New Australopithecine Endocast, SK 1585, from Swartkrans, South Africa

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ABSTRACT   The new SK 1585 endocast, found by Dr. Brain at Swartkrans, 1966, is that of a robust australopithecine, matching the endocast of the Olduvai Hominid 5 in volume, and being almost identical to it in morphology. Aside from Olduvai Hominid 5 it is the only robust australopithecine endocast complete enough to permit easy reconstruction, as only a small portion of the frontal lobe is missing. While the gyral and sulcal patterns are not clear, there are a number of features indicating that the brain is not that of a pongid, but that is has been reorganized to a hominid pattern, particularly the occipital, parietal, and temporal lobes.

A new undistorted endocast, presumably that of a robust australopithecine, was discovered in January, 1966, by Dr. C. K. Brain in the hillside dump rubble at Swartkrans (Brain, '70, '67). At the kind suggestion of Dr. Brain, I was invited to describe this endocast while visiting in Johannesburg during the early part of 1969. I am greatly indebted to Dr. Brain and Prof. P. V. Tobias for this opportunity.

This report will be limited to the description of the endocast, and its quantitative comparison with the Olduvai Hominid 5 endocast described by Tobias ('67), as the research for a comprehensive comparison of all australopithecine endocast specimens from both East and South Africa is still in progress.

MATERIALS AND METHODS

Plaster endocasts of the earlier discovered australopithecines, STS 5, STS 60, Taung, and Olduvai hominid 5 were used for comparison. Latex rubber endocasts of one adult male gorilla and one chimpanzee filled with plaster were also used as a basis for comparison for the various cerebral indices. Both the original and plaster copies of the SK 1585 were utilised, the latter measuring the same as the original.

The description of the morphology of the SK 1585 endocast was made on the basis of visual inspection, after the surface of the cast had been lightly rubbed with carbon shavings to enhance the surface detail. Various combinations of lighting were employed to bring out features of cerebral morphology.

The volumetric determinations by water displacement were carried out on plasticine reconstructed plaster copy, first checked for its accuracy against the original endocast. A fuller discussion of the methods used, particularly on the Taung endocast, have been given by Holloway ('70). The volume of 530 cc is based on an average of five readings.

The SK 1585 and Olduvai Hominid 5 endocasts were photographed together to emphasize their similarity. Hemi-endocasts of each were prepared by selecting three points along the midsagittal plane of each endocast. Using these three points to define a plane parallel to a flat table surface, a thin scribe was used to mark the midsagittal plane along the entire circumference of each cast. These were next sawn close to the line, and then smoothed exactly to the line with a belt sander. The left portion of Olduvai Hominid 5 was then placed against the right half of SK 1585, using both frontal and occipital poles for alignment. Once aligned, the two halves were secured tightly with a rubber band, and the whole was then photographed.

Fig. 1   Photograph of endocast with bone matrix, kindly provided by Dr. C. K. Brain. Note openness of sutures.

All chord measurements were taken with either sliding or spreading calipers to the nearest millimeter, and all arc measurements were made with an anthropometric flexible metal tape. The direct measurements for the Taung endocast were not included with the SK 1585 skull, since the former is that of a child, but the indices, based on ratios of measurements, were used in table 2.

Description

SK 1585 is a natural endocast of the right side of the cranium, formed by the infiltration of very fine-grained sediments through the foramen magnum into the braincase, and subsequently hardened *in situ* by calcium carbonate. The skull must have rested on its right side, with the posterior portion inclined downward, as only the frontal portion and left side are missing, and both occipital lobes and cerebelli are present. This fact allowed for accurate determination of the midsagittal plane, so that a complete hemi-endocast could be reconstructed.

When first examined, the endocast was still partially covered with a highly frangible, eroded bone layer (see fig. 1); with Dr. Brain's permission, this covering, plus part of the petrosal-filled matrix, was carefully removed with a vibrator tool, and saved for future analysis.

Clearing away this bone disclosed two important facts: (1) the sutures of the skull were still patent, indicating a subadult individual; (2) there were three

areas in the frontal region just anterior to the coronal suture (see figs. 2, 4), suggesting that the bone had been fractured, probably at death, and that one fracture was produced by a sharp point.

The endocast is almost totally undistorted and complete, and thus a minimum of plasticine reconstruction was necessary to prepare a complete hemi-endocast. The only areas requiring plasticine additions were the tip and rostrum of the frontal lobe, the inferior portion of the medulla to the level of the foramen magnum, the hypophysial region, the remainder of the sigmoid vein, and a few minor pits and depressions in the fractured zone anterior and posterior to the coronal suture (see fig. 3).
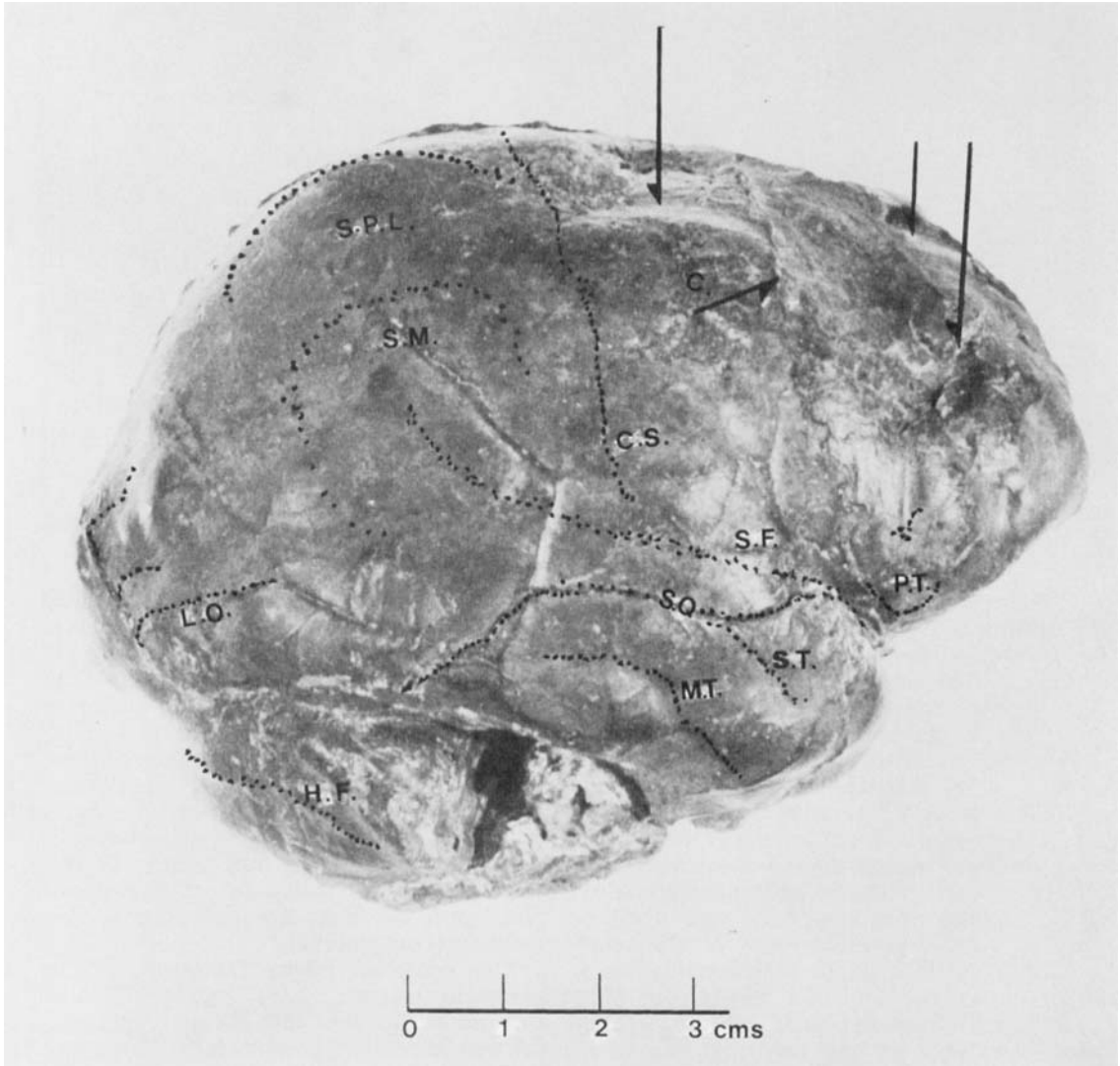

Fig. 2 Lateral view of cleaned endocast. Arrows show locations of fracture zones, the middle one being that of a conical point. Gyri and sulci are approximate only. P.T., pars triangularis; C, coronal suture; S.F., sylvian fissure; C.S., central sulcus; S.Q., squamous suture; S.T., superior temporal sulcus; M.T., medial temporal sulcus; H.F., great horizontal fissure of cerebellum; L.O., lateral occipital or prelunate; S.M., supramarginal gyrus; S.P.L., superior parietal lobule.
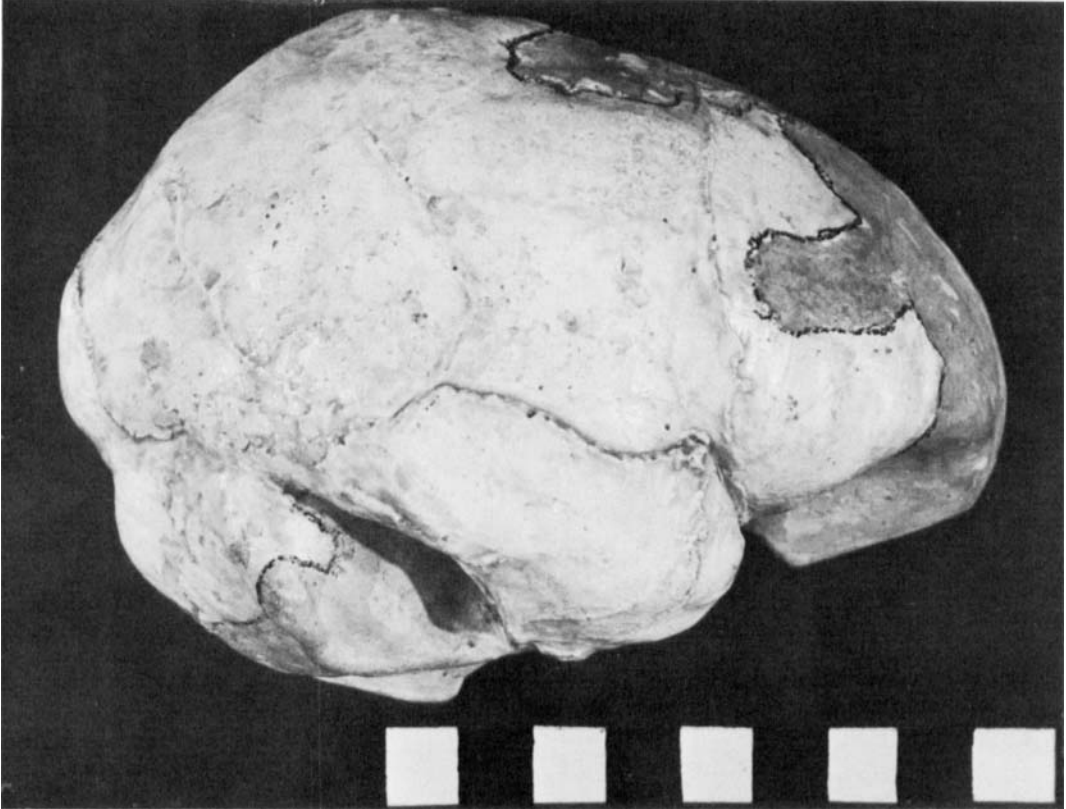
Fig. 3   Lateral view of reconstructed endocast — gray areas are plasticine.

This reconstruction permitted very accurate water displacement measures described elsewhere (Holloway, '70), giving a hemi-endocast capacity of 265 cc, thereby a total volume of 530 cc, which is exactly the same as that for the Olduvai Hominid 5 ("Zinj") as given by Tobias ('67). It is possible that this value is slightly on the low side, as the imprint of the squamosal suture suggests a very slight degree of movement of the temporal bone upward over the inferior margin of the parietal, running from the sylvian region to the posterior part of the temporal lobe. This slight displacement was surely postmortem, and would not significantly affect the final volume. While the openness of the lambdoid, sagittal, coronal, and squamous sutures suggests a subadult individual, it does not seem likely that any further significant growth of the brain would have been realised if the individual had lived longer.

Because of the extremely fine-grained sediments which entered the cranial cavity to produce the endocast, and lack of any evidence for disturbance during its filling, the surface detail of this endocast is truly remarkable with respect to meningeal patterns. Compared with all the remaining australopithecine endocasts, even the superb original Taung specimen, SK 1585 has the greatest detail. However this detail does not apply to the cerebral gyri and sulci, for on this endocast, most of them are not suitable for cortical reconstruction.

The occipital lobes, posterior to the lambdoid suture, are "puckered" and asymmetrical, the left being displaced downward relative to the right. The gyral configuration immediately anterior to the lambdoid suture does not provide an unequivocal lunate sulcus which in primate brains separates the visual sensory cortex (areas 17, 18, 19) from the posterior pari-
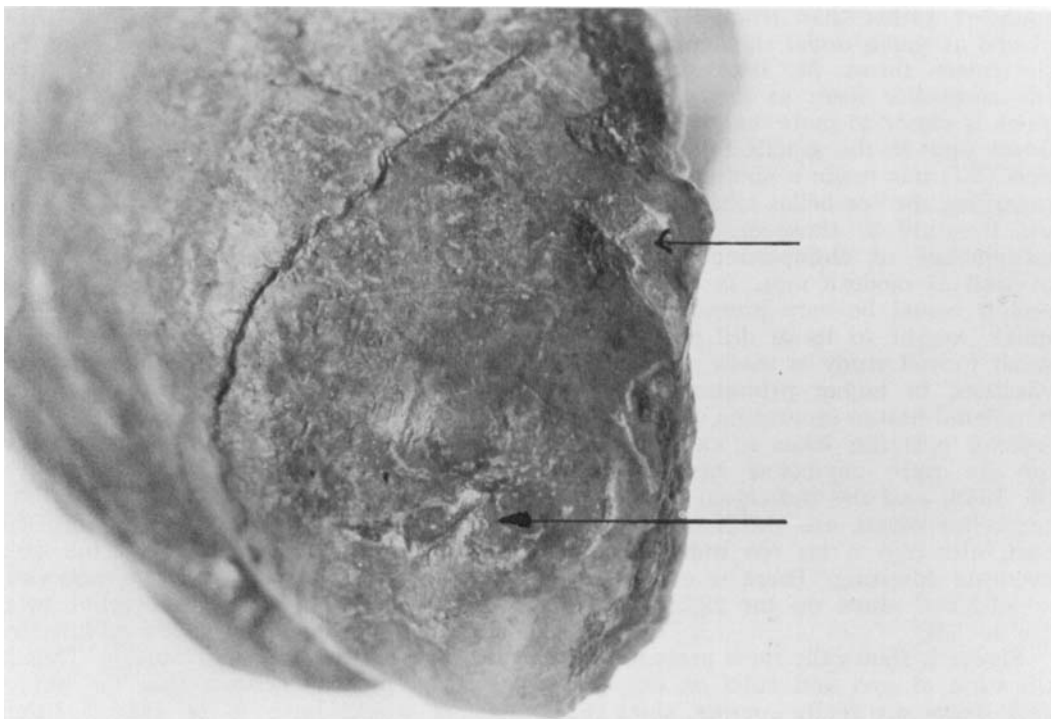
Fig. 4 Enlargement of frontal portion of original endocast, showing fracture regions with dark arrows.

etal "association" cortex. The constriction caused by the lambdoid suture probably occurs over the lunate sulcus, for anteriorly there is no indication of a sulcus which could be interpreted as the lunate. Indeed, the gyri anterior to the suture all appear to bend and retroflex somewhat anterior to the suture, and immediately behind the suture in the upper portion of the occipital lobe is a small lipping, the most superior ridge of which may represent the lunate. In any event, the lunate sulcus must be placed well posterior to the position found on pongid endocasts (see Connolly, '50). Similarly, both the expanded posterior and inferior aspect of the temporal lobe, and its anterior tip, show a hominid rather than pongid conformation (see fig. 2).

The inferior convolution of the frontal lobe immediately superior to the sylvian indentation, and just anterior to the coronal suture suggests an advanced disposition of the so-called Broca's region, relating to motor aspects of vocalization. The basis for this conclusion is that this area appears larger and more rounded than in pongid brain endocasts. The surface detail is not strong enough to differentiate safely the orbital, opercular, and triangular gyri of this region, however. Similarly, the gyral and sulcal configuration of the parietal lobe is not strong enough to delineate clearly angular and supramarginal gyri, but this endocast gives the strong impression that the parietal lobe was well developed in this regard, and that the inferior parietal lobule is certainly more expanded than in any pongid brain. Again, this conclusion is based only on visual examination, and the higher degree of curvature in this region.

The cerebellar lobe, most complete on the right side, is well-developed, well under the cerebral cortex, triangular in form, with the lateral lobe expanded anteriorly and laterally. The cerebellar form of SK 1585 is most clearly comparable to that of Olduvai Hominid 5 in size and shape. The gracile australopithecine cerebellar lobes (Taung, STS 5, STS 60, MLD 19) with the exception of STS 19, are more

rounded, rather than triangular, and not placed as much under the cerebrum as in the robust forms. My impression is that the cerebellar form in the robust endocasts is closer to more advanced hominid forms than in the gracile fossils, and Tobias ('67) has made a similar observation regarding the cerebellar lobes of the Olduvai Hominid 5. However, the cerebellar morphology of chimpanzee and gorilla, as well as modern man, is very variable and it would be very premature to give much weight to these differences, until some formal study is made of cerebellar variation in higher primates. The great horizontal fissure separating superior from inferior posterior lobes is clearly evident on the right cerebellar hemisphere of SK 1585, and the individual folia of the cerebellar cortex are visible on the endocast, although a bit too indistinctly for accurate counting. There is evidence for a collateral sinus on the right side, but not the left.

Figure 2 shows the most probable identification of gyri and sulci on this endocast. These are really guesses, since there is no way to offer positive proof without actual electrode stimulation or recordings. Some guesses, however, are more probable than others, and only those that seem most reasonable are drawn on the photograph of the cast. In the frontal lobe, just anterior to the lower portion of the coronal suture there are suggestions of the pars triangularis and pars orbitalis of the lower frontal gyrus. Approximately 3.2 cm behind the upper portion of the coronal suture there is a mild depression or valley between two bumps which could be the superior portion of the central sulcus. If one holds the cast in the lateral position, and then slowly revolves it by turning the midsagittal plane away from the eyes, one can follow the valley downward, forward, and see it then proceed further downward and forward. Somewhat lower than half the distance between sagittal and squamous sutures there are again two large knuckles which would fall roughly in the thumb and hand area of the homunculus maps for primates figured by Penfield and Roberts ('59). At this level, there is a good suggestion of a large portion of the precentral gyrus. If this identification of the central sulcus

is correct, the parietal cortex can be roughly divided into superior and inferior parietal lobules, even though the interparietal sulcus is not visible. The differentiation can only be done on the basis of degree of curvature and shape, and by holding the endocast with the occipital portion toward the eyes, rotating the cast counterclockwise. Under appropriate lighting, a small valley is evident between two convexities, the superior one being the larger, or most convex, i.e., with the shorter radius of curvature. There is a slight suggestion of the ascending ramus of the superior temporal sulcus coursing upward to help form the angular and supramarginal gyri of the inferior parietal lobule with the ascending part of the sylvian fissure. Posterior to this general region, there are no vertical sulci, until the lambdoid suture is reached, and the horizontally aligned gyri (probably representing superior and inferior occipital gyri) curve sharply downward a few millimeters anterior to the lambdoid suture. This is the best proof, I believe, that the lunate sulcus would have to be placed either under the lambdoid suture, or posterior to it, a fully human configuration.

None of the temporal gyri and sulci are clearly indicated in an uninterrupted pattern. The inferior temporal sulcus is not visible. The middle temporal sulcus shows an interrupted course, and is mainly evident in the middle portion of the lobe. The superior temporal sulcus most probably coincides with the anterior portion of the squamous suture, and is thus displaced. There is a sulcus leading from the lambdoid suture, about two-thirds of the way down, which courses anteriorly, and which could fuse with the middle temporal sulcus. If this is so, the posterior portion would most likely be the prelunate (transverse occipital) sulcus. It curves sharply downward at its most posterior part, giving more support to the interpretation made thus far of the lunate sulcus. There is a clear parieto-occipital notch, but no good evidence for the parieto-occipital fissure in the superior portion of the endocast. There are some slight impressions for the orbital gyri on the inferior surface of the frontal lobe.

The meningeal pattern best replicates the type IIb of Giuffrida-Ruggeri's ('12)

five types. The anterior and posterior rami of the middle meningeal artery separate immediately upon issuing from the foramen spinosum, with the anterior division of the posterior ramus appearing to be the larger. The anterior and posterior branches of the anterior ramus divide approximately at the sylvian region, suggesting a pattern most like type IV. This description is thus somewhat different than that given by Tobias ('67) for the Olduvai Hominid 5. As it is well known that these patterns do not appear to follow any particular phylogenetic plan, and are variable in all hominoid genera, it is pointless to go beyond this description.

Measurements

Table 1 provides the measurements taken on the original specimen where possible, and on the reconstruction where indicated. Included are measurements taken on the original Olduvai Hominid 5 endocast, supplied by Prof. Tobias. Included are the comparable measurements for a gracile australopithecine endocast, STS 60. It should be stressed that these measurements are only approximations. Landmarks on the endocranial casts are seldom discrete points, and measurements, particularly those of arc distances by metallic tape, are difficult to standardize without proper anchoring devices. The purpose of these measurements, despite their imperfections, is only to quantify and demonstrate empirically the remarkable similarity between the SK 1585 and Olduvai Hominid 5 endocasts. Indeed, the major differences in the measurements

TABLE 1

Some measurements taken directly on the endocasts

		SK 1585	Old. Hom. 5	STS 60
1.	A-P length			
	chord	12.9 *	12.6–0.9	11.5
	arc (dorsal)	19.0	17.1	15.5
	arc (lateral)	16.5	16.7	15.2
2.	Maximum width, superior temporal			
	chord	9.8 [1]	10.0	9.6
3.	Maximum depth, vertex to lowest cerebellar point			
	chord	8.7	8.3	8.1
4.	Bregma-lowest cerebellar point			
	chord	9.5	9.4	8.9
5.	Vertex-deepest temporal			
	chord	8.6	8.5	7.9
	arc	12.6	12.5	12.0
6.	Occipital pole-anterior, temporal pole			
	chord	9.2	10.4	8.9
	arc	11.7	13.7	11.8
7.	Maximum width just anterior to coronal suture	4.4	4.4	4.0
8.	Maximum width, sigmoid sinus	8.2	8.5 [2]	—[3]
9.	Inter-occipital pole	2.4	2.4	—[3]
10.	Lambda-Bregma			
	chord	8.1	8.4 [4]	6.9
	arc	9.6	9.5	7.2

* All measurements taken on reconstructed endocast.
[1] 4.9 on hemi-endocast.
[2] Estimated, since excrescences are on cast.
[3] Cannot be measured.
[4] Bregma estimated.

reflect a temporal lobe too large for the latter endocast, as can be seen in the arc and chord measurements from occipital pole to anterior temporal tip, and from the superpositioning of the two endocasts in figure 8, in the basal view. The Olduvai Hominid 5 endocast is not complete, and had to be reconstructed in its central portion, thus resulting in some error in the positioning of the anterior pole of the temporal lobe. Such a difference, however, is minor, and would not represent more than about 5–10 cc in volume.

Table 2 provides a few indices based on four dimensions taken directly on the casts rather than dioptrographic tracings. L = maximum anterior-posterior length from frontal pole to occipital pole; W = maximal biparietal or supratemporal width; B = distance from bregma to deepest cerebellar projection; H = maximum height from vertex to the deepest temporal lobe portion, when the endocast is oriented in a horizontal plane defined by the maximum frontal pole-occipital pole distance. These indices have no value aside from demonstrating the near identity of the SK 1585 and Olduvai Hominid 5 endocasts (see Weidenreich, '41, for discussion) in size and proportions. Included are two adult male pongid endocast measurements for comparative purposes. Figures 6, 7 have been included to emphasize the extreme similarity between the two robust forms, when the hemi-endocasts are positioned together along the mid-sagittal plane by orienting the frontal and occipital poles together.

DISCUSSION AND CONCLUSIONS

Reference has been made in the description to the fracture marks in the frontal region just anterior to the coronal suture as occurring most probably at death. Naturally, it is impossible to substantiate this opinion, for such fractures could have occurred after death, but prior to any hardening of the sediments which eventually filled the cranium. These could have been caused by rock falls or carnivore/scavenger activity. The small fractures make rock falls unlikely, as one would expect more massive crushing. The fracture marks certainly do *not* provide the startlingly clear case that can be seen on the SK 54 (Brain, '70) frontal and parietal bones. In that case (SK 54), the marks are clearly punctures caused by a conical point, which happen to match perfectly the intercanine distance of leopard mandibles (Brain, '70). The distance between the small conical point depression and other fractures on SK 1585 do not match those of the SK 54 case. In my opinion, these marks on SK 1585 are too ambiguous to warrant any conclusions about causation.

Endocasts, particularly those of the higher primates, are quite variable in the degree to which the representation of cortical morphology is impressed with the overlying dural membranes into the bones of the skull. The main quest of my examination was to discern whether any clear evidence exists for a hominid rather than pongid status of cortical organization, rather than to localize each particular cerebral gyrus and sulcus. No methodology yet exists that "proves" the existence and placement of any particular gyrus or sulcus. One can only offer what appears to be the most probable interpretation based on careful examination of a comparative series, and an understanding of the variability of these features. It is

TABLE 2

Some indices based on measurements on casts

	SK 1585	Old. Hom. 5	Taung	STS 60	STS 5	Chimp.	Gorilla
W/L	0.759	0.781	0.728	0.834	0.737	0.871	0.731
H/L	0.666	0.664	0.703	0.704	0.746	0.734	0.671
B/L	0.738	0.734	0.779	0.817	0.860	0.798	0.753
H/W	0.877	0.850	0.965	0.843	1.011	0.842	0.918
B/W	0.969	0.940	1.069	0.979	1.116	0.915	1.300
H/B	0.905	0.904	0.902	0.861	0.866	0.919	0.891

W = maximum width; L = maximum length, frontal poles; B = bregma to deepest cerebellum; H = vertex to deepest temporal lobe portion.
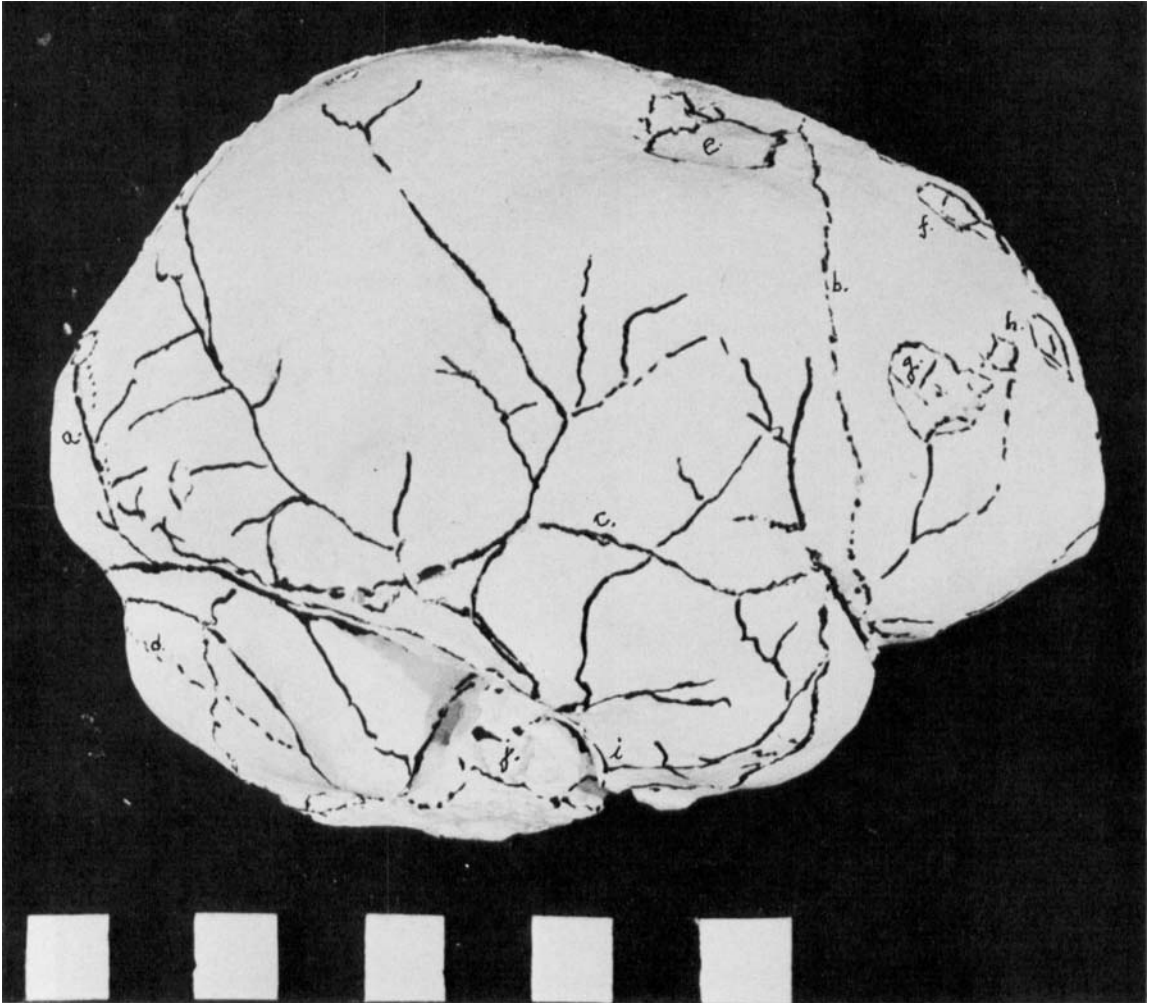
Fig. 5 Lateral view of unreconstructed cast, with major features inked. *a*, lambdoid suture; *b*, coronal suture; *c*, squamous suture; *d*, great horizontal fissure of the cerebellum; *e, f, g, h* are fracture zones; *i*, origin of middle meningeal artery; *j*, matrix.

my opinion, based on many examinations of this endocast and others, as well as the actual brains of pongids and man, that the morphological patterns of the SK 1585 clearly show evidence of a reorganization along human lines. The lunate sulcus of SK 1585 must be placed well posterior to the position found on pongid endocasts (see Connolly, '50, for illustrations and discussions). Such a position underlines the basic hominid status of this endocast. The functional significance of this posterior position is that it indicates an increase in the relative, if not absolute, volume of the posterior parietal and temporal cortex, with concomitant decrease in striate (area 17) and parastriate (areas 18 and 19) visual cortex on the surface. One cannot know the infolding under the surface. This is "proof," however tenuous, that the brains of these hominids were indeed reorganized (Holloway, '66, '68) whatever the low volumes within pongid ranges. The argument can then be extended to the subcortical nuclei, such as the pulvinar of the thalamus, since this and the inferior parietal and posterior temporal cortex are in two-way
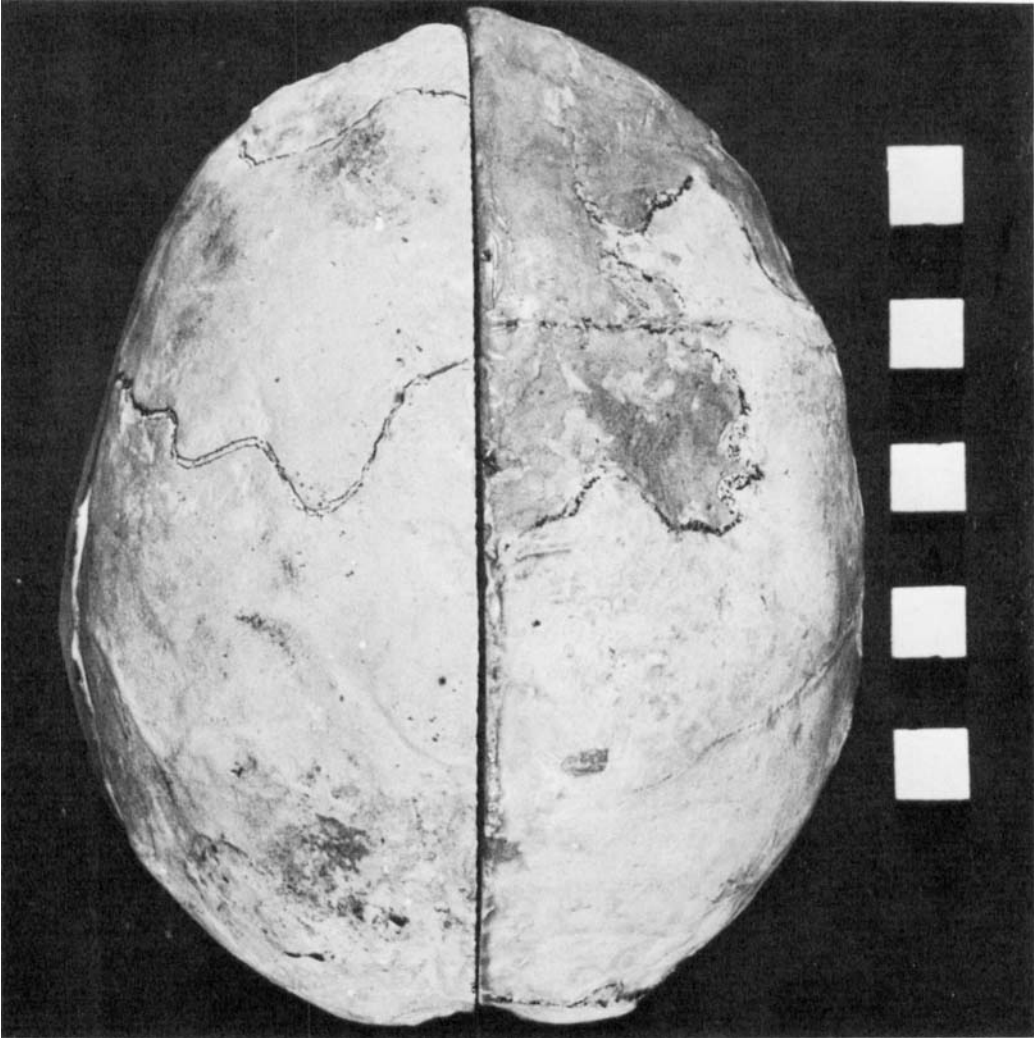
Fig. 6   Dorsal view of SK 1585 on right, and Olduvai Hominid 5 on left, oriented together
on midsagittal plane, with frontal and occipital poles aligned in horizontal plane.

up-and-down connection. One can only guess at what selection pressures existed to bring about this reorganization, but it is concordant with the suggestion of an increased facility for communication and problem-solving ability. The inferior convolution of the frontal lobe suggests a more advanced disposition of the so-called Broca's area, which again is concordant with the parietal and temporal region discussed above. Whether or not this appraisal is true, it cannot be claimed that this hominid was capable or incapable of language. The minimal statement that can be made is that there is nothing in the cortical morphology of the endocast which necessarily precludes language ability, and much is in its favour. The reorganization is not limited only to the posterior portion of the brain, but also the frontal lobe, the expanded posterior and inferior aspect of the temporal lobe, its anterior tip, the cerebellum, and the posterior parietal region and occipital cortex. As the posterior parietal cortex has been recently underlined by Geschwind ('65) as an important part of the receptive and associative func-
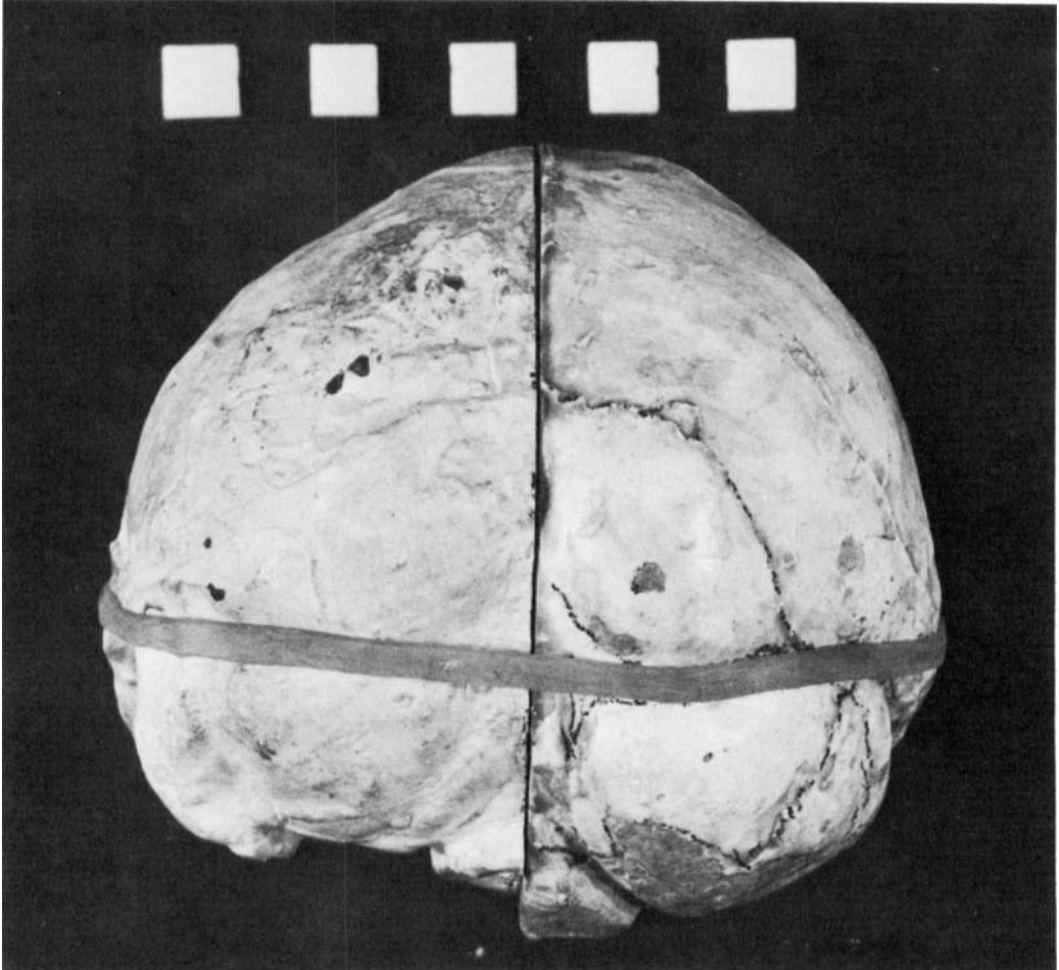
Fig. 7   Occipital view, as in figure 6.

tioning of language behavior, the possibility of australopithecine language behavior becomes more enhanced.

The cerebellar morphology of SK 1585, which shows a typically hominid form, and contrasts with those gracile forms so far discovered (STS 5, STS 60, STS 19, and MLD 1), leads to the need for a critical re-appraisal of the usual view of the robust forms as somehow more primitive in terms of locomotory and tool-using/making abilities. I share Tobias' ('67) observation of the advanced morphology of this region in the Olduvai Hominid 5, but it should be noted that not only are there very few specimens available, there are also no good studies available on the

variability in shape of the cerebellar lobes in primates in general, or in African pongids in particular. Thus it is unwise to speculate here about the possibility of a more advanced behavioral level in the robust forms, except to note that the question should remain open.

The most obvious conclusion to be drawn from this description is the near identity of the two forms. Obviously, a sample of two will not settle any taxonomic questions. My own conviction, not based on endocasts only, is that the SK 1585 and Olduvai Hominid 5 specimens are not separable beyond the subspecific level. The differences between these two cases are less than those existing be-
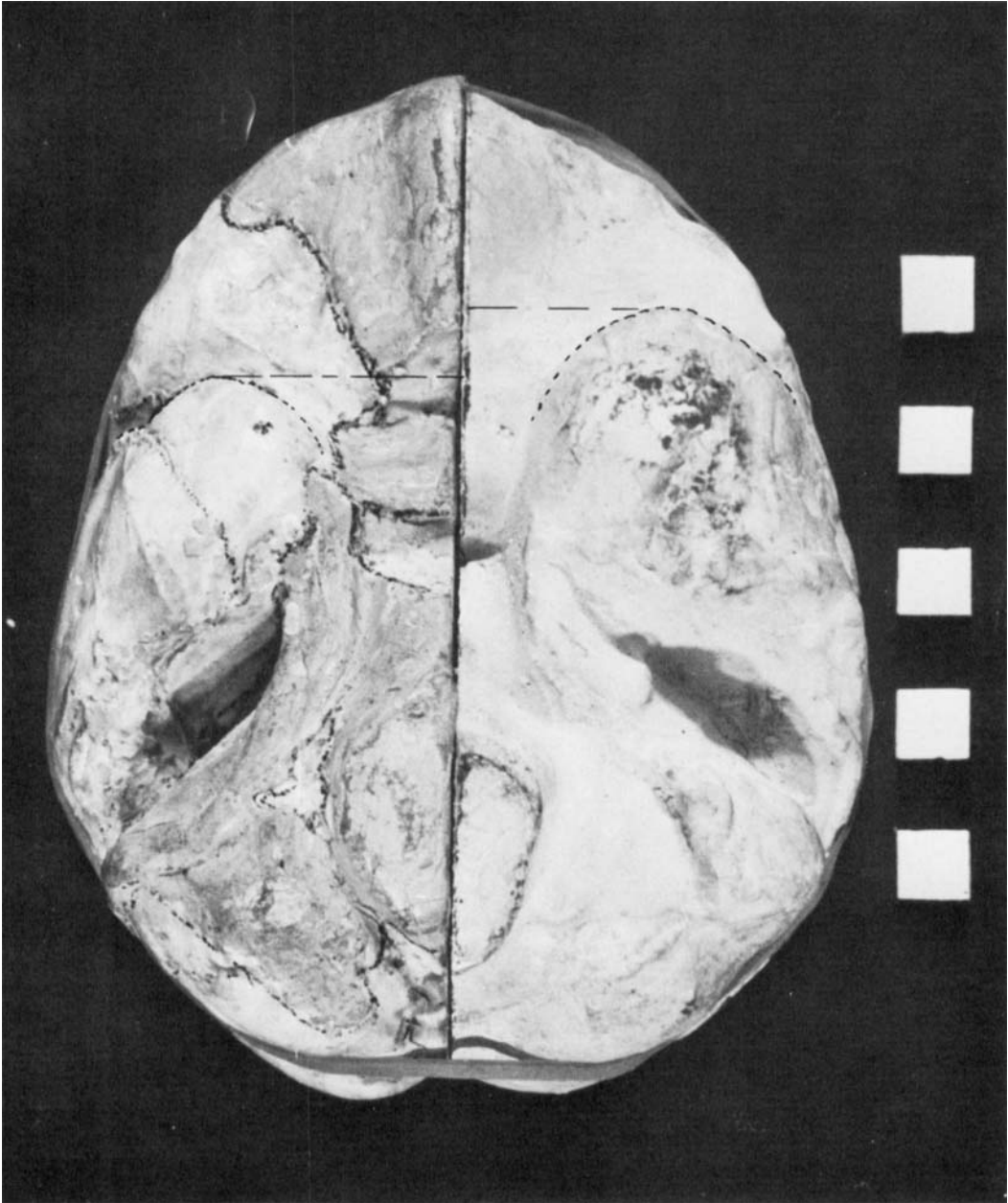
Fig. 8   Ventral or basal view, SK 1585 on left, Olduvai Hominid 5 on right. Anterior tips of temporal lobes are indicated by dotted lines, and projected to midline to show small error in tip reconstruction of Olduvai Hominid 5.

tween modern *Homo sapiens* and Neandertal endocasts. Secondly, there are clear differences between these two endocasts and those of gracile australopithecines that go beyond the possibility of simple sexual dimorphism. Male and female gorillas, which have as high a degree of sexual dimorphism in size as any primate, still maintain a morphological identity that is easily discerned on the endo-

casts by simple visual inspection. The same can be said for the chimpanzee. Similarly, if one were confronted with a male chimpanzee and a male gorilla endocast, one would readily recognize differences in shape and size of at least an equal order as between robust and gracile australopithecine.

In summary, these australopithecine endocasts are more advanced in terms of morphological patterns than pongids, whatever the few indices given may indicate, or whatever their cranial capacities. The most pronounced differences between these and any pongid brains are: (1) reduction of occipital parastriate and striate visual cortex and a concomitant expansion of both parietal and temporal cortex; (2) a more complex frontal lobe, particularly in Broca's region; (3) a more human-like shape, size, and disposition of the cerebellar lobes, reflected by the lateral (or neocerebellar) lobe enlargement, possibly related to locomotor and manipulatory functions. There is nothing about the surface morphology of these endocasts which provide for or against the possibility that *A. robustus* made and used stone tools. That evidence must come from analyses other than brain morphology. Similarly, there is nothing in the endocast morphologies of either gracile or robust forms which prove the genus *Australopithecus* capable or incapable of human cognition, or primitive language ability. The casts cannot be used for these purposes.

Finally, this question emerges: which of these forms appears the most advanced on the basis of the endocranial casts? The gracile forms suggest more folding of the cortex, although the forms that show this (Taung, STS 60, and type 3, in Broom and Schepers, '46), are young forms. The robust types, Olduvai Hominid 5 and SK 1585, suggest more modernness in overall size, shape, expansion of parietal cortex, and most particularly,

the shape and disposition of the cerebellum.

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