

A Reanalysis of the South African Australopithecine Natural Endocasts

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ABSTRACT Sulcal patterns of six previously available South African australopithecine natural endocasts are reexamined and compared to sulcal patterns of 17 human, 12 gorilla and six chimpanzee brains. In addition, a seventh natural endocast, from STS 58, is described for the first time and compared to an artificial endocast from the same specimen. Using the Taung endocast as a focal point, it is shown that sulcal patterns reproduced on natural endocasts of australopithecines appear to be pongid-like rather than human-like. Contrary to earlier descriptions, the lunate sulcus occupies a rostral position similar to that found in pongids. Since South African australopithecine brains do *not* appear to be reorganized along human lines at a gross external neuroanatomical level, the concept of neurological reorganization is best applied at finer neurological levels, perhaps at the level of the neuron or at a neurochemical level. Thus, future studies by comparative neuroscientists are more likely to elucidate the fine details of neurological reorganization that occurred during early human evolution than are studies by paleontologists who directly observe the australopithecine fossil record of natural endocasts.

The South African gracile australopithecines have long been viewed as ape-men, or missing links, which were direct ancestors of *Homo*. Many of the early arguments for the gracile australopithecines' humanity centered upon interpretations of their endocranial casts (Dart, 1925, 1956; Broom and Schepers, 1946; Broom et al., 1950; Clark, 1947). More recently, the supposed caudal position of the lunate sulcus in the Taung endocast has been interpreted as evidence that the brains of South African gracile australopithecines were reorganized in a human direction (Holloway, 1972, 1975). According to some authors (e.g., Johanson and White, 1979), *Australopithecus afarensis* has replaced the South African gracile australopithecines (*A. africanus*) as the Plio/Pleistocene hominid most likely to have given rise to *Homo*. According to this view, the South African gracile australopithecines are with the robust australopithecines on a sidebranch of the hominid phylogenetic tree that became extinct between 1.0 and 1.5 million years ago. In light of this reinterpretation of the hominid

fossil record, it would be interesting to review the status of the South African australopithecine natural endocasts. Were they, or were they not, human-like in appearance? In this paper, all six (five gracile, one robust) of the available previously described South African australopithecine natural endocasts will be reviewed in an effort to answer this question. Because so much speculation has centered upon its sulcal pattern, the Taung endocast will be described and discussed in detail. An additional seventh natural endocast, from the gracile calvarium STS 58 that was recently discovered in a storage room at the Transvaal Museum by R.J. Clarke, will also be described for the first time.

MATERIALS AND METHODS

There has been much controversy about the reliability of determining primate sulcal patterns from endocasts. Symington (1916) compared endocasts of modern human skulls with the corresponding brains and concluded that

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very little information about sulcal patterns can be determined from human endocasts. Clark et al. (1936) reproduced six endocasts from chimpanzee skulls and compared them to the corresponding chimpanzee brains and arrived at equally pessimistic conclusions regarding the reliability of chimpanzee endocasts as replicators of sulcal patterns. Connolly (1950) also compared endocasts with corresponding brains of apes and humans and he too concluded that endocasts do not reproduce many details of hominoid sulcal patterns.

Radinsky (1968, 1972, 1974) has used latex endocasts to investigate sulcal patterns of prosimians and fossil anthropoids and I have used the same method to study sulcal patterns of cercopithecoid (Falk, 1978a,b,c) and ceboid (Falk, 1979a) monkeys. Radinsky and I both selected skulls with maximum internal relief for casting. Endocasts prepared from most prosimian and *carefully selected* monkey skulls do reproduce details of external brain morphology including much or all of the cerebral sulcal pattern, sutures, and positions of some cranial nerves, veins, and arteries. Thus, latex endocasts prepared from selected prosimian and monkey skulls reproduce clear sulcal patterns; endocasts prepared from pongid and human skulls (even if carefully selected) do not. This poor reproduction of brain surface features on pongid and human endocasts has been attributed to relatively thick, masking meningeal structures situated between the brains and the skulls of hominoids (Holloway, 1974).

Several of the existing australopithecine natural endocasts (Table 1), on the other hand, reproduce a surprising amount of detail of external brain morphology. These natural endocasts are all from South Africa and are associated with limestone deposits. According to Broom and Schepers (1946:168), these endocasts consist of "a natural, lime-impregnated, windblown, sandy dust." Artificial endocasts prepared from reconstructed australopithecine and the somewhat larger *Homo habilis* skulls do not reproduce the amount of detail shown by some of the australopithecine natural endocasts. (See Tobias, 1971, for photographs of natural South African and artificial East African australopithecine and *H. habilis* endocasts.)

There are two possible reasons why australopithecine natural endocasts show more detail than australopithecine and *H. habilis* artificial endocasts:

1) Perhaps artificial endocasts do not reproduce as much detail of sulcal pattern as do nat-

ural endocasts because they are usually reproduced from reconstructed skulls (Tobias, 1971), whereas natural endocasts were formed from unreconstructed calvaria, or portions thereof. That is, endocasts reproduced from cranial fragments that have been patched together or endocasts constructed by cementing together pieces of endocasts reproduced from separate cranial fragments will reflect any discontinuities or errors inherent in the reconstruction process.

2) The difference in natural and artificial endocasts may be a question of taphonomy. Perhaps the more detailed portions of natural endocasts were formed by the replacement of the brain tissue and pia/arachnoid mater by fine lime-impregnated dust *before* disintegration of the overlying dura mater, rather than being formed by the casting of an entirely emptied calvarium by natural sediments. A taphonomist could explore this possibility by determining which parts of the cranial contents disintegrate first when skulls are exposed to the elements. Is the dura mater the last to go? If so, do portions remain longer in some parts of the calvarium than in others?

For whatever reasons, the sulcal patterns reproduced on South African australopithecine natural endocasts are worthy of study. Table 1 lists all six of the gracile australopithecine natural endocasts available for study, as well as the robust australopithecine natural endocast SK 1585. It should be noted that Clarke and I were unable to locate two natural and one artificial or natural endocast from Sterkfontein, listed by Broom et al. (1950:89): *Plesianthropus transvaalensis* V (STS 5), VII (STS 71), and VIII (STS 19). According to Schepers, the STS 5 natural endocast represented the "right parieto-occipital as well as the left central and parietal portions," STS 71 contained frontal fragments of natural limestone cast, and STS 19 had "an almost perfect cast of the posterior and middle cranial fossae." Clarke searched thoroughly the storage rooms of the Transvaal Museum for these specimens and we questioned authorities at the Transvaal Museum and the nearby Department of Anatomy at the University of Witwatersrand as to their whereabouts. We were unable to learn anything about these natural endocasts and think that they have been missing for at least several years.

Since white plaster copies facilitate identification of features not readily apparent on darker original fossils, the natural endocasts listed in Table 1 were cast in alginate molding

TABLE 1. South African australopithecine natural endocasts¹

Specimen designation	Presumed type	Repository	Cortical area represented	Quality of endocast	Original description
1. Taung	g	W	<i>rgt hem</i> : missing fro & tem poles	good fro, tem; fair occ; poor par. Damaged several areas	Schepers (Broom and Schepers, 1946)
2. Sterkfontein NO. 1 (STS 60)	g	T	<i>lft hem</i> : missing tem pole <i>rgt</i> : medial portions fro, par	fair fro; poor elsewhere. Damaged lft orbitofrontal cortex & posterior par/occ.	"
3. Sterk. NO. 2	g	T	<i>rgt</i> : fro, rostral par, small part tem <i>lft</i> : medial fro <i>rgt, lft</i> : par/occ	good fro; fair tem; poor elsewhere. Damaged rgt fro/par area	"
4. Sterk. NO. 3	g	T	<i>rgt, lft</i> : par/occ	poor. Damaged lft occ, distortion lft par.	"
5. STS 58 ²	g	T	<i>rgt, lft</i> : par/occ. missing lateral medial parts	poor. Fracture rgt par	this report
6. STS 1017	g	T	<i>rgt</i> : par, small part fro, tem	good fro, tem; poor par.	Falk, 1979b
7. SK 1585	r	T	<i>rgt hem</i> : missing fro pole <i>lft</i> : medial par/occ	poor	Holloway, 1972

¹ Endocasts are from presumed gracile (g) or robust (r) individuals and most specimens are housed in the hominid collection at the Transvaal Museum (T), although the Taung endocast is located at the Department of Anatomy, University of Witwatersrand (W). Abbreviations: fro, frontal lobe; hem, hemisphere; lft, left; occ, occipital lobe; par, parietal lobe; rgt, right; tem, temporal lobe. See text for discussion of each endocast.

² It should be noted that this natural endocast comprises part of the so-called NO. 8 specimen. Although Schepers (Broom et al., 1950:89) originally described an *artificial* endocast from STS 58, this report includes the first description of the *natural* endocast.

compound from which white plaster copies were prepared. Both the original specimens and their white plaster copies were studied and compared to each other. The original specimens were photographed. The newly discovered natural STS 58 endocast (see below) was compared to, and photographed with, the artificial STS 58 endocast described by Schepers (Broom and Schepers, 1950). I studied, sketched, and described the sulcal, suture, and vascular patterns of each specimen. (Connolly's (1950) terminology was used for sulci.) After I completed my descriptions, I compared my findings with those of Schepers (Broom and Schepers, 1946; Broom et al., 1950).

Casts of the seven available australopithecine natural endocasts were compared with 150 latex endocasts of monkeys, two chimpanzee endocasts, 20 cercopithecine brains, six chimpanzee brains, 12 gorilla brains, and 17 human brains. These brains were photographed in right, left, and occipital views to document the range of variation in sulcal patterns.

As noted above, much speculation has been based on the interpretation of the sulcal pattern of the Taung endocast. Since various workers (Connolly, 1950; Clark, 1947) have relied on Schepers' illustration of the Taung endocast rather than firsthand examination of the specimen, a main focus of this paper will be a reassessment of the sulcal pattern of the Taung endocast.

OBSERVATIONS

The Taung endocast

Frontal lobe. Figure 1 compares Schepers' (Broom and Schepers, 1946:188) illustration and sulcal identifications of the Taung endocast (A) with my own (B). Schepers identifies the central (*c*), subcentral (*sc*), precentral superior (*pcs*), and "intermediate fosset" (*ifo*) sulci on the frontal lobe of the Taung endocast. I was unable to see, feel, or in any other way identify these sulci on either the original specimen or its white plaster copy (Fig. 1). I believe Schepers mistook the coronal suture for the central sulcus. My observations confirm Schepers' identification of the frontalis superior (*fs*), rostral portion of the frontalis medius (*fm*), and precentral inferior (*pci*) sulci. In addition, I have identified a ramus horizontal (*h*) of *pci* (see Fig. 7A for a similar configuration of *fm/h/pci* in *Pan*).

The sulci labeled *fo* and *sf* in Schepers' illustration are *not* sulci (except the caudal aspect of *fo* which I have not labeled, see below). Two approximately equal-sized gyral bulges de-

lineate the lateralmost edge of the Taung endocast orbit. The two so-called sulci of Schepers represent the lateral contours of the orbit. The NO. 2 australopithecine endocast from Sterkfontein (Fig. 4) exhibits similar orbital bulges. The other natural australopithecine endocasts are incomplete in this area, although the NO. 1 specimen exhibits the rostral bulge and a small portion of an adjacent bulge in a partially damaged area caudal to that (Fig. 4).

The sulcus separating the two orbital bulges in the Taung endocast has been identified by me as the fronto-orbital (*fo*) sulcus, after Connolly (1950). Connolly typically figures *fo* for chimpanzees and gorillas but not for humans. My study of 17 human, six chimpanzee, and 12 gorilla brains confirms the observations that 1) *fo* typically incises the orbitolateral border of the frontal lobe of chimpanzee and gorilla brains, and 2) a similar configuration of *fo* is rarely if ever present in human brains. (See Fig. 2.) Connolly attributes the difference in the sulcal patterns of the frontal lobes of pongids and *Homo* to opercularization of the frontal cortex in *Homo* displacing *fo* caudally so that it "becomes the anterior limiting sulcus of the insula, at least in its lower part" (1950:330). Thus, *fo* is not visible on the lateral surface of the human brain. See Connolly (1950:330) for further discussion.

In other words, the shape and sulcal pattern of the orbital edge of the frontal lobe differs markedly in pongids and humans. Unlike the *fo*-divided orbits of *Pan* and *Gorilla*, approximately 75% of the 34 human hemispheres that I observed exhibited a gyrus oriented in a rostro-caudal direction at the caudolateral edge of the frontal lobe (Fig. 2C, above). Although this lateral gyrus is broken up by branches of the inferior frontal (*fi*) in the remaining 25% of the human hemispheres (Fig. 2C, below), a pongid-like *fo* is rarely if ever seen in humans, although conceivably the horizontal branch of the Sylvian fissure could occasionally be mistaken for *fo* in humans (e.g., see R' in Connolly, 1950:329D). Figure 2 illustrates the range of variation in frontal lobe sulcal patterns in *Pan*, *Gorilla*, and *Homo*. The Taung specimen looks decidedly pongid-like in this portion of the endocast.

The sulcus on the Taung endocast that I have labeled *fo* has been identified as the diagonal (*d*) sulcus by Schepers. Commenting on Schepers' figure, Connolly (1950:294) notes that *d* is never found rostral to *fo* in anthropoid or human specimens, thus questioning Schepers' identifications. My identification of *fo* and its

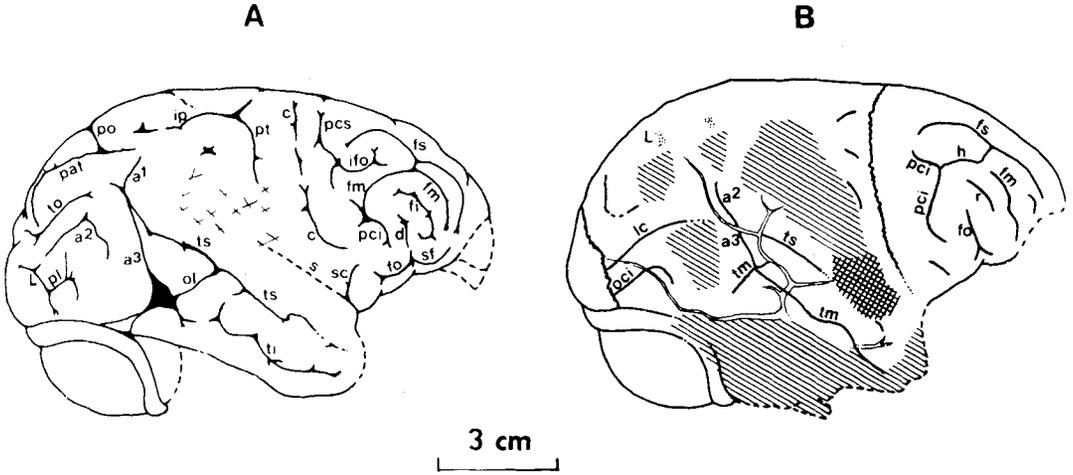


Fig. 1. The natural endocranium from the Taung specimen of *Australopithecus africanus*. A, from Broom and Schepers (1946:188); B, this report. The coronal and lambdoid sutures, vessels, and all damaged areas are illustrated in B but not in A. Crossed hatching in B indicates adhering bony fragment. Abbreviations of sulci modified after Connolly (1950): a¹, parallelus superior of ts; a², angularis; a³, anterior occipital; c, central; d, diagonal; fi, frontalis inferior; fm, frontalis medius; fs, frontalis superior; h, horizontal ramus pci; ifo, intermediate fosslet; ip, intraparietal; L, lunate; lc, lateral calcarine; oci, inferior occipital; ol, lateral occipital; pat, parietalis transversus; pci, precentral superior; pcs, precentral superior; pl, prelunate; po, parieto-occipital; pt, postcentral; r, rectus; s, Sylvian; sc, subcentral; sf, subfrontalis; ti, temporalis inferior; tm, temporalis medius; to, transverse occipital; ts, temporalis superior.

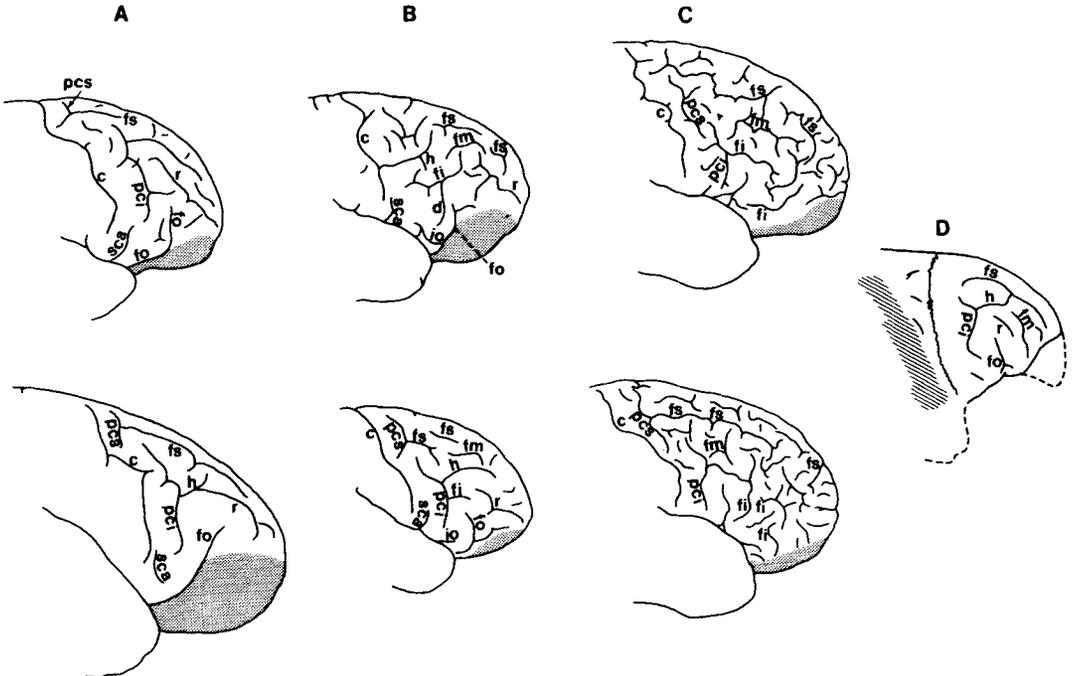


Fig. 2. Frontal lobes of hominoid brains, selected to show range of variation. Right lateral views, reversed from left if necessary. A, *Gorilla*: after Connolly (1950:99, 93); B, *Pan*: after Connolly (1950:114, 108); C, *Homo*: after Connolly (1950:188, 191); D, the Taung endocranium. The simplicity and configuration of the sulcal pattern of the Taung specimen resembles those of *Pan* and *Gorilla* rather than the more complicated patterns of *Homo*. Note the pongid-like fo of the Taung endocranium and see text for discussion. Not to scale. Abbreviations of sulci: io, incisura opercularis; sca, subcentral anterior; other abbreviations as in Figure 1.

relationship to *pci*, *h*, and *r* are in keeping with Connolly's terminology and figures for anthropoid brains.

The sulcus that I have labeled the rectus (*r*) has been identified as the inferior frontal (*fi*) sulcus by Schepers. I have identified *r* as such because its lateral end is rostral to *fo* and its medial end is surrounded by *h* and *pci*. This configuration is frequently seen in primate brains of an approximately equal size and complexity of sulcal pattern (Fig. 2). Connolly also questioned Schepers' identification of *fi* (my *r*), noting that it occupied a "very anterior position." Schepers was consistent in his identifications. He labeled *r* as *fi* in both the NO. 1 and NO. 2 specimens (Broom and Schepers, 1946), and according to Connolly (1950:294): "In Schepers' Figure 3B of the orang brain, showing sulci after Kappers, a sulcus extending close to the frontal pole is obviously the sulcus rectus, but interpreted as the frontal inferior sulcus."

Connolly (1950) discusses the position of *pci* relative to the temporal pole in Schepers' illustration, noting that in man and in many specimens of *Pan*, *pci* is located more caudally than in the Taung endocast. It is difficult to be sure of the relative position of *pci* since the entire rostral portion of the temporal lobe (not just the temporal pole, as indicated by Schepers) is missing in the specimen. Unfortunately, this is also the case for the NO. 1 and NO. 2 specimens and STS 1017. The only specimen that shows the temporal pole is the robust SK 1585, which unfortunately does not reproduce *pci* (Holloway, 1972). I have left unlabeled a small sulcus caudal to *fo* because without *c* and the rostral part of the temporal lobe, I cannot tell if it is the diagonal sulcus (*d*), the opercular sulcus (*io*), or simply an unnamed secondary sulcus.

According to Clark (1947:312), "the first impression obtained by an examination of the original casts of *Australopithecus*. . . is that the sulci on the frontal lobe are, in fact, rather more numerous and close-set than they are in the brains of modern anthropoid apes." My observations of the Taung specimen and the other australopithecine natural endocasts disagree with those of Clark. Neither my, nor Schepers', illustration of the Taung endocast's frontal lobe shows more sulci than are typically present in pongid frontal lobes (Fig. 1 and 2). The sulcal pattern of the frontal lobe of the Taung endocast and the shape of its orbital edge could easily be taken for that of a chimpanzee or gorilla. On the other hand, the frontal lobe sulcal pattern of the Taung endocast is different from,

and more convoluted than, that of any genus of monkey (Falk, 1978c; 1979a). Thus, the frontal lobes of the Taung endocast (and the other australopithecine natural endocasts, see below) look more pongid-like than human-like.

Parietal lobe. Schepers identifies the intraparietal (*ip*) and postcentral (*pt*) sulci in the Taung endocast. I was unable to see or feel these sulci. A larger portion of the parietal area is damaged than is apparent from Schepers' illustration. A ramus of the superior temporal (*ts*) sulcus (*a*¹ = parallelus superior of Schepers; *a*² = angularis, this report) is visible (see below). The indentation that Schepers labeled *po* is most likely the location of the medial portion of the lunate (*l*) sulcus (below). No part of the sylvian (*s*) sulcus is visible on the Taung specimen due to damage and an adhering bony fragment in this area. The only australopithecine natural endocast that exhibits well-defined *c* and *s* is the newly discovered STS 1017 (Falk, 1979b). This specimen shows a *c* that is arched in its lateral extent rather than straight as was depicted for SK 1585 (Holloway, 1972). Most, but not all, of *c* figured for pongids by Connolly (1950) are less curved in their lateral extent than is *c* of STS 1017. However, my observations of *c* in 18 pongid and 17 human brains suggest that its lateral curvature is too variable to permit generalizations about the human-like or pongid-like configuration of *c* in australopithecines. The parietal lobe of the Taung endocast reproduces a portion of the posterior parietal meningeal artery, as do all of the parietal lobes of the other australopithecine natural endocasts. Although all seven of the available australopithecine natural endocasts reproduce portions of the parietal cortex, details are not clear on any of the specimens. Consequently, we do not yet know what the sulcal pattern looks like in this portion of the australopithecine brain.

Temporal lobe. Contrary to Schepers' interpretation, adhering matrix prevents observation of the lateral border of the temporal lobe in the Taung endocast. The sulcus that Schepers has identified as the temporalis inferior (*ti*) has been identified by me as the temporalis medius (*tm*) sulcus, in keeping with Connolly's terminology for monkeys, apes and humans.

According to Schepers (Broom and Schepers, 1946:195):

The deep fossa between the anterior occipital sulcus and the superior temporal and inferior temporal sulci is probably produced as

a transitory growth phenomenon. But a sulcus, which probably represents the lateral occipital sulcus of Anthropoids can still be observed in this region. It is likely that it may have disappeared as adjacent gyri developed to attain the adult state of organization.

I am unable to confirm the existence of the lateral occipital (*ol*) sulcus, although there is a rostrally directed spur where a^3 (see below) meets *tm*. This spur terminates rostrally where it is crossed by the posterior parietal meningeal artery.

The branch of *ts* that Schepers has identified as the superior parallel sulcus (a^1) has been figured by him at a slightly more rostral angle with respect to *ts* than it actually occupies. Since this branch is continuous with the anterior occipital sulcus (a^3) and since it does not arch rostrally in its medial extent, this sulcus does not appear to me to be a^1 . I have labeled this sulcus the sulcus angularis (a^2) based on numerous diagrams of a^1 , a^2 , and a^3 for *Pan* and *Homo* (Fig. 7 and Connolly, 1950). If a^1 was present in the Taung endocast, it may have been located rostrally in the damaged parietal regions (Figs. 1 and 7).

Schepers has identified an anterior occipital sulcus (a^3) on the Taung endocast. While I agree that the medial portion of this sulcus represents a^3 , I think that the lateral portion constitutes a caudal continuation of *tm*, with which it is continuous. The relationship between a^2 , a^3 , and *ts* shown in my illustration of the Taung endocast is typical for chimpanzees and gorillas but not for humans (Connolly, 1950). In general, the human sulcal pattern is more convoluted in this region and a^2 and especially a^3 may be separate from *ts*, and they are usually separate from each other (Fig. 7 and Connolly, 1950). Similarly, the abrupt lateral course of *tm* in its caudal extremity shown in Taung is seen frequently in *Pan* and *Gorilla* where *tm* occasionally links up with *oci* (Connolly, 1950:94, 111). A single, long coursing *tm* is not typical of humans in whom *tm* has usually been broken up by convolutions of the temporal lobe. Thus, in its temporal lobe, the Taung endocast again resembles the African pongid rather than the human condition. There is nothing in the temporal lobes of the other australopithecine natural endocasts to dispute this observation.

Occipital lobe. My identifications in the occipital lobe of the Taung endocast differ completely from those of Schepers. The endocast has been damaged in two occipital regions. These damaged areas were intact prior to

Schepers' description (see Fig. 5 of Dart, 1925) but Schepers neglected to indicate them in his illustration. Schepers has figured a sulcus which seems to me to be arched around one damaged area and he has identified it as the angularis sulcus (a^2). Clark et al. (1936:268) disagree with this identification:

the angular sulcus in *Australopithecus* is, in its abrupt edges and its depth, unlike any marking which we have seen on our endocranial casts. The angular sulcus certainly does not produce a furrow of this type in the chimpanzee. . . . we think that such an interpretation must be highly problematical.

While I agree that there is a sulcus (*lc*, see below) directed caudally from the medial edge of the damaged area, I am unable to see or feel the portion which Schepers figured as arched around the rostral end of the area. The portion of the sulcus that is present in the Taung endocast cannot be a^2 , as identified by Schepers, because it is caudal to a^3 , which is the reverse of the human condition where a^2 is always rostral to a^3 (see Connolly, 1950:224-225). In *Pan* and *Gorilla*, a^2 is typically continuous with a^3 (Connolly, 1950:91, 108). Based on the angle and location, this sulcus clearly appears to be the lateral calcarine (*lc*). See Figures 1 and 3.

Schepers has identified another relatively long sulcus as the transverse occipital (*to*) sulcus. The rostral end of this sulcus is in fact not detectable because it is terminated by a second damaged occipital area (not included by Schepers). Hence, my counterpart to this sulcus is much shorter than Schepers' *to* and, I believe it most likely is a superior ramus of *lc* ($= u$)—a sulcus that is commonly seen in monkeys and apes. I have not labeled *u* in Figure 1 because I am less certain of this identification than I am of the other sulci—e.g., it could also be a post-lunate (*ptl*) sulcus. Radinsky (personal communication) has asked whether this sulcus might not be a portion of the lunate, but I think that this is unlikely since its lateral extension would intercept *lc*. Schepers has identified a long parietalis transversus (*pat*) sulcus in the Taung endocast. I am unable to confirm the existence of the entire longitudinally oriented segment of this sulcus in either the original specimen or its plaster copy. The small transverse portion of Schepers' *pat* is included in my tentative identification of *u* (Figs. 1 and 3).

Sutures are readily distinguished from sulci on endocasts (Falk, 1978c), since sulci are represented by grooves and sutures are represented by protruding lines that often look like sutures. The landmark that Dart (1925) and

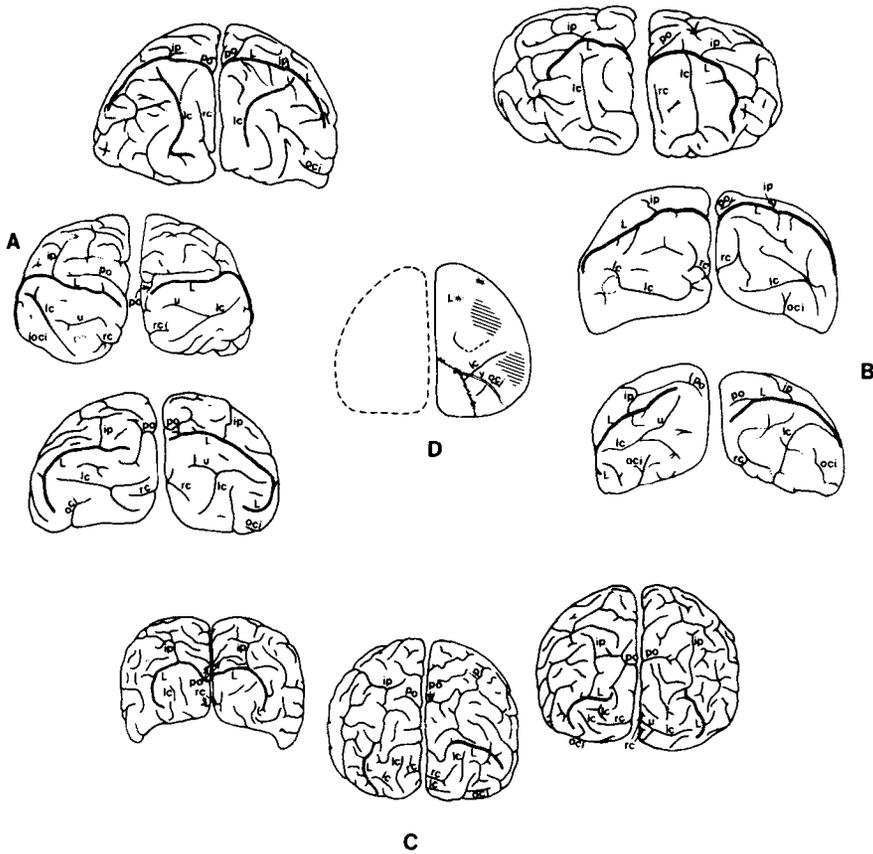


Fig. 3. Occipital views of hominoid brains, selected to show range of variation. Lunate sulci darkened. A, *Gorilla*: top, NMNH 292165; middle, NMNH 292164; bottom, after Connolly (1950:95). B, *Pan*: top, author's collection; middle, NMNH 292176; bottom, NMNH 292178. C, *Homo*: after Connolly (1950:316, 242, 239). D, the Taung endocast: *lc* and *oci* are crossed by a vessel (*v*). The unlabeled sulcus medial to *lc* may be its superior ramus (*u*). Notice that in all genera, *L* is rostral to *lc*. Placement of *L* caudal to the unlabeled lambdoid suture in the Taung endocast would violate this arrangement. Thus, the identification of the medial portion of *L* shown here is in keeping with the relative position of *L* in other hominoids. See text for discussion. Not to scale. Abbreviations of sulci: *rc*, retrocalcarine; *u*, ramus superior of *lc*; other abbreviations as in Figure 1.

Schepers (Broom and Schepers, 1946) identified as the lunate (*l*) sulcus is definitely the lambdoid suture, as suggested by Clark et al. (1936:268). Schepers has identified the sulcus rostral to this suture as the prelunate (*pl*). This sulcus appears to me to be the inferior occipital (*oci*) sulcus (see Figs. 1 and 3). Schepers has identified the parieto-occipital sulcus (*po*) in the Taung endocast. This sulcus is rarely, if ever, reproduced on human (Connolly, 1950), ape (ibid; Clark et al., 1936), or monkey (Falk, 1978c) endocasts. I think that *po* of Schepers represents the medial end of the lunate sulcus (*l*). If so, the course of the lateral portion of *l* may be obscured either by the nearby damaged

area or by the nearby branch of the posterior parietal meningeal artery (Fig. 1). Schepers also identified *l* on the NO. 2, NO. 3, and NO. 8 specimens. I could neither see nor feel *l* on these specimens (see Figs. 4 and 6 and below for further discussion on *l*).

The occipital lobe of the Taung endocast appears to be smooth caudal to the lambdoid suture. It seems likely that sulci were present but simply were not reproduced in this region of the endocast, since comparable areas in hominoid endocasts do not reproduce sulci although sulci do exist in the corresponding parts of hominoid brains. Since the occipital regions of the other australopithecine natural endocasts also are

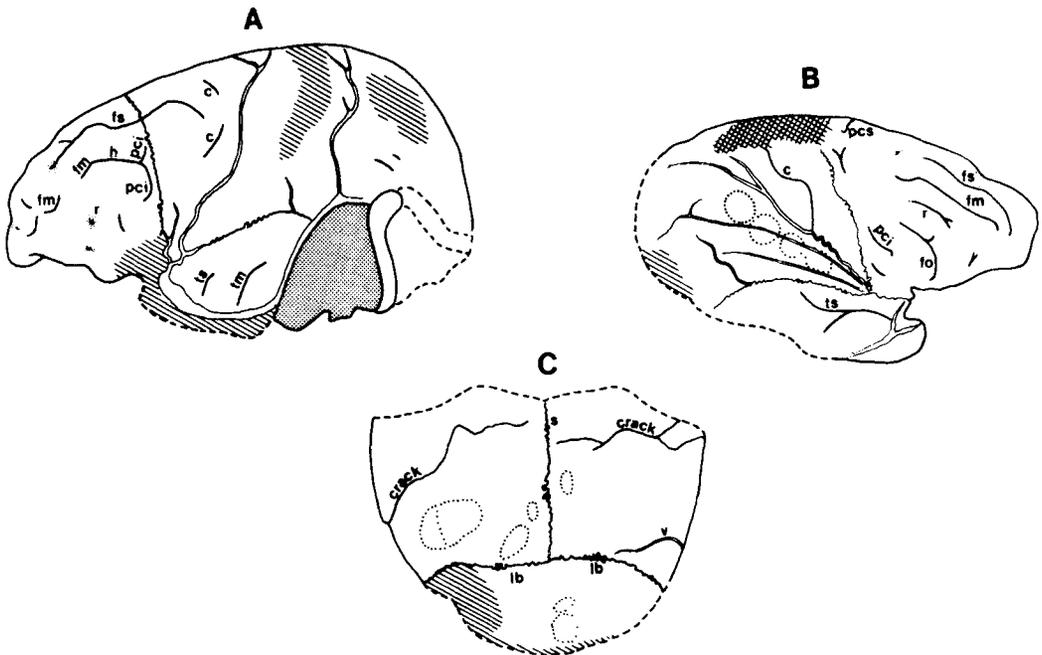


Fig. 4. Sulcal patterns of three australopithecine natural endocasts from Sterkfontein. A, NO. 1 (STS 60); B, NO. 2; C, NO. 3. Sutures and vessels are indicated and damaged areas have been hatched. Crossed hatching in B indicates a dented-in region. Schepers (Broom and Schepers, 1946) originally figured these specimens but in all three cases he identified many more sulci than I have been able to verify in either the original specimens or their copies. See text for discussion. Abbreviations: *lb*, lambdoid suture; *s*, sagittal suture; other abbreviations as in Figure 1.

blank, we do not yet have a good description of the sulcal pattern in the occipital lobe of australopithecines. The Taung endocast is the best example, and the occipital sulcal pattern rostral to the lambdoid suture in this specimen appears to be relatively simple—i.e., more ape-like than human like, especially in the location and size of *lc* (Fig. 3).

The Sterkfontein NO. 1, NO. 2, and NO. 3 endocasts

Figure 4 illustrates my identifications of the sulci on the left hemisphere of STS 60 from Sterkfontein (NO. 1), the right hemisphere of the NO. 2 specimen, and a dorsal view of the Sterkfontein NO. 3 specimen. In both the NO. 1 and NO. 2 specimens, the sulcal pattern of the frontal lobe appears similar to that of the Taung endocast. Unfortunately, the NO. 3 specimen fails to reproduce specific details of the occipital sulcal pattern, although gentle contours are visible rostral to the lambdoid suture in the left hemisphere. These specimens have also been illustrated by Schepers (Broom and Schepers, 1946:185, 187, and 191), who

identified many more sulci than shown in Figure 4. As was the case for the Taung endocast, I was frequently unable to see or feel sulci figured by Schepers in either the original fossils or their plaster copies (see discussion). Adequate figures and identifications of sulci of SK 1585 and STS 1017 may be found in Holloway (1972) and Falk (1979b) respectively.

The STS 58 natural endocast

The STS 58 natural endocast reveals little about the external morphology of australopithecine brains. However, since it was recently discovered in a box at the Transvaal Museum by Doctor Ronald Clarke and since it was previously not known to exist, I will describe it and discuss its history.

According to Broom et al., (1950), the Sterkfontein NO. 8 specimen (*Plesianthropus transvaalensis* VIII) consisted of the STS 19 cranial base and the STS 58 calotte. Clarke (personal communication) thinks that there is no reason to assume that these two specimens belong to the same individual. Schepers (Broom et al., 1950:84) reconstructed the endocast of the NO.

8 specimen "by the addition of an *almost perfect cast* of the posterior and middle cranial fossae to an accurate *impression* made from the posterior two-thirds of the calvarium" (emphasis mine). Clarke was not able to locate the nearly perfect endocast from STS 19, but did find the artificial (plaster) endocast from STS 58 and, much to our surprise, a *natural* endocast from STS 58. This latter specimen has not been mentioned by Schepers. Thus, Clarke's search produced the rare opportunity to compare an artificial endocast with a natural endocast from the same australopithecine individual (Fig. 5).

Figure 6 illustrates the small amount of cerebral morphology that is visible on the STS 58 natural endocast. With the exception of two small sulci (one in each hemisphere) directly behind the coronal suture (*possibly* the precentral superior sulci), no sulci are clearly delineated on this specimen. One can see portions of the sagittal, lambdoid, and coronal sutures, sagittal sinus, and cerebral vessels. Although sulci are not reproduced, there are very slight bulges in the occipital regions, especially on the left side. The natural, but not artificial, endocast reproduces a buckled area in the right parietal region. This may have been the result of buckling from internal pressure during the process of fossilization.

The artificial plaster endocast from STS 58 reproduces fewer details of the cerebral cortex than does the natural endocast. This is due largely to the fact that 75% of its surface is covered with bone pulled away from the endocranial surface (evidently Schepers chose not to remove the bone from the plaster endocast). The STS 58 calvaria has large cracks which are not represented on either of the endocasts. These cracks extend through the shattered and chisel-marked massive breccia in which the calvaria is embedded. The pieces have been glued together and the breccia plastered. It is clear that the calvaria was damaged first by the artificial endocast that removed large areas of endocranial surface and secondly by the chiseling that appears to have been an attempt to remove the calvaria from the breccia at some time *after* removal of the artificial endocast. Schepers described only the artificial endocast from STS 58 (Broom et al., 1950:107, 109). As noted above, Schepers' illustrations show many sulci that I am unable to detect on either the natural or the artificial endocast.

DISCUSSION

A comparative study of the cerebral cortices of chimpanzee, gorilla, and human brains, and

australopithecine endocasts suggests that sulcal patterns reproduced on natural endocasts of South African australopithecines are more pongid-like than human-like. A comparison of the sulcal pattern of the approximately 5- to 6-year-old Taung "baby" (Fig. 1B) with the sulcal patterns of a young chimpanzee (Fig. 7A) and a 5-year-old *Homo sapiens* (Fig. 7B) will serve to illustrate the pongid-like affinities of the external morphology of the australopithecine brain.

Previous workers have concentrated on the position of the lunate sulcus as evidence for human-like attributes of the australopithecine brain. The lunate sulcus is a crescent-shaped sulcus that delimits the primary visual or striate area rostrally on the lateral surface of the occipital lobe in monkeys and in apes. In a sample of 120 human brains (Connolly, 1950:252), a continuous *l* was present in approximately 58% of the hemispheres. According to Connolly (1950:232), the area striata lies slightly caudal to the lunate sulcus in human brains. See Figures 3 and 7 for illustrations of the variation in the position of *l* for humans and African pongids.

The position of *l* in australopithecines has long been the subject of debate. According to Dart (1925), *l* occupied a relatively caudal position in the Taung endocast, similar to the position of *l* believed to be typical for humans and indicative of an expanded parietal association cortex. Clark et al. (1936) suggested that Dart mistook the lambdoid suture for *l* and that *l* should be located rostral to this suture in australopithecines, as it is in chimpanzees. Later, in a curious reversal, Clark (1947:312) concluded that "it must be inferred that a sulcus lunatus, if present in typical form, must have been at least as far back as sulcus 18" (i.e., *l* of Schepers = the lambdoid suture). Clark's later statements were based on Schepers' diagram of the Taung endocast (Fig. 1). Clark reasoned that if *l* were rostral to the lambdoid suture it would have to be as far forward as Schepers' occipital anterior sulcus (*a*³) because between these two locations (1947:312) "the convolutions are disposed in an approximately antero-posterior direction, and they are clearly enough marked on the cast to exclude the possibility of a transversely disposed sulcus lunatus in this position." Clark stated that this rostral location of *l* was untenable because *l* would be further forward than in any modern ape.

Clark's reasoning against a rostral location of *l* does *not* hold for my identifications of the Taung endocast's sulci. As discussed above, I

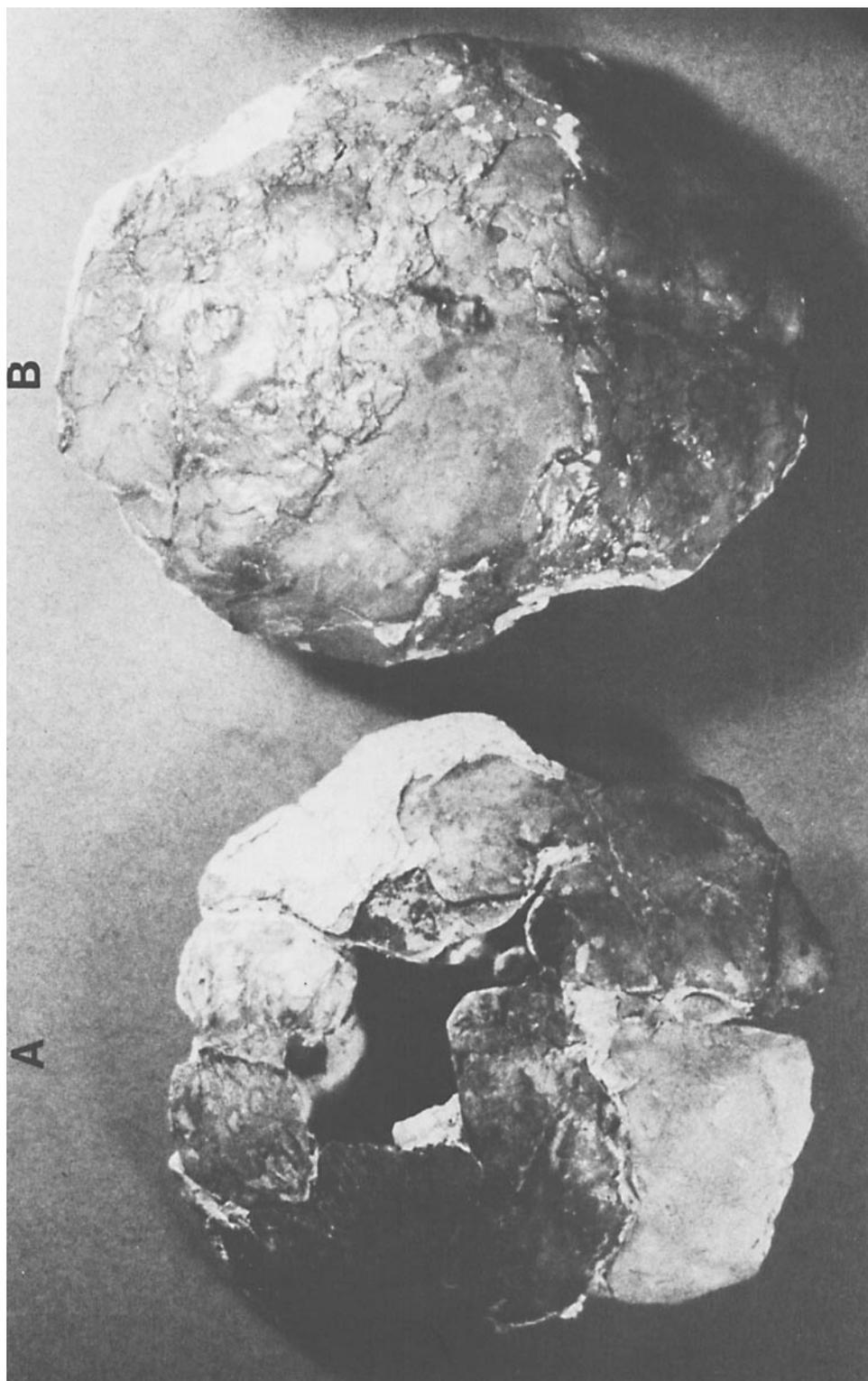


Fig. 5. Natural (A) and artificial (B) endocasts from the same australopithecine calvarium (STS 58). The natural specimen shows more details of cerebral cortex than does the artificial endocast. See Figure 6 and text for discussion of the interesting history of these specimens.

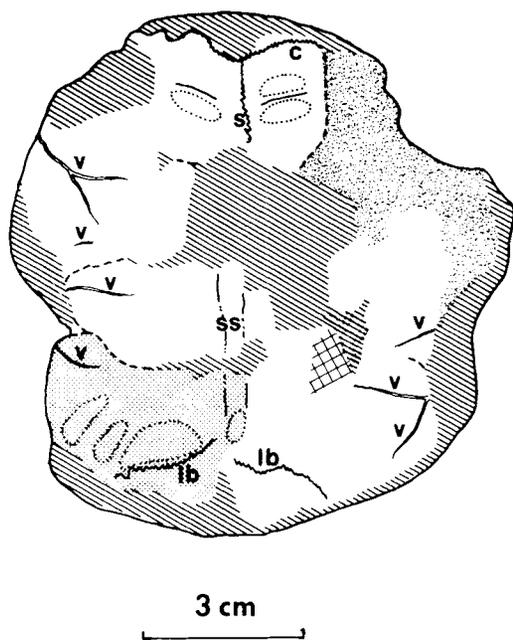


Fig. 6. Illustration of the natural endocranium from STS 58 which consists of an eggshell-thin layer of hard lime that has been supported with a plaster backing. Hatched areas damaged or missing, double-hatched area represents buckled area of right parietal lobe not visible in the artificial endocranium. Stippling represents plaster endocranium, and plain shading indicates area of adherent bone from the endocranial surface. Although two sulci are reproduced in the right and left hemispheres near the coronal suture, their identities remain ambiguous because of lack of other sulcal landmarks. Abbreviations: *c*, coronal suture, *lb*, lambdoid suture; *s*, sagittal suture; *ss*, sagittal sinus; *v*, vessel; other abbreviations as in Figure 1.

was unable to see or feel the rostral portions of the occipital sulci identified by Schepers (his *pat*, *to*, and *a*²). Furthermore, the position of *l* suggested by me for the Taung endocranium is perfectly in keeping with the position of *l* in African pongids (Clark et al., 1936; Connolly, 1950; and Figs. 3 and 7). It should be noted that *l* is rostral to the lambdoid suture in monkeys (Falk, 1978c), *Pan* (Clark et al., 1936) and some humans (Connolly, 1950:316, 318; Crafts, 1966:464–465). Finally, if *l* is caudal to the lambdoid suture in the Taung endocranium, this would be a unique feature because no other anthropoid endocraniums or brains that I have seen have *l* caudal to *lc* rather than rostral to it! See Figures 3 and 7. Thus, I believe that, although its lateral extent is not visible in the Taung endocranium, the lunate sulcus must have been lo-

cated rostral to the lambdoid suture. As noted above, the most likely position to have been occupied by the medial portion of *l* is the depression that Schepers identified as *po*. The lateral course of *l* could have been obscured by either the nearby damaged occipital area or nearby branch of the meningeal vessel (Fig. 1), or perhaps *l* was even a bit more caudal than the meningeal vessel and simply did not become reproduced on the natural endocranium.

Unfortunately, the supposed caudal position of *l* in australopithecines is well entrenched in the modern literature. According to Holloway (1972:198), the "minimal interpretation" of the caudal position of *l* is that by the time of the Taung child, the hominid brain was already reorganized in a human direction, regardless of the chimpanzee-like size. . . . Holloway (1975) also suggests that the Taung endocranium shows a human shape that is different from the shape of African pongid endocraniums. In order to compare heights of brains, Holloway provides a number of indices for hominid endocraniums, among them mean L/H indices (ratio of chord length between frontal and occipital poles to chord length from vertex to lowest plane of temporal lobe) for various hominids, including the Taung endocranium. Lower indices indicate greater cortical height relative to length. The mean figure for L/H of *Homo sapiens* ($n = 4$) is 1.40, the mean for *Pan troglodytes* ($n = 29$) is 1.47, and that for *Gorilla gorilla* ($n = 36$) is 1.53. Holloway's L/H index for the Taung endocranium is 1.41. Since neither the frontal pole nor the lowest plane of the temporal lobe is present in this specimen, this index must be viewed tentatively. I have calculated a mean L/H index of 1.36 for six orangutan endocraniums and Holloway (1980) provides mean H/L indices, the reciprocals of which yield L/H figures of 1.62 for Solo ($n = 5$) and 1.49 for *H. s. neandertalensis* ($n = 4$). Furthermore, as Holloway points out (1975:23), L/H indices for *Homo erectus* fail to conform to a pattern of greater cortical height in hominids than in African pongids. Thus, L/H indices do not separate pongids (even just African apes) from hominids.

I have shown that the lateral edge of the frontal lobe of the Taung endocranium appears to be pongid-like in shape rather than human-like. Even if quantitative analyses of australopithecine endocraniums did suggest that certain areas were shaped like comparable areas in human endocraniums, I agree with Radinsky (1979:21) that "the differences in shape of *Australopithecus* vs. chimp and gorilla endocraniums may be a packaging phenomenon"—i.e., these differences

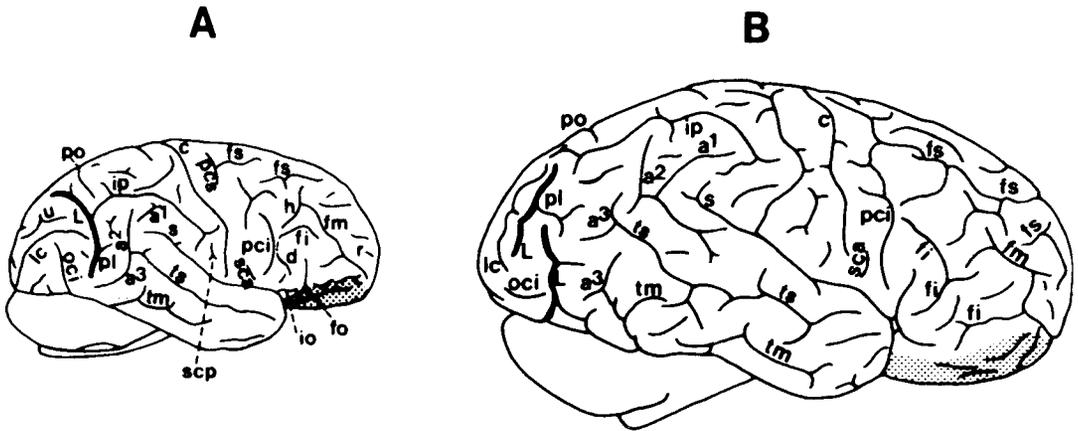


Fig. 7. A chimpanzee and a human brain, right lateral views. Lunate sulci darkened. A, *Pan*: young male, after Connolly (1950:108). B, *Homo*: 5-year-old male, after Connolly (1950:177). Not to scale. Compare with the endocast from the Taung specimen (an individual who lived to be approximately 6 years old) in Figure 1B. Abbreviations of sulci: *io*, incisura opercularis; *sca*, subcentral anterior; *scp*, subcentral posterior; *u*, ramus superior of *lc*; other abbreviations as in Figure 1.

may simply be due to the relatively larger brain-to-skull size in the former. Finally, it should be noted that the ratios between brain size and body size (i.e., relative brain size) of australopithecines is considerably smaller than that of modern humans (McHenry, 1975). (See Falk, 1980 for further discussion.)

CONCLUSIONS

The observation that sulcal patterns reproduced on natural endocasts of South African australopithecines appear to be pongid-like rather than human-like is contrary to the early descriptions of australopithecine endocasts as well as to current consensus. Two factors may help account for the disparity between Schepers' descriptions of australopithecine endocasts and my own.

First, a good deal of the disparity in endocast descriptions is the result of different techniques for "reading" sulcal patterns. Schepers (Broom and Schepers, 1946:178) acknowledges that his figures are characterized by "a much larger number of convolutions . . . than could be . . . identified by direct observation. These could be added one by one only in most cases." In addition to direct observation and palpation of endocasts, Schepers used a variety of techniques to identify sulci: 1) shading in with pencil of grooves and depressions on plaster copies of endocasts, 2) oblique illumination and photography of plaster copies, and 3) rubbing soot on plaster copies to highlight details of sulcal

pattern. Clark et al. (1936) have shown that the latter method produces inaccurate and distorted sulcal patterns. The "carbon method" (and the "pencil method") may result in vessels and sutures being mistaken for sulci (Clark et al., 1936), as is demonstrated by a comparison of Schepers' and my illustrations of the Taung endocast (Fig. 1). Anyone who has photographed endocasts or brains knows that lighting can easily create an inaccurate impression of sulcal patterns. Photography certainly should not be used to discover sulci that are otherwise unobservable. For the above reasons, my sulcal identifications are based solely on visual inspection and palpation.

Second, the early descriptions of australopithecines should be viewed in historical context. After his announcement of the discovery of the Taung specimen in 1925, Raymond Dart had to defend the contention that "the specimen is of importance because it exhibits an extinct race of apes *intermediate between living anthropoids and man*" (Dart, 1925:195). Later, Dart's colleague Robert Broom discovered other australopithecine "ape-men" and defended their status as missing links. Perhaps it was in an effort to answer critics who dismissed the importance of these finds, that early workers such as Schepers (Broom's co-author) emphasized the human-like features of australopithecines and downplayed their pongid-like features.

Although australopithecine brains average

approximately 450 cc and human brains average about 1400 cc (Holloway, 1970 and 1975), human and australopithecine (and pongid) brains have the same basic sulcal pattern. 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.

I want to make it quite clear that I am not saying that australopithecine brains were identical to those of pongids. The fact that australopithecines and pongids differ in posture, locomotion, dentition, other aspects of skeletal morphology, and inferred ecological niche suggests that the nervous systems of these hominoids also differ. These differences are not manifest at the level of cortical sulcal patterns, however, but may have existed at finer neurological levels, perhaps at cellular or molecular levels.

The most important conclusion of this paper is that the australopithecine lunate sulcus was not located in a caudal human-like position, as first reported by Dart (1925) and now generally believed. Rather, the australopithecine lunate sulcus was relatively rostral, as in pongids. Although Holloway's (1967, 1972, 1975) concept of reorganization of australopithecine brains was based, in part, upon acceptance of a caudal lunate sulcus, we must be careful not to throw out the reorganization baby with the lunate sulcus bathwater. Neurological reorganization remains the best concept for explaining evolution of the human brain (Holloway, 1975:34):

one important aspect of the large increase in brain size seems attributable to the reorganization of numerous component structures. That is why I believe comparisons based on cranial capacities alone are meaningless. One cc. of chimp or australopithecine cortex is not equivalent to one cc. of modern human, Neanderthal or *Homo erectus* cortex. It is changes in the spatial relationships between elements that provide our great neural complexity.

Future studies by comparative neuroanatomists (e.g., Armstrong, 1979:80a,b) will hopefully elucidate the fine details of neurological reorganization that occurred during human evolution.

Finally, although South African australopithecines appear to be pongid-like in the gross details of cerebral cortex, this paper should *not* be construed as supporting placement of *Australopithecus africanus* on a sidebranch of the human phylogenetic tree (Johanson and White, 1979). No derived features were found in the cerebral cortices of South African australopithecines that would preclude their being ancestral to *Homo sapiens*.

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