

<sup>5</sup>Since the lunate sulcus curves back toward the midsagittal plane, 30° is the limit of angular deviation from the horizontal plane. A more accurate stereoplotting device is currently being built to measure at intervals of 1°, rather than at 10° or 5° intervals.

<sup>6</sup>Both visual inspection and palpation were utilized.

<sup>7</sup>Falk notes that only "carefully selected" endocasts were used. My endocast collection is *not* "carefully selected" except that they are all adult, unbroken specimens. I too have examined the primate brains at the Smithsonian Institute, as well as other Institutions, but I found many of them to be distorted given the number of years they have been lying around in fixative solution and jars.

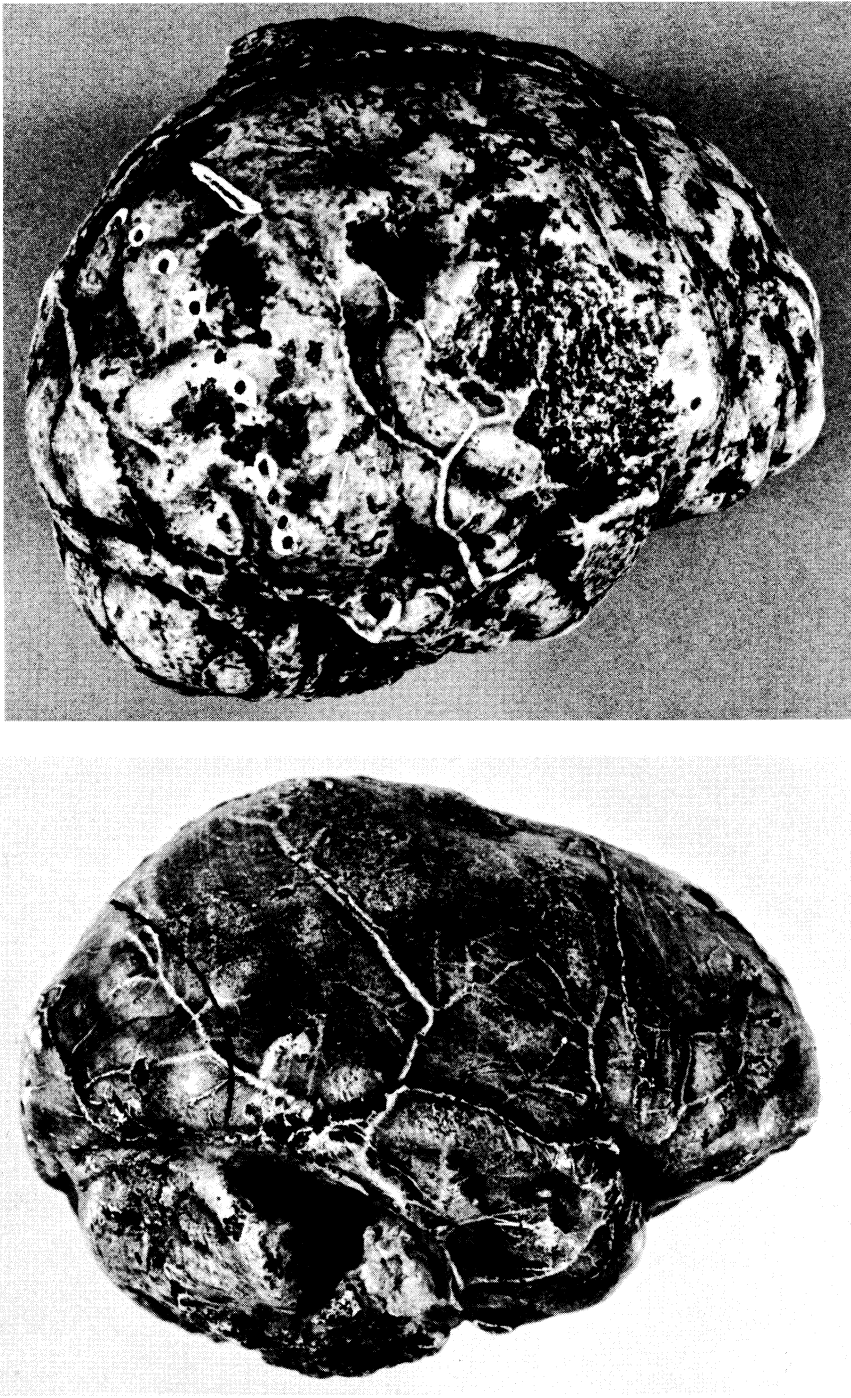


Fig. 3. Photographs of the Taung and SK1585 unreconstructed endocranial casts showing the position of the averaged Chimpanzee *brain* cast coordinates of the lunate sulcus. The Taung endocranial is superior, and has been rotated such that the occipital section (left) is forward. The dotted lines repre-

sent *Pan troglodytes* coordinates, and the upper mark is where Falk proposes the lunate sulcus to be. Note that it is about  $10-15^\circ$  above the *Pan* coordinates. Note also that the *Pan* coordinate-curve transects at least four clear gyri, and does *not* line-up with any sulci.

TABLE 1. Coordinates of the lunate sulcus on five chimpanzee brains cast<sup>1</sup>

Angle (in degrees)	Chimpanzee casts					Average
	1	2	3	4	5	
Horizontal +0°	50°	52°	53°	53°	56°	52.8°
Horizontal +10°	46°	51°	50°	50°	55°	50.4°
Horizontal +20°	37°	44°	37°	39°	46°	40.6°
Horizontal +30°	30°	38°	— <sup>2</sup>	35°	35°	34.5°
Vertical at midsagittal plane	29°	30°	29°	27°	29°	28.8°
Approximate endocast volume (ml)	330	245	288	414	290	313.4

<sup>1</sup>Approximate coordinates of the lunate sulcus for five chimpanzee brains, right side, except for #4, which is the left side of Dr. Welker's chimpanzee brain. The angles under columns 1 through 5 are those measured in the horizontal plane, and each 10° above it. Note the wide range in approximate volumes, yet relative constancy of coordinates.

<sup>2</sup>Not able to measure.



Fig. 4. Occipital view of the Taung endocast (right) and *Pan* brain cast provided by Dr. Welker, positioned in the same approximate orientation. The dots on the Taung endocast are the coordinates from the chimpanzee brain casts, and the short line in Falk's lunate placement. Note the detail of convolutional relief anterior to the lambdoid suture,

but its complete absence inferior to it. The lateral calcarine is deep in *Pan*, and goes as far caudad as the occipital pole. Note how the lateral calcarine as defined by Falk on the Taung endocast is truncated anterior to the lambdoid suture.

sulcus. Neither the Taung or SK 1585 endocasts show convolutional patterns in this region, a fact that Falk (1980a:532) also notes. On the other hand, of those endocasts of *Pan troglodytes*, *Pan paniscus*, and *Gorilla gorilla* studied, the following observations can be made:

1. The lunate sulcus, in its total extent can only be seen in about three cases for each of the two taxa, giving a percentage of somewhat less than 8%.
2. The lateral calcarine sulcus can be seen in about 40–50% of the endocasts, but only in its more rostral extent. It is almost never visible

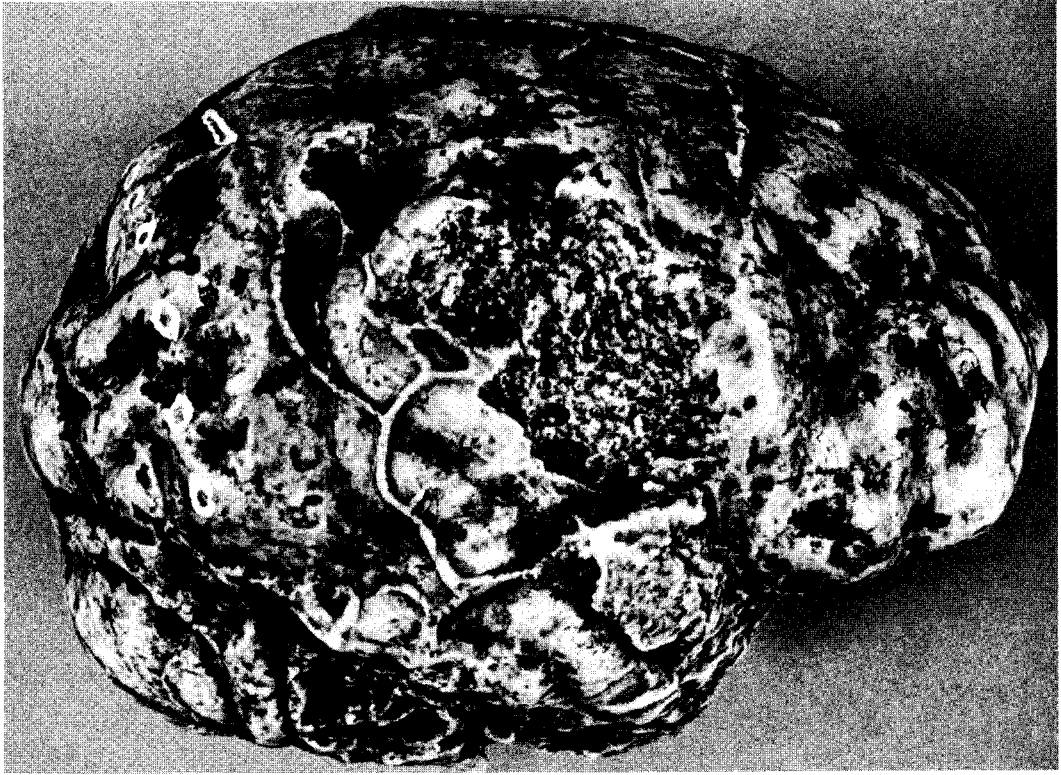


Fig. 5. An enlarged lateral view of the Taung endocranium to show details of meningeal arteries, gyri and sulci, pits and flake scar, and sutures, in relationship to *Pan* brain cast co-

ordinates (dots) and Falk's placement. Compare to Falk's (1980a:529) Figure 1B.

in the occipital pole region. These comments do not apply to gorilla or orang endocrania as these features are not visible.

3. The most inferior portion of the lunate sulcus can be seen in about 50–60% of the endocrania with variable clarity, and when present is always approximate to the sigmoid sinus, but these observations apply only to *Pan troglodytes* and *Pan paniscus*.<sup>8</sup>

#### DISCUSSION

##### *The lunate*

The major conclusion to be drawn from these studies is that the placement of the lunate sulcus in a typical pongid position on either the Taung or SK 1585 endocrania violates the morphological pattern available. This is not to be construed as a proof that the lunate sulcus on these endocrania is where Dart, LeGros Clark, Schepers, or myself believed it to be. It is sim-

ply an indication that there is no secure evidence that its position is typically pongid. *We cannot prove where the lunate sulcus is located, but only demonstrate where it is not.*

This leaves two alternatives: one, that its position is more caudal, and two, that it is more rostral. As the latter suggestion is tantamount to suggesting a cercopithecoid pattern, the burden of proof should rest on those so inclined to interpret it so. There is not a single indication on either the Taung or SK 1585 endocrania to support such an interpretation except for the one small ambiguous depression which

<sup>8</sup>Only one chimpanzee endocranium (*troglodytes*) provides a clear impression of the central sulcus. Falk's comments (1980a:526) regarding taphonomy are very interesting, and it is hoped that such studies will be pursued. However, Falk does not explain why this particular set of taphonomic circumstances *only* took place with the Taung and Sterkfontein endocrania. I believe it is dubious at best to expect the consolidation of detritus within the cranium prior to dissolution of the dura mater, particularly given the strong meningeal impressions.

TABLE 2. Encephalization quotients (E.Q.'s) adapted from Table VIII (Holloway, 1976b:116) and Table I (Holloway and Post, n.d.)

Taxon	Body weight (g)	Brain weight (g)	Author	Encephalization quotients by different formulas. (E.Q.'s in % of modern <i>Homo</i> ) <sup>1</sup>				
				1	2	3	4	5
<i>Homo sapiens</i>								
<i>Pan troglodytes</i>	46,000	420	Stephan, 1970	39.7	39.3	41.2	38.6	39.5
<i>A. africanus</i>	28,020	442	McHenry, 1975	61.9	56.4	63.2	54.2	57.4
<i>A. robustus</i>	36,550	530	McHenry, 1975	62.2	57.2	61.9	55.7	57.9
<i>A. africanus</i>	23,900	442	Holloway, 1976b	68.7	62.4	71.4	59.5	63.6
<i>A. africanus</i>	21,700	442	Holloway, 1976b	73.2	66.3	76.8	62.9	67.7
<i>A. robustus</i>	31,500	530	Holloway, 1976b	68.7	62.9	69.3	60.7	63.8

A comparison of McHenry's (1975) bodyweight estimates for *Australopithecus* based on the 12th thoracic and 5th lumbar vertebrae from STS 14 and SK 3891. McHenry used averaged diameters. My results are based on multiple linear regression of the actual diameters so kindly provided to me by McHenry. (See Holloway, 1976b:116 for details.) Note that *Pan* E.Q.'s expressed as a percentage of modern *Homo* E.Q. average about 40. When heavier body weights are used (per McHenry above), *Australopithecus* percentages of modern *Homo* E.Q. are still considerably larger than *Pan* relative values. The five equations are all derived from the empirical data expressed in grams for both brain and body weights, as provided by Stephan et al. (1970).

<sup>1</sup> Equations used:	Constants	Exponents	Modern <i>Homo</i>		Remarks
			E.Q. score		
1	0.12	0.66	6.91	Jerison, 1973	
2	0.0429	0.63	28.8	Stephan et al., 1970 (Basal insectivores)	
3	0.0991	0.76237	2.87	All primates, no <i>Homo</i>	
4	0.6216	0.58152	3.4	Pongids only	
5	1.0	0.64906	1.0	"Homocentric"	

garding comparative neuroanatomy, and the lunate sulcus in particular.

#### *Some comments on relative brain size*

In Falk's article (1980a:537), she cites McHenry (1975) and herself (Falk 1980b) to the effect that the relative brain size . . . "of australopithecines is considerably smaller than that of modern humans . . ." This is premature, given that we do not possess any demonstrably accurate estimates of body-size. Falk does not take into account the following: using McHenry's (1974, 1975) data on the 12th thoracic and 1st lumbar vertebrae of STS 14 and SK 3891, a simple stepwise multiple regression on the original dimensions, rather than averaged diameters, gave lower body-weights than McHenry's estimates. The technique also gave a higher multiple *R* and smaller residuals. These observations were published by Holloway (1976b:83). The encephalization quotients (E.Q.) are, as Falk is aware, significantly greater than chimpanzee E.Q., regardless of which equation is used to calculate E.Q. (Holloway and Post, in press). Table 2 shows these figures.

#### *Other morphological observations*

It is not my intention to debate all of the assignments of gyral and sulcal labels that Falk has provided.<sup>9</sup> In my estimation, almost none

can be identified with any certitude. This is particularly true for the frontal lobe, and especially for its inferior lateral edge. These regions are either missing or damaged on the australopithecine endocasts. Even on STS 60, which has the most complete frontal portion, the orbital surfaces on both sides are damaged. This is a pity, because the chimpanzee brains and endocasts suggest a rather sharply angulated and very concave orbital region, commencing almost immediately anterior and superior to the beginning of the Sylvian fissure. The Taung endocast is "silent" on this matter, but the STS 60 endocast suggests less angulation and concavity in that region than in extant pongids. There is simply too much damage and lack of clarity on the rest of the frontal lobe of the Taung specimen to attempt such categorical labeling of gyri and sulci. Radinsky's (1979:21) suggestion that " . . . the differences in shape of *Australopithecus* vs. chimp and gorilla endocasts may be a packaging phenomenon," is a moot point, since one cannot demonstrate this suggestion as either true or false on the basis of present materials.

<sup>9</sup>Any careful appraisal of the lateral surface of the Taung endocast will reveal the appalling fact that its surface is considerably damaged, and some of that damage is located precisely where Falk has decided to locate the lunate sulcus. Her diagram B of Figure 1 is not a good representation of the damage, and the readers should observe the endocast themselves on this point.



Similarly, Falk (1980a:538) declares that the "... difference between a human and an australopithecine (or pongid) brain is that the larger human brain has a greater number of secondary sulci. This is in keeping with the allometric expectation for mammalian neocortex, and it is possible that gross morphological differences in sulcal patterns of small and large hominoids are due entirely to allometry. That is, it is possible that an australopithecine (or pongid) brain would look like a human brain if it were enlarged to human size."

Perhaps, but the burden of proof falls on Falk to demonstrate this. This is very curious reasoning, considering the lengths to which Falk went in trying to prove the pongid-like rather than human disposition of the Taung endocast's convolutions. It is all the more puzzling to me given the actual, empirical evidence I presented in two recent papers (1976a, 1979), particularly the latter, which shows that human visual striate cortex (area 17) is considerably *less* than expected on purely allometric grounds. The facts of the matter are simple: apes and humans differ in their convolutionary patterns, and australopithecine brains did not enlarge to the human size. Consequently, we simply do not know what a pongid or australopithecine brain "... would look like if it were enlarged to human size" (p. 538).

#### *The temporal lobe*

The temporal lobe is difficult to interpret, and my remarks should not be construed as a necessary disagreement with Falk's interpretation as indicated on her Figure 1B. Her designation of *tm* (temporalis medius) is certainly a needed correction to Scheper's designation of *ti* (temporalis inferior), which is never seen so laterally situated on hominoid brain casts. The large bony flake still adhering to the natural endocast in the Sylvian region is not helpful, of course, but if Falk is suggesting that taphonomic processes were propitious for preserving the lunate sulcus and many other convolutional patterns, it is curious that the Sylvian primary fissure cannot be found. Both palpation and visual examination show that the lower margin of the crosshatched flake on her Figure 1B diagram is *clearly* a continuation of *ts*. Falk has drawn *ts* as a single curved line, but on the endocast it deflects inferiorly about 4 mm behind the most posterior portion of the flake. Between Falk's A<sup>2</sup> and the posterior branch of the meningeal artery, there is a pit, the anterior edge of which *suggests* a sulcal imprint, but that is a guess. If so, then

her A<sup>2</sup> is entirely and continuously confluent with the *ts* sulcus. Where, then, would be the superior end of the primary Sylvian fissure? The minimal distance from *ts* and A<sup>2</sup> moving superiorly and frontally is about 7 mm to any form of depression that could be reckoned as the Sylvian fissure. This produces a diagonal distance of 32 mm to the inferior margin of the temporal lobe at the sigmoid sinus. On the chimpanzee brain casts I have, this distance is maximally 27 mm. This distance of 32 mm is large compared to the distance on any chimpanzee brain cast, and should caution us about the sanctity of the *ts* identification. Additionally, from all the diagrams in Connolly, (1950:108, 113, 114), the *ts* always leads into an A<sup>1</sup> limb that tends to flex anteriorly. If Falk's *ts* is secure, where is A<sup>1</sup>? As A<sup>2</sup> is drawn by Falk, it is continuous with A<sup>3</sup>, which is a guess at best, but it is indicated as flexing downward and forward, the opposite of what it normally does in pongid brains, which is to run diagonally from the end of *ts* downward and *backward*.

Another question arises from Falk's claims. The A<sup>2</sup> limb in its most superior limit is not far removed from the interparietal (*ip*) sulcus, which runs in an anteroposterior direction, *but which always intersects the lunate sulcus in Pan*.

There simply are no indications on the Taung endocast of such a pongid pattern. Looking for an *ip* to intersect any continuation of Falk's lunate sulcus is an exercise in frustration, particularly as Falk extends the lateral calcarine (*lc*) almost to the meningeal branch posterior to her A<sup>2</sup>. *If there is always some distance between the most anterior end of the lc and the margin of the lunate sulcus, the only remaining location for the inferior part of the lunate sulcus is Falk's A<sup>3</sup>!* Something is most unpongid here. Falk (1980a:531) conveniently places A<sup>1</sup> as most probably "... located rostrally in the damaged parietal regions..." A<sup>1</sup> and A<sup>2</sup> are usually joined in pongid brains, and A<sup>1</sup> is always anterior to A<sup>2</sup>. The "damaged" portion of the Taung endocast anterior to A<sup>2</sup> (per Falk) is located a good gyrus away. While Scheper's designation of A<sup>1</sup>, A<sup>2</sup>, and A<sup>3</sup> are very suspect, his A<sup>1</sup> is more in accord with the true nature of the Taung endocast, than Falk's proposed location of A<sup>1</sup>. This region is simply not well-enough preserved to make these identifications secure.

#### *The frontal lobe*

As for the frontal lobe, I do not find her interpretation any more convincing than Schep-

ers'. First of all, the Taung is that of a young child. All of her drawings for pongids and *Homo* are from adult specimens. The loss of the prefrontal portion on Taung makes it extremely difficult to be certain of any of the more rostral gyral and sulcal patterns. I thoroughly agree that Schepers was wrong on the central sulcus. That is the coronal suture. The whole region anterior to the lower end of the coronal is too distorted to provide gyri and sulci that can be so confidently labeled. The designated *fm*, *fs*, and *r* are guesses, depending on what features one regards as the midsagittal plane. If the endocast is oriented as per Falk's Figure 1B, so that the pits and coronal suture are in the same position, one cannot see the *fs*, which could well mean that what Falk has indicated *fs* is really *fm*.

The third inferior convolution, just anterior to the coronal suture, is clearly showing more complexity than she has drawn in the Figure 1B. It is guess work to attempt to do more, but that little unidentified line under *pci* is not all of the story, which could well mean that her interpretation of "fo" leaves room for different interpretations. The same criticism applies to her Figure 4A, of the STS 60 frontal portion. The two limbs of *pci* cannot be so easily defined on the actual endocast. The whole Broca cap region shows more detail than she has rendered in her Figure 4A. Also, there is no evidence for the most superior part of the central sulcus *c*, on the actual endocast. Falk *may* be right about the lower part, but who knows? *Pci* could very well be just slightly caudal to the coronal suture.

Falk's identification of *pci* more than 10 mm anterior to the coronal suture is somewhat a problem. Cunningham's (1892) memoir, with its beautiful plates, consistently shows the precentral gyrus to be *posterior* to the coronal suture (see Plates VI, VII, and VIII), although the chimpanzee illustration of Plate VIII is that of a young specimen and *part* of Cunningham's (ibid) *pci* coincides with the coronal suture. Figure 73 in Kiss and Szentágothai (1960: 68) again shows (for modern human) a coronal suture well anterior of the precentral gyrus, and the *pci* that anteriorly delimits the gyrus. Unfortunately, the elaborate and exquisite work of Cunningham's (1892) volume does not provide the necessary data for variability in the juxtapositioning of such features in pongids. Looking at Figure 1 of Shantha and Manocha's (1969:191) illustration, one finds a *pci* only somewhat superior to the third inferior frontal convolution, which is approximately

where Falk (1980a:529) has placed *pci* on her Taung reconstruction in Figure 1B. Visual inspection *and* palpation are dubious empirical guides in the case of Taung. The lower end of the coronal suture is a very prominent and rather sharply unguled bump, and the clefts anterior to it that Falk labels as *pci* could be postmortem distortions or damage to the once overlying pterionic region.

The fronto-orbital sulcus (*fo*) in chimpanzee (and other pongid) brains is a rather deep sulcus, which extends deeply into the orbital cortex of the frontal lobe, coursing downwards to the temporal pole. What Falk has called *fo* on the Taung specimens *does not* show that deeply incised pattern in its inferior aspect just superior to where the orbital plate of bone is still adhering to the natural endocast. Consequently, I do not agree that *fo* on the Taung frontal lobe is typically pongid; nor does her small branching of the inferior end of *fo* appear demonstrable on the Taung endocast.

In fact, the convolutional morphology of the hominoid frontal lobe is notoriously variable, as any reading of Connolly's (1950) or Shantha and Manocha's (1969) discussions make obvious. None of the australopithecine endocasts, particularly Taung, STS 60, or #2, are preserved well enough to make unambiguous designations. Falk's *fo* could well be Connolly's *fi* (frontalis inferior), or Shantha and Mocha's *ca* (subcentralis anterior).

Hirschler (1942), however, did conclude that in pongids, the precentral gyrus was positioned either under or slightly anterior to the coronal suture.

#### *The occipital and parietal lobe*

There is no dispute regarding Schepers' figure of Taung. It is incorrect. But neither is Falk's drawing accurate (B, Figure 1). The two diagonal fractured zones on the posterior portion are not accurate in anterior-posterior extent, particularly the upper one just under her "1" for the lunate sulcus. The intact portion between the two scarred portions is not simply a blank space; it is a nicely rounded gyrus that goes anteriorly for about 2 mm from the lambdoid suture to roughly the edge of the posterior meningeal vessel, and it is uninterrupted by any pit or depression running from top to bottom. Falk then identifies the lower extent of this gyrus as the lateral calcarine, "*lc*," which she draws as a sulcus extending right to the edge of the meningeal vessel, but does not represent the flaked-off pits of the surface that she is apparently including as "*lc*." The lateral

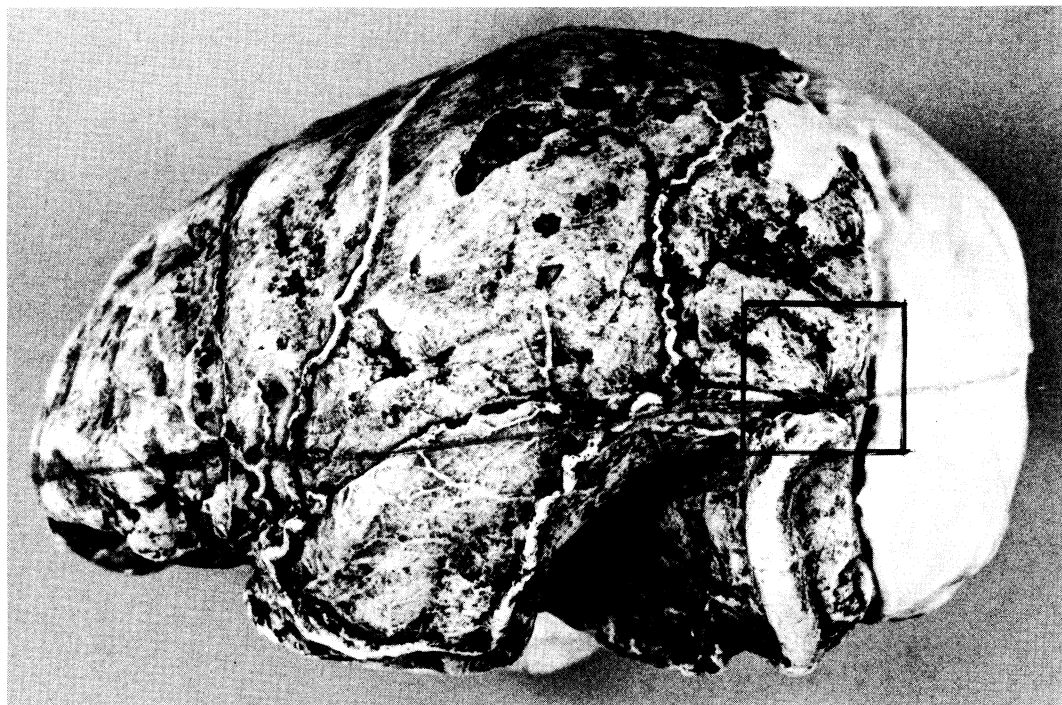


Fig. 6. Lateral view of left side of STS60 endocranial cast, with rectangle enclosing region just superior to the sigmoid sinus. No vertically-oriented sulci can be seen in this region,

which would be where the inferior part of the lunate sulcus should be located in *Pan*.

calcarine does not go that much anteriorly, even in pongids.

Anterior to the lambdoid suture, but posterior to the flaked surface zone, is a line (unnamed). If one *looks* and *feels*, that line is the rostral limit of a sulcus that has a caudal limit just at the lambdoid suture.

Falk's A<sup>2</sup> is partly a pit, not represented on her drawing. A<sup>3</sup> is purely guess work. Falk has the *oci* (inferior occipital) going in exactly the opposite direction of that in any chimp brain represented in Connolly's (1950) book. In all three cases (on pp. 108, 113) the *oci* goes from inferior to superior, rostral to caudal; i.e., \ as opposed to her /.

If one looks very carefully at the lower course of the lambdoid suture from an inferior view, i.e., with the cerebellum toward one's eyes, there is a distinct depression just anterior to the ridge of the suture, which is probably the most reasonable place to put *oci*. Furthermore, on her Figure 1B rendition, Falk totally ignores an obvious sulcus that goes all the way

inferiorly to the sigmoid sinus. She represents the upper part of it as *oci*, but ignores the rest of it. About 1.5 cm anterior to it is a large pit that she labels "*tm*." Her "pits" and those on the endocranial cast do not match.

Similarly, the inferior occipital sulcus (*oci*), when readily visible, is always caudally placed with respect to the lower end of the lunate sulcus. The *oci* is quite variable on the brains, casts, and diagrams I have examined (see above), and when present, most often courses from rostral to caudal, inferior to superior. While Falk's identification of this minor sulcus appears opposite to most cases, the variability of this sulcus should be kept in mind. The main point, however, is that on the inferior occipital-parietal region of the Taung endocranial cast, there are no sulcal features just rostral to Falk's *oci* which suggest an anterior sulcus identifiable as the lunate. It is possible that what Falk calls the *oci* is the sulcus prelunatus (PLE of Shanthi and Manocha, 1969:202; see Figure 6 in particular). The left hemispheric brain cast

provided by Dr. Welker offers such a possibility, and the PLE may even extend somewhat rostral of the lunate, as it appears to in Shanthia and Monoca's Figure 6 (p. 203). This region on the Taung endocast is very difficult to describe, however, and Falk's interpretation could be correct. If *oci*, however, one is hard-pressed to find a suitable morphological anterior boundary to it suggestive of a lunate sulcus. Puzzling too, is the lack of any indication of the lateral calcarine caudal to the lambdoid suture on the Taung endocast, a condition not shared by *Pan* brains: that is, in *Pan*, the *lc* usually extends to the occipital pole (see Fig. 4 and legend).

What Falk calls "l" for the lunate sulcus could be the parieto-occipital (*po*) sulcus, which in *Homo* is always rostral to the lunate. If what she is calling "lunate" is where she has it, then *po* would be in an unusually anterior position. Furthermore, on just about any pongid endocast, at least chimpanzee, the lower end of the lunate is always at the level of the sigmoid sinus. On STS 60, in that position, there is no evidence for a lunate sulcus there, just as there isn't for the Taung (see Fig. 6).

Some other features of the occipital lobe require discussion. In Figure 1B, Falk has extended the lateral calcarine (*lc*) almost to the small meningeal vessel of the posterior branch of the middle meningeal artery. In all of the cases of *Pan* brain casts I have examined, the actual brains, as well as the numerous diagrams in Connolly (1950), Cunningham (1892), Smith (1903, 1904, 1907, 1929), Retzius (1906), and Shanthia and Manocha (1969) (to mention but a few), the lunate sulcus is always anterior to the most rostral extension of the lateral calcarine. It is impossible to place a lunate sulcus anterior to Falk's representation of the lateral calcarine without violating the basic morphology of the Taung endocast, that is, the gyral convexities.

Finally, with respect to the upper, or most superior end of the lunate sulcus, it is most usually continuous with the primary fissure, the parieto-occipital (*PO*), in all of the *Pan* brain casts examined, and in the various diagrams referenced above. Falk's placement of the lunate provides no continuity with any feature suggestive of the *PO* on the Taung endocast. The best indication of *PO* is within the lambdoid sutural region, but this cannot be taken as a conclusive placement either. The stereoplotted *Pan* coordinates onto the Taung endocast are completely in violation of a pongid *PO*, as their superior, most medial

placement is purely gyral (see footnote 4). In this respect, Schepers' labeling is most incorrect: There is no visible *pat* (transverse parietal), *PO* (parieto-occipital), or *to* (transverse occipital). Schepers' placement of *A*<sup>2</sup> is likewise incorrect, as Falk correctly demonstrates. This leaves, however, a curious unnamed gyrus on Falk's Figure 1B diagram, which is the U-shaped depression rostral to the lambdoid suture. In most *Pan* brains, this is a part of the lateral calcarine, being the upper branch of it. This is not drawn correctly in Schepers' Figure 1A, and its most superior bend is not present in Falk's Figure 1B. If it is truly a part of the *lc*, it should somehow connect with Falk's *lc*, but it does not do so. Frankly, I do not know what it is.

### Indices

Falk's use of L/H indices is unusual. The frontal pole of the Taung is of course missing, but unless a better reconstruction of the endocast is produced, the index of 1.41 for Taung is reasonably secure.<sup>10</sup> The L/H or H/L indices for *Homo erectus*, Solo, or Neandertals are beside the point, given their known platycephaly, and larger volumes. The chimpanzee values are meaningful *only* in comparison to the Australopithecine endocasts, given that both brain weights and body weights are more commensurate. Twisting the arguments by injudicious use of indices unfortunately camouflages the very important fact that the height of australopithecine cerebral cortex above the cerebellum was relatively greater than in pongids.

### Other comments

A few final comments deserve to be made. In her article, Falk (1980a:538) notes the "future studies of comparative neuroanatomists (e.g., Armstrong, 1979, 1980a,b)" as providing us with the "fine details of neurological reorganization that occurred during human evolution." It would be well to remind the reader that any such information will only come forth on current, extant, presently terminal branches of evolutionary development, i.e., pongids and *Homo sapiens*. For the evolutionary picture of our own lineage, it will be the endocasts that so

<sup>10</sup>The amount missing is extremely small, and the frontal bone portion of the original Taung cranium clearly indicates that only a tiny portion is required for a reasonably accurate reconstruction of the whole. A similar position can be readily defended with regard to the temporal pole. But these minor points aside, any comparison of the Taung with a chimpanzee endocast, as viewed posteriorly when aligned together, will indicate a higher cerebral hemisphere for the Taung, although some *Pan paniscus* endocasts come very close.

inform us of the changes in cortical sulcal and gyral patterns that we will interpret as evidence for neurological reorganization. What Falk apparently means to say is that cortical convolutional structures may not be the best neuroanatomical units for studying evolutionary change in hominoids, particularly given the small sample we possess of early hominid endocasts and their frustrating ambiguity of interpretation. The "fine details of neurological reorganization that occurred during human evolution" (Falk 1980a:538) are not available from current studies such as Armstrong's given the very small sample sizes of particular taxa. It remains to be seen just what units of neural structure are most useful (Holloway 1969, 1970, 1976a, 1979), and I suggest that only a careful and selective approach combining both comparative and paleoneurological levels will help.

Falk has shown considerable courage (as did Schepers) in attempting to reinterpret the Australopithecine endocasts, but given secondary convolutional variability in living hominoids, and the incompleteness of the fossil materials, this writer remains as skeptical as he did in 1969 during his first encounter with the Taung endocast. That encounter, of several months duration, led me to restrict my "phrenological" endeavors to hopefully defining only a very few but key primary or secondary fissures, i.e., the central or Rolandic, lunate or "affenspalte," Sylvian, and interparietal. In the particular case of Taung, finding the most probable location of the lunate sulcus is a goal well worth the effort, although Falk and I are in complete disagreement about its location. Hopefully, the newer methods used in this paper add in a positive sense to the solution of that particular riddle. With regard to the rest of the endocast's convolutional features, I am wholly skeptical, and along with Le Gros Clark (1947) demur from providing a convolutional map.

Finally, some comments on the other endocasts. Through Dr. Falk's kindness, I saw a cast of STS 58. It's convolutional vacuity is depressing. Numbers 2 and 3 from Sterkfontein are without much value, but for different reasons. Number 3 is distorted, mostly missing, and without convolutional relief. Number 2 has tantalizing possibilities in the frontal region, but it is so badly distorted that any interpretations are risky. The left frontal is displaced with respect to the small portion of temporal lobe available, there is distortion along the coronal suture, and the right prefrontal portion is displaced with respect to the same

portion on the left side. All of the frontal convolutions in Falk's (1980a:533) Figure 4B course rostrally. Any examination of the endocast shows anything but such a simple pattern. The *fo* designation is far deeper and more extensive than that on any *Pan* brain cast I have seen. The *pci* cannot be realistically placed given the relative forward displacement of the temporal and parietal regions toward the frontal lobe, as the very raised ridge of the patent coronal suture indicates. The central sulcus, *c*, is purely guess work. The *fs* and *fm* have anecdotant horizontal limbs that Falk does not place on her Figure 4B.

As for Falk's (1980a:534) remarks regarding the STS 58 and STS 19 endocasts,<sup>11</sup> I am regretful that Dr. Clarke's search did not uncover STS 19, which I examined at the Transvaal Museum in 1969 and 1972.

#### CONCLUSIONS

1. While Falk's reanalysis of the Taung endocast correctly points to several errors of Schepers' earlier analysis, her arguments regarding an essentially pongid convolutional pattern on the Taung endocast are not empirically founded.

2. When the coordinates of the lunate sulcus are determined for *Pan* braincasts and replotted back onto either the Taung or SK 1585 endocasts, the resulting placement violates the morphology present on these endocasts. Falk's placement of a pongid-like lunate sulcus pattern crosses a number of clear gyri, and is considerably anterior to a pongid lunate sulcus.

3. The assignment of the lateral calcarine (*lc*) and inferior occipital (*oci*) sulci by Falk on the Taung endocast to their respective locations require that a lunate sulcus be located anterior to their most rostral limits. There are no indications of such a placement on the Taung endocast.

4. It is highly unusual for sulci such as the lateral calcarine or inferior occipital to appear on an endocast without a clear representation of the lunate sulcus. Similarly, on pongid brains, the lunate and parieto-occipital fissure are most usually confluent.

Falk's placement of the upper end of the lunate does not provide a relief pattern commensurate with such a basic pongid morphology.

<sup>11</sup> Puzzled by Falk's comments regarding STS 19, I examined my old 1969 notes, in which I was listing all specimens that appeared to be good candidates for endocasting. My entry: "STS-19 basal fragment fantastically good for casting basis craniae." Then follows a page and a half of measurements. May 1972, at the Transvaal Museum, offered another opportunity to examine STS 19 as my notes indicate.

There is a clear gyrus where there ought to be a parieto-occipital fissure.

5. Almost all pongid occipital lobes have a strong calcarine sulcus extending to the inferior aspect of the occipital pole. The Taung endocast is without any suggestion of a lateral calcarine in that position. In fact, the most caudal limit of Falk's *lc* is truncated well-anterior to the lambdoid suture.

6. On pongid endocasts (*Pan*, *Gorilla*, *Pongo*) where there is evidence for a lunate sulcus, the inferior end is invariably approximate to the sigmoid sinus. None of the Australopithecine endocasts (Taung, STS 60, SK 1585) show any indication of a lunate in such a position.

7. The frontal lobes on the Taung, STS 60, and Type 2 endocasts are extremely difficult to interpret, given the fact that they are either missing some portions (Taung), damaged (STS 60), or distorted (Type 2). Falk's location of the inferior precentral sulcus (*pci*) is problematical, given that it is usually located either caudal to, or approximate to, the coronal suture, rather than well anterior to the suture. The placement of the fronto-orbital (FO) sulcus on the Taung, STS 60, and Type 3 endocasts must remain as guess-work, until better fossil specimens are discovered.

8. Falk has misread LeGros Clark's (1947) paper on the Australopithecines. LeGros Clark did work directly on the specimens and not merely with Schepers' figures.

9. The relative brain size of the Australopithecines, expressed in terms of E.Q.'s, appear significantly advanced beyond pongid (e.g., *Pan*) values, approximating 60% of the modern human value, rather than the 40% figure for *Pan troglodytes*.

10. Indices expressing degrees of platycephaly are not relevant to the question of cortical reorganization in *Australopithecus*. The cerebral height of the Taung and SK 1585 endocasts are relatively high compared to the greater majority of pongid endocasts, approached only by the species, *Pan paniscus*.

11. The combination of a more human-like placement of the lunate, higher percentage of modern *Homo* E.Q. values, and a higher cerebral height all suggest a reorganizational pattern of Australopithecine brains toward a *Homo* rather than pongid pattern.

12. Comparative neuroanatomical approaches (e.g., the thalamus per Armstrong, 1979, 1980a, b) are valuable but cannot answer questions regarding fossil hominid brain evolution. More objective methods of analyzing endocasts must be developed, as the only empirical

evidence for early hominid brain evolution rests upon the endocasts.

13. Detailed convolutional maps depicting secondary gyri and sulci are practically impossible given the poor quality and incompleteness of these hominid endocasts. Efforts at depiction should be limited to a few selected convolutional landmarks only.

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