

THE PAST, PRESENT, AND FUTURE SIGNIFICANCE OF THE LUNATE  
SULCUS IN EARLY HOMINID EVOLUTION

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INTRODUCTION

This Jubilee of the Taung discovery, and Prof. Raymond Dart's extraordinary prescience in realizing its significance, provide an opportunity to look once again at a controversial issue of great importance to our nascent understanding of human brain evolution. There is a certain irony to it all: 60 years ago, the position and importance of the lunate sulcus on the Taung endocast were integral parts of the debates of those times; 60 years later, the issue would appear to be unresolved, surrounded by a veritable penumbra of doubt, confusion, and alas, ignorance.

Several "anniversaries" are worth mentioning at the outset of this paper, which is unabashedly an homage and tribute to one man so instrumental in setting my own career in the perfidious endeavours of paleoneurology. 1986 will mark the 60th anniversary of Dart's (1926) re-assertion that the Taung lunate sulcus was in a non-pongid posterior position. 1986 will be the 50th anniversary of the Clark et al (1936) paper which attempted to rebut Dart's earlier claims, and as will be shown below, holds an important key to the puzzle of both Taung and Hadar interpretations (Holloway 1981a, 1983,a,b,c, 1984). 1987 will be the 40th "anniversary" of Clark's (1947) classic paper which, while not definitively identifying the position of the cerebral landmarks on the Taung specimen, nevertheless supported most of Dart's original perceptions, including the lunate sulcus. 1986 will mark the 40th anniversary of Schepers' (1946, 1950) attempts to interpret those convolutional details

which brought him to an unusual statement of positive accord. 1986 will mark the 30th anniversary of Dart's (1956) paper which recognized the reorganization of brain structures in early hominid evolution as something equally important as mass, or size (if not more so).

#### THE ISSUE OF THE LUNATE SULCUS

"Whatever the total dimensions of the adult brain may have been, they are not lacking evidences that the brain in this group of fossil forms was distinctive in type and was an instrument of greater intelligence than that of living anthropoids... The pithecoïd type of parallel sulcus is preserved, but the sulcus lunatus has been thrust backwards toward the occipital pole by a pronounced general bulging of the parieto-temporo-occipital association areas...

"The expansion in this area of the brain is the more significant in that it explains the posterior humanoid situation of the sulcus lunatus. It indicates... the fact that this group of beings... had profited beyond living anthropoids by...a...much larger area of cerebral cortex to serve as a storehouse of information concerning their objective environment... They possessed to a degree unappreciated by living anthropoids the use of their hands and ears and the consequent faculty of associating with the colour, form, and general appearance of objects, their weight, texture, resilience, and flexibility, as well as the sounds emitted by them... They had laid down the foundations of that discriminative knowledge of the appearance, feeling, and sound of things that was a necessary milestone in the acquisition of articulate speech." (Dart 1925:197-198; see also Dart 1926:324-327 for comments regarding the size of the Taung brain and expansion of posterior parietal association cortex, and McGregor 1925.)

Perhaps the language is a bit more optimistic or piquant than modern descriptions of cerebral regions and functions, but Dart's (1925) quotation above compares favorably with conclusions drawn from modern neurobiology (c.f. Geschwind 1965; Damasio, Geschwind 1984; Hyvarinen 1982; Angevine, Smith 1982; Jones 1984, Eidelberg, Galaburda 1984), regarding both the sensory and integrative functions of anterior occipital and posterior parietal cerebral cortex, i.e., areas 18 and 19 per Brodmann, or peristriate cortex.

The lunate sulcus is the anterior boundary of primary visual striate cortex, which has a particular cytoarchitectonic appearance, as it contains the stria of Gennari, densely composed of stellate neurons. This is koniocortex, and is the first way-station in the cerebral neocortex for the termination of the radiating visual fibers leaving the lateral geniculate body of the thalamus. It is a crescentic furrow or sulcus, concave posteriorly, and is invariably in an anterior position in Anthropoidea. The function of striate cortex is almost totally sensory, although the anterior margins have some integrative functions. The striate cortex's nearest anterior neighbor is parietal "association" cortex, better known for its integrative functions in cognition, although its posterior margin also subserves visual sensory tasks. Damage within the striate cortex produces scotopias, or areas of visual blindness. Ablations in parietal "association" cortex do not normally produce scotopias.

In Pan, Pongo, Gorilla and Hylobates, the lunate sulcus is readily visible, always anterior to the lateral calcarine sulcus, and always posterior to the interparietal sulcus whose posterior portion abuts against the lunate sulcus (see Holloway 1983b for diagrams). In modern Homo sapiens, the lunate is often present, and when visible is in a decidedly posterior position (see Levin 1936, and Connolly 1950 for frequencies). Interestingly, Smith (1904a) found an unusual exception to this general condition in one Egyptian woman's brain. Smith (1904a, 1904b, 1907a,b, 1927, 1929) spent years studying the distribution, development and comparative aspects of the lunate sulcus. This does not mean that invoking his name is, as Falk (1983a: 487) described it, "argumentum ad verecundiam", but rather an indication that as Dart did study under Smith, he (Dart) had probably heard of the lunate sulcus, and did not cast his eyes upon the Taung endocast as an unknowledgeable virgin who would confuse the lambdoid suture with the lunate sulcus! But in the interest of Latin scholarship, Falk missed this essential point. Falk (1982:86) claims that one looks in vain for any reorganization in the human brain, despite her earlier (1980a:104) examples from Armstrong's (1979, 1980) work. Passingham and Ettlinger (1973:241-242), using Stephan's (1969) data showed that the human value for primary visual striate cortex fell well beneath the log-log equation of striate cortex vs. brain volume. In 1979, I

showed the same results with 4 independent samples, and had discussed such findings in 1976 as a response to Jerison's (1973) critique of the reorganization concept.

On Stephan et al's (1981) newer data base, the Homo sapiens value for visual striate cortex is 66% less than expected for a primate of its brain size. The lateral geniculate body is 106% less than expected! (These are for the Anthropoidea only. If prosimians are included, the deviations are 121% and 147% respectively.) Sometime in the course of human evolution, primary visual striate cortex became relatively reduced, and posterior parietal cortex enlarged. This is not some mere "packaging problem" (Radinsky 1979) whom Falk cites (1983a: 488) "argumentum ad verecundiam", without a single empirical observation to prove it, but rather a true reorganizational feature important to cognitive functioning. Results with stereoplotting techniques (Holloway 1981b, 1984) point to the same conclusion. The questions are, when did this happen, and how can it be demonstrated unambiguously?

#### BACK TO THE ENDOCASTS

The problem with the Taung endocast, as both Dart and Clark (and others) knew, was that the lunate sulcus could not be unambiguously demonstrated, given the position and openness of the lambdoid suture. Schepers (1946), too, realized this, but opted for placing the lunate sulcus in the approximate position followed by the lambdoid sutural ridge.

"The identification of the lunate sulcus (18) in Australopithecus africanus, originally made by Dart, provoked a great deal of adverse criticism on the part of many scientists, notably Keith (1929). Being ordinarily situated relatively far forward on the dorsolateral surface in living anthropoids... and just behind the parallel sulcus (24), the suggestion that it may be represented by the curved sulcus near the tip of the occipital pole, which lay almost opposite the lambdoidal suture-line, was widely taken to signify over-enthusiasm on the part of the sponsors of the hominid status of the Taungs fossil. As far as is known, none of these critics have had access to the original cast. Even Dart studied a partially cleaned cast. Since the adherent cortical lamellae have been removed there can be little doubt as to the precise identification of the

various occipital sulci, and Dart's original homology for the lunate sulcus must be sustained." (Schepers 1946:192).

Falk's (1980b: 531-532) response was as follows:

"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 Schepers (Broom and Schepers 1946) identified as the lunate sulcus is definitely the lambdoid suture, as suggested by Clark et al (1936:268)" (Falk 1980b: 531-532.)

It comes as a surprise to me that Clark (1947) should reverse his earlier position (Clark et al 1936) after working on the originals rather than a cast and six chimpanzee brains and associated endocasts. In fact, as Clark et al (1936) indicated, the lambdoidal suture and the lunate sulcus did overlap (approximately) in one chimpanzee specimen, and Hirschler (1942:17,31,54) in his review and studies found this conjunction to occur occasionally. Incidentally, there is nothing in Schepers' (1946) discussion to suggest he confused the lambdoid suture with the lunate sulcus, as alleged by Falk (1980b).

Falk's (1980b) solution to this problem was to define a small sulcal depression well anterior to where it would occur on any pongid brain, as the lunate, even though its superior portion was interrupted by a longitudinal gyrus just lateral to the midsagittal plane, and without any inferior crescentic morphology. The normal Pan position, based on 6 Pan brain casts, violated all cerebral morphology when placed on the Taung endocast (Holloway 1981a). To rebut this demonstration, Falk (1983) introduced some undefined "shape factor" (p. 487) to account for the discrepancy, based on ratios taken from arc measurements on unscaled photographs of Pan brain casts. The actual measurements (Holloway 1984) indicate Falk's lunate position on Taung to be 2.52 S.D.'s anterior to that in a typical pongid pattern (Fig. 1).

In 1983c, in a preliminary report on the AL 162-28 posterior endocast portion of a reputed A. afarensis (Holloway 1983c), groove or furrow "B" was defined not as the lunate sulcus, but as a depression caused by the inferior lip of the parietal bone. Falk (1985) now regards this as a true lunate and, by incorrectly orienting her

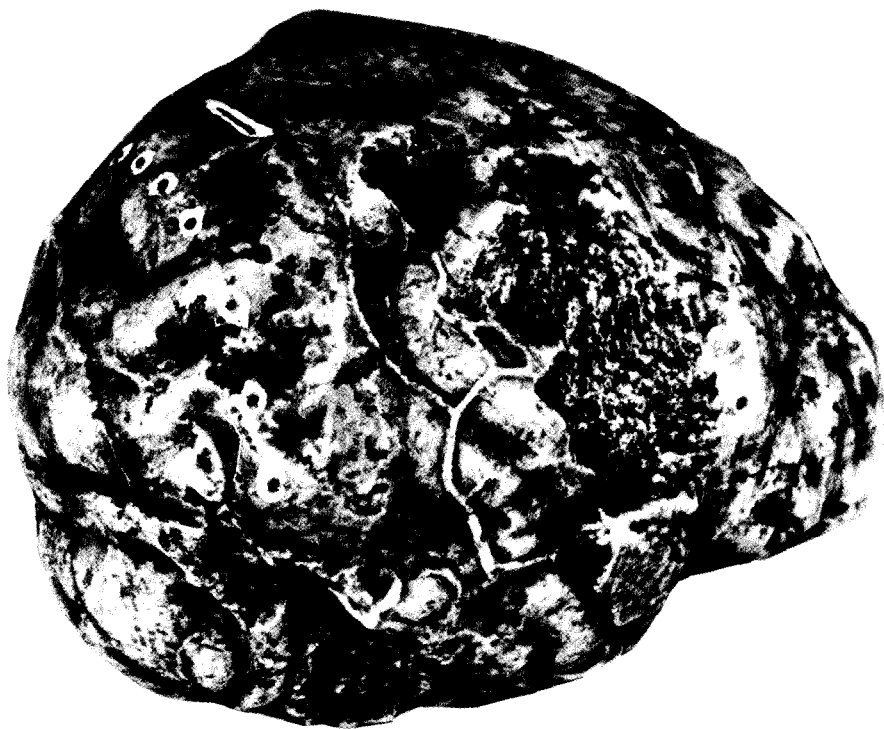


Fig. 1

Lateral view of the Taung endocranial cast, slightly rotated from the midsagittal plane to show the convolutional patterns more thoroughly. The small line marked at top left is Falk's (1980b) placement of the lunate sulcus. To the left is an arc of white dots containing black dots, which represents the average location of the lunate sulcus in Pan, based on six brain casts (c.f. Holloway 1981a). Falk's "line" falls 2.5 standard deviations outside of the Pan average (Holloway 1984). Note how the typical Pan placement violates the transversely disposed convolutional detail between the lambdoid suture and Falk's line.

drawing by an anterior rotation of the endocast fragment, claims it (the furrow) to be a lunate sulcus in an anterior position. As shown below, her conclusions are erroneous, and her placement actually strengthens the argument for a posterior position of this sulcus.

CLARK ET AL (1936) AND CLARK (1947)

In this paper, Clark and his colleagues studied six chimpanzee brains, and drew their convolutional details (their Figs. 1-6). They also made endocasts from the same crania whence came the brains. Soot was deposited on the endocast surfaces and then wiped off with a cloth stretched over a flat board. Thus soot was erased from prominences (gyri) and left intact in the furrows (sulci).

They compared the two configurations and discovered that gyri and sulci were seldom replicated on the endocasts by the impressions left by the once pulsating brains on the endocrania. This was particularly true of the lunate sulcus! They used this demonstration to argue forcibly that Dart was incorrect in perceiving the Taung lunate as non-pongid:

"The lunate sulcus, surprisingly enough, produces only ill-defined depressions on the cast. With the possible exception of the left hemisphere on specimen No. 1, and the left hemisphere of No. 2, it is very doubtful whether the course of the sulcus could be inferred correctly from the casts. On the other hand, the lambdoid suture always produces a conspicuous furrow which might readily be mistaken for a lunate sulcus, the more so because the occipital pole bulges rather conspicuously behind this furrow..."

"The furrow taken by Dart to represent the sulcus lunatus resembles precisely in its position and appearance the furrow on all the chimpanzee endocranial casts caused by the lambdoid suture. There can be little doubt, therefore, that this is the correct interpretation..." (Clark et al, 1936:268; (see also Cunningham 1892).

An important clue appears to have been ignored in their paper. In each case, a groove "X" was found in a posterior position, and it was caused by the posterior inferior lip of the parietal bone in the lambdoidal sutural margin! Groove

Figure 2b

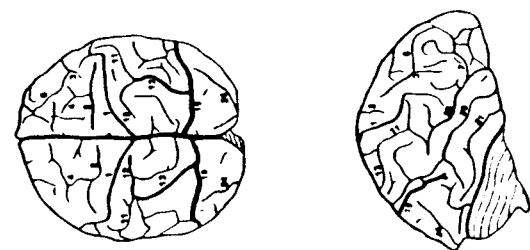


Figure 2a

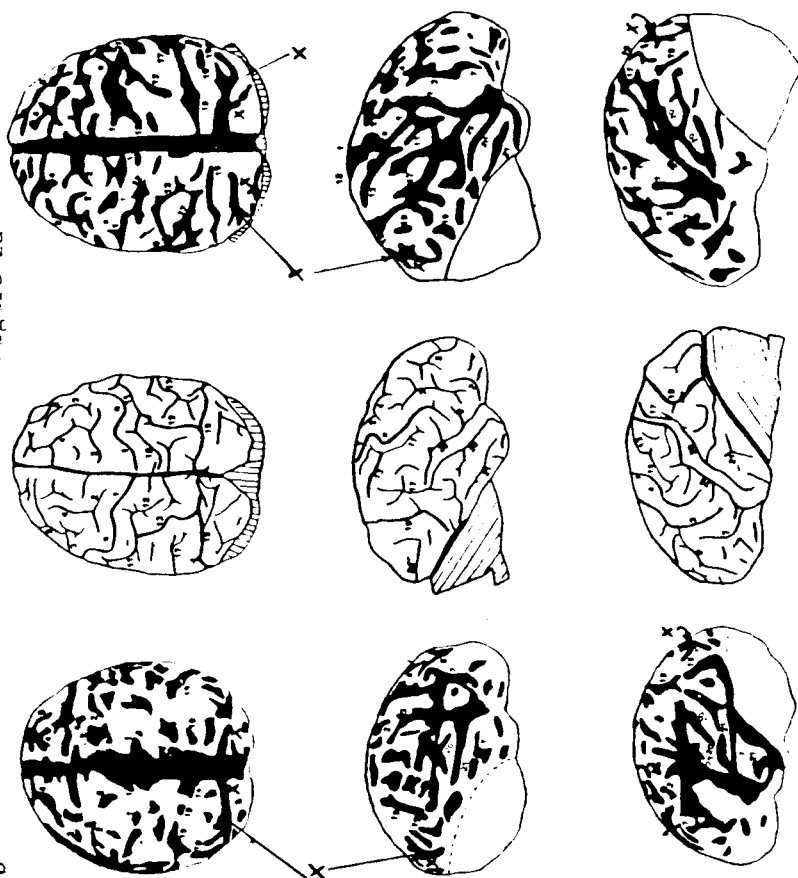


Fig. 2. Figures adapted from Clark et al's (1936) Figs. 2 and 3, pp. 254-256. Note how furrow "x" is clearly posterior to sulcus 19, the lunate, on both dorsal and lateral views.



"X" always transects the lateral calcarine sulcus and always appears well posterior to the lunate sulcus (Fig. 2). It is a striking morphological pattern and can be readily seen on almost every Pan brain that this author has examined, as well as on the endocasts.

Unpublished observations on 36 Pan troglodytes endocasts in my laboratory show this groove to present in pronounced form in 30 cases, and less pronounced in the remainder. It is seldom if ever coincident with the lunate sulcus on these endocasts, which can seldom be seen, an observation fully in accord with Clark et al's (1936) study, and Hirschler's (1942) review.

The AL 162-28 specimen shows this groove ("X" of Clark et. al.) clearly and the interparietal sulcus abuts this groove posteriorly. Falk (1985) agrees with my identification of the interparietal (IP). When the endocast fragment is oriented properly, the groove is quite posterior, as is the caudal end of the interparietal sulcus. Unless the AL 162-28 A. afarensis specimen represents a freak of hominoid brain morphology as yet undiscovered in any living or fossil specimens, one must conclude that if the lunate sulcus did exist, it did so in a posterior non-pongoid position. But let us return to Clark:

"A close study seems to make it fairly clear that, if the sulcus lunatus is farther forward than the depression numbered 18 in Schepers' diagram, it must be at least as far anterior as the depression marked 26 (for between 18 and 26 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. But a sulcus lunatus in the position of the depression marked 26 would be much farther forward (relative to the distance between frontal and occipital poles of the cerebral hemisphere) than in any modern ape, and would indicate an area striata of an extent and complexity beyond reasonable expectation. Thus it must be inferred that a sulcus lunatus, if present in typical form, must have been at least as far back as sulcus 18. On the other hand, the impression on the cast which has been interpreted as sulcus 18 is very ill-defined, and may simply be related to an elevation of bone along the line of the lambdoid suture and not to a cortical sulcus at all. Whichever interpretation may be

correct, the evidence provided by the cast can certainly be taken to indicate that the brain belonging to the Australopithecus skull did not possess a lunate sulcus of the typical simian type. (Clark 1947: 312, emphasis mine).

Falk (1980b), in error, misread Clark (1947), and proclaimed Schepers' (1946) groove (21, parieto-occipital fissure) to be the lunate sulcus. In the stereoplotting (Holloway 1981b) and arc-chord measurements (Holloway 1984) papers, both, techniques concurred in showing Schepers' (1946) grooves (21) and (26) to be far more anterior than any in the chimpanzee. (The latter paper found Falk's 1983a placement by traditional arc-chord techniques to be 2.5 S.D.'s anterior to a true pongid position of the lunate sulcus). I believe Clark's studies of the original specimen, along with Schepers' diagrams, led Clark to regard the lunate as either not present, or posteriorly positioned, as a lunate in the intervening regions would completely violate the remaining cerebral morphology (Fig. 1).

Clark could be wrong in his acceptance of some of Schepers' (1946) convolutional details, but Clark was guarded over accepting some of them. In particular he was hardly confusing the lambdoid suture with the lunate sulcus.

#### SOME NEWER EVIDENCE FROM HADAR

Falk's (1985) criticism of my study of the Hadar AL 162-28 endocast (Holloway 1983) provides a basis for further hypothesis testing. As she agrees with my depiction of the posterior end of the IP sulcus, it is simple to measure the distance from OP (occipital pole) to IP (interparietal) and compare that distance with values from chimpanzee brains, most of which are smaller in volume than the Hadar 162-28 specimen. The results are quite dramatic (Table I), as the distance from OP to IP in AL 162-28 is roughly 1/2 that found on chimpanzee brains. Even the infant case, with a brain weight of 136 grams, has a larger value! Similarly, the distance from OP to what Falk regards as lunate sulcus is on AL 162-28, roughly 1/2 of the distance found on chimpanzee brains. Clearly, if there was a lunate on AL 162-28, it was in a very posterior position compared to the chimpanzee, and, one assumes, any other pongid brain. These measurements thus disprove her contention of an anteriorly-placed, pongid-like lunate sulcus for AL 162-28. Falk's orientation of the endocast is almost 40° in error from proper anatomical placement of the cranial fragment (Kimbel et al 1982; Holloway and Kimbel, in press).

Table 1

| <u>SPECIMENS</u>          | <u>VOLUME (ML)</u> | <u>DISTANCE FROM<br/>OP TO IP (mm)</u> |
|---------------------------|--------------------|--|
| <u>Hominid</u>            |                    |  |
| AL 162-28                 | 375-400            | 16                                     |
| <u>Chimpanzees</u>        |                    |  |
| infant                    | 140                | 25.5                                   |
| 1                         | 407                | 34                                     |
| 2                         | 320                | 30                                     |
| 3                         | 290                | 30                                     |
| 4                         | 295                | 29                                     |
| 5                         | 270                | 28                                     |
| 6                         | 250                | 29.5                                   |
| 7                         | 300                | 33.5                                   |
| 8                         | 400                | 32.5                                   |
| 9                         | 275                | 27                                     |
| Chimpanzee Mean $\bar{x}$ |                    | 30.39                                  |
| S. D.                     |                    | 2.43                                   |

Number of S.D.'s of AL 162-28 from chimpanzee average = 5.92.

Table 1

Figures showing OP (occipital pole) to IP (interparietal sulcus, caudal end) distance in mm (adapted from Holloway and Kimbel, in press). Note that most chimpanzee brain casts are smaller than the AL 162-28 endocast, yet the OP-IP chord distance is approximately double in chimpanzee.

## DISCUSSION

There is a considerable difference between saying that a brain shows some human-like features and saying it is human, fully human, or does not retain any pongid features. In my papers on human brain evolution, I have not said that australopithecine brains were human. A more human-like disposition of the primary visual striate cortex is a far cry from a fully human brain. After all, these creatures lived about 2-3 m.y ago, and it would be amazing if no primitive features of cerebral morphology were retained from ancestral pongid-like forms.

More recently, Falk claims to have discovered a pongid-like morphology of the frontal lobe in australopithecines (Falk 1982, 1983a, b, 1984). She claims a fronto-orbital sulcus is visible in Taung, STS60, and KNM-ER 1805 from Kenya. With all due respect, the following must be said: (1) The inbedded frontal lobe region of the Taung endocast renders such an observation impossible. (2) The crushed and distorted type 2 endocast from Sterkfontein does not show that region intact. (3) STS 60 similarly lacks any clear indication of that sulcus, given the broken surface morphology in that region. (4) The original KNM-ER 1805 endocast was made by me. Both frontal and temporal lobe regions are damaged and eroded, and on the original endocast, the fronto-orbital sulcus cannot be seen on either side. The line drawings in Falk's (1983b) article are at odds with photographs of the original. Indeed, her fronto-orbital sulcus could be interpreted as an inferior frontal or horizontal limb of the Sylvian sulcus.

In conclusion, a plea is made for newer and more objective methods to be developed, to locate convolutional details. Careful metric and stereoplotting tests of hypothesized hominid sulci are an apparent improvement, but newer approaches would be welcome.

## Acknowledgements

I am grateful for the support of the L.S.B. Leakey Foundation, and to NSF (BNS-79-11235 and BNS-84-18921) which permitted me to cast the chimpanzee brains. I am very grateful to Mrs. Beverley March for her patience and skill in typing this paper. I owe countless thanks to Drs. P.V. Tobias, R.A. Dart and Mr. Alun Hughes for all their help, interest and hospitality since 1969.

## References

- Angevine JB Jr., Smith MS (1982). Recent advances in forebrain anatomy and their clinical correlates. In: Thompson RA and Green JR (eds), "New Perspectives in Cerebral Localization." New York: Raven, p.l.
- Armstrong E (1979). A quantitative comparison of the hominoid thalamus. I. Specific sensory relay nuclei. *Am J Phys Anthropol* 51: 365.
- Armstrong E (1980). A quantitative comparison of the hominoid thalamus. II Limbic nuclei anterior principalis and lateralis dorsalis. *Am J Phys Anthropol* 52: 43.
- Broom R, Schepers GWH (1946). "The South African Fossil Ape-Men: The Australopithecinae," *Transvaal Mus Mem* 2:1
- Clark WE LeGros (1947). Observations on the anatomy of the fossil Australopithecinae. *J Anat* 81: 300.
- Clark WE LeGros, Cooper D Zuckerman S (1936). The endocranial cast of the chimpanzee. *J Roy Anthropol Inst* 66: 249.
- Connolly CJ (1950). "External Morphology of the Primate Brain," Springfield Ill: CC Thomas.
- Cunningham DJ (1892). Contribution to the surface anatomy of the cerebral hemispheres. *Roy Irish Acad Sc Cunningham Memoirs*, No. VII, Dublin.
- Damasio AR, Geschwind N (1984). The neural basis for language. *Ann Rev Neurosci* 7:
- Dart RA (1925). Australopithecus africanus: the man-ape of South Africa. *Nature* 115: 195.
- Dart RA (1926). Taungs and its significance. *Nat Hist.* 26: 315.
- Dart RA (1956). The relationship of brainsize and brain pattern to human status. *S Afr J Med Sci* 21: 23.
- Eidelberg D, Galaburda AM (1984). Inferior parietal lobule. divergent architectonic asymmetries in the human brain. *Arch Neurol* 41: 843.
- Falk D (1978). External neuroanatomy of Old World monkeys (Cercopithecoidea). *Contrib Primatol* 15: 1.
- Falk, D (1980a). Hominid brain evolution: the approach from paleoneurology. *Yearbook of Phys Anthropol* 73: 93.
- Falk, D (1980b). A reanalysis of the South African australopithecine natural endocasts. *Amer J Phys Anthropol* 53: 525.
- Falk, D (1982). Primate neuroanatomy: an evolutionary perspective. In Spencer F (ed): "A History of American Physical Anthropology, 1930-1980," New York: Academic

- Press, p. 75.
- Falk, D. (1983a). The Taung endocast: A reply to Holloway. *Am J Phys Anthropol* 60: 479.
- Falk, D (1983b). Cerebral cortices of East African early hominids. *Science* 222: 1072.
- Falk, D (1985). Hadar AL 162-28 endocast as evidence that brain enlargement preceded cortical reorganization in hominid evolution. *Nature* 313, 45.
- Geschwind N (1965). Disconnexion syndromes in animals and man. *Brain* 88: 237, 585.
- Hirschler P (1942). "Anthropoid and human endocranial casts." Amsterdam: N.V. Noord-Hollandsche Uitgevers Maatschappijen.
- Holloway RL (1976). Paleoneurological evidence for language origins. *New York Acad Sci* 280: 330.
- Holloway RL (1979). Brainsize, allometry, and reorganization: toward a synthesis. In Hahn ME, Jensen C, Dudek BC (eds): "Development and Evolution of Brain Size: Behavioral Implications." New York: Academic Press, p 59.
- Holloway RL (1981a). Revisiting the South African Taung australopithecine endocast: the position of the lunate sulcus as determined by the stereoplotting technique. *Am J Phys Anthropol* 56: 43.
- Holloway RL (1981b). Exploring the dorsal surface of hominoid brain endocasts by stereoplotter and discriminant analysis. *Philos Trans R Soc Lond B* 292: 155.
- Holloway RL (1983a). Human brain evolution: a search for units, models and synthesis. *Canad J Anthro* 3: 215.
- Holloway RL (1983b). Human paleontological evidence relevant to language behavior. *Human Neurobiol* 3: 105.
- Holloway, RL (1983c). Cerebral brain endocast patterns of the AL 162-28 Hadar A. afarensis hominid. *Nature* 303: 420.
- Holloway, RL (1984). The Taung endocast and the lunate sulcus: a rejection of the hypothesis of its anterior position. *Amer J Phys Anthropol* 64: 285.
- Holloway, RL, Kimbel, WH (in press). Brain reorganization in the Hadar AL 162-28 endocast: A reply to Falk. *Nature*, N.D.
- Hyvarinen J (1982). "The Parietal Cortex of Monkey and Man," (Studies of Brain Function, Vol. 8) Berlin: Springer-Verlag.
- Jerison HJ (1973). "Evolution of Brain and Intelligence." New York: Academic Press.
- Jones EG (1984). History of cortical cytology. In: Peters

- A, Jones EG (eds) "Cerebral Cortex," Vol. 1. New York Plenum p. 1.
- Keith A (1929). "The Antiquity of Man." London: Williams and Norgate.
- Kimbel WH, Johanson DC, Coppens Y (1982). Pliocene hominid cranial remains from the Hadar Formation, Ethiopia. *Am J Phys Anthropol* 57: 453.
- Levin G (1936). Racial and "inferiority" characters in the human brain. *Am J Phys Anthropol* 22: 345.
- McGregor JH (1925). Recent studies on the skull and brain of Pithecanthropus erectus. *Nat Hist* 25: 544.
- Passingham RE, Ettlinger G (1973). A comparison of cortical functions in man and other primates. *Int Rev Neurbiol* 16: 233.
- Peter A, Jones EG (eds) (1984). "Cerebral Cortex. Vol. 1 Cellular Components of the Cerebral Cortex." New York; Plenum.
- Radinsky LB (1979). The fossil record of primate brain evolution. James Arthur Lecture, New York: Amer Mus Nat Hist.
- Schepers GWH (1946). The endocranial casts of the South African Ape Men. In Broom R, Schepers GWH "The Australopithecinae." Transvaal Mus Mem 2.
- Schepers GWH (1950). The brain casts of the recently discovered Plesianthropus skulls. Part II of Broom R, Robinson JT, Schepers GWH. "Sterkfontein Ape-Man Plesianthropus." Transvaal Mus Mem 4.
- Smith GE (1904a). Studies in the Morphology of the human brain with special reference to that of the Egyptians. No. 1. The occipital region. Records. Egyptian Govr School Med 2. 725.
- Smith GE (1904b). The morphology of the occipital region of the cerebral hemispheres in man and apes. *Anat Anz* 24: 436.
- Smith GE (1907a). A new typographical survey of the human cerebral cortex. *J Anat* 41: 237.
- Smith GE (1907b). New studies on the folding of the visual cortex and the significance of the occipital sulci in the human brain. *J Anat & Phys* 41: 198.
- Smith GE (1927). "Essays on the Evolution of Man." Oxford: University Press.
- Smith GE (1929). The variations in the folding of the visual cortex in man. Mott Memorial volume.
- "Contributions to Psychiatry, Neurology, and Sociology." London.
- Stephan H. (1969) Quantitative investigations on visual

structures in primate brains. Proc. 2nd Internat. Congr. Primates 3: 34.

Stephan H, Frahm H, Baron G (1981). New and revised data on volumes of brain structure in Insectivores and Primates. Folia Primatol 35: 1.