

The Natural Endocast of Taung (*Australopithecus africanus*): Insights From the Unpublished Papers of Raymond Arthur Dart

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ABSTRACT Dart's 1925 announcement of *Australopithecus africanus* (Dart: Nature 115 [1925] 195–199) was highly controversial, partly because of an interpretation of the Taung natural endocast that rested on an erroneous identification of the lambdoid suture as the lunate sulcus. Unpublished materials from the University of Witwatersrand Archives (Dart, unpublished material) reveal that Dart reacted to the controversy by: 1) describing and illustrating the entire sulcal pattern on the Taung endocast, in contrast to just two sulcal identifications in 1925, 2) identifying a hypothetical part of the lambdoid suture and revising his description of the lunate sulcus, and 3) bolstering his argument that Taung's brain was advanced by detailing expansions in three significant cortical association areas. Four unpublished illustrations of Dart's identifications of sulci and sutures on the Taung endocast are compared here with those published by Keith (Keith: New discoveries relating to the antiquity of

man (1931)), Schepers (Schepers: The endocranial casts of the South African ape-men. In: Broom R, Schepers GWH, editors. The South African fossil ape-men; the Australopithecinae [1946] p 155–272), and Falk (Falk: Am J Phys Anthropol 53 [1980] 525–539), and the thorny issue of the location of the lunate sulcus is revisited in light of new information. Archival materials reveal that Dart believed that Taung's brain was reorganized globally rather than in a mosaic manner, and that the shapes of certain cortical association areas showed that *Australopithecus* was closer to *Pithecanthropus* than to the living apes. Although a few of Dart's hitherto-unpublished sulcal identifications, including his revision for the lunate sulcus, were questionable, his claim that the Taung endocast reproduced a shape that was advanced toward a human condition in its prefrontal cortex and caudally protruded occipital lobe was correct. Yrbk Phys Anthropol 52:49–65, 2009. © 2009 Wiley-Liss, Inc.

Raymond Dart's description of the fossilized face, jaw, and associated natural endocast from Taung (now Taung) and his naming of *Australopithecus africanus* (Dart, 1925) were received with skepticism by British anatomists, which contributed to the fact that it was decades before the importance of his discovery was accepted (Tobias, 1984, 1992, 1996, 2008) (see Fig. 1). Dart had identified what he thought was a posteriorly (caudally) positioned lunate sulcus (*L*) on the Taung endocast (Fig. 2a). This deep crescent-shaped sulcus approximates the rostral boundary of primary visual (striate) cortex (Brodmann's area [BA] 17) in monkeys and apes, and is located much further forward (more rostrally) on their brains than is the case for lunate sulci that have been identified for humans (Connolly, 1950). Because of this, it had long been thought that *L* was displaced caudally as the brain's parietotemporo-occipital association cortices enlarged during the course of hominin evolution (Smith, 1903, 1904a,b, 1927). Dart's identification of *L* in a humanlike position on the Taung endocast was surprising because of its small apelike volume, and it was the main reason he concluded that Taung's brain had been derived toward a humanlike condition (Dart, 1925).

Dart's description of Taung's endocast as appearing humanlike despite its small apelike size contributed to the initial skepticism of scientists, including Arthur Keith (1925, 1931), Grafton Elliot Smith (1925), and Arthur Smith Woodward (1925). Some of Dart's

colleagues recognized that his conclusion rested heavily on a questionable identification of the lunate sulcus (Keith, 1931; Clark et al., 1936). Although skeptics eventually accepted the importance of Dart's discovery, as well as the fact that certain shape features of Taung's endocast were, indeed, derived, few of them ever accepted Dart's specific identification of *lb* as *L* (Clark et al., 1936; Clark, 1947).

In 1980, I published an independent analysis of the sulcal patterns reproduced on the Taung endocast and six other australopithecine natural endocasts, and concluded that they appeared apelike rather than humanlike (Falk, 1980) as others had suggested (Schepers, 1946; Holloway, 1975). Ralph Holloway critically examined my identifications of sulci on Taung, and stated that in his "estimation, almost none can be identified with any certitude" (Holloway, 1981, p 51). Having championed Dart's interpretation of a caudal position for *L* in Taung (Holloway, 1975), Holloway took particular exception to my identification of a relatively rostral depression on Taung's endocast as the likely medial end

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Fig. 1. Phillip Tobias elucidated the academic politics between the British scientific establishment and Raymond Dart that were one of the reasons it took decades for the importance of *Australopithecus africanus* to become recognized (Tobias, 1984, 1996). Here, Tobias is shown displaying the original Taung fossil in the Wits Anatomy Department. Photographs courtesy of Harry Jerison. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

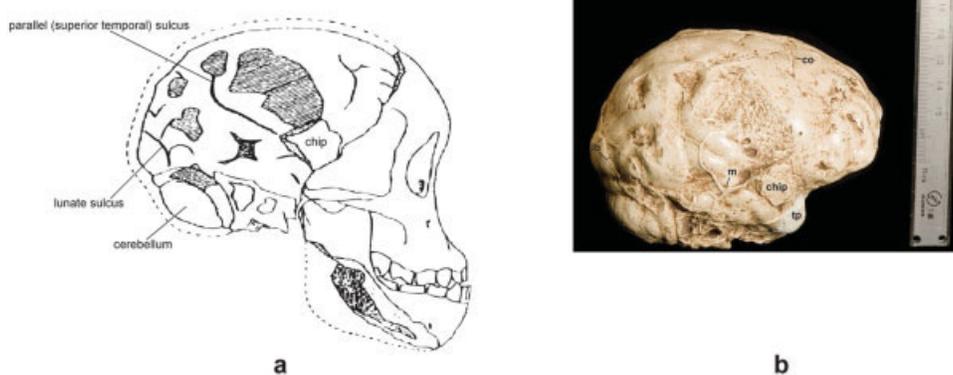


Fig. 2. The Taung fossil. (a) Dart's 1925 illustration of the Taung endocast, in which he identified only two sulci: the superior temporal (parallel) sulcus; and a caudally positioned lunate sulcus that was actually the lambdoid suture (*lb*). Modified from Dart, 1925). (b) A copy of the Taung endocast that includes its right temporal pole (*tp*), which was restored by Ron Clarke by attaching a cast made from its fossilized impression in the back of Taung's face (Falk and Clarke, 2007). The lambdoid (*lb*) and coronal (*co*) sutures, and an adhering bony chip are labeled. Notice, also, damaged (rough) areas and meningeal blood vessel (*m*). The chip, sutures, and vessels are superficial to other features. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

of that sulcus (Holloway, 1981). Subsequently, we debated the position of *L* on a number of australopithecine endocasts, and neither of us changed our general views about australopithecine sulcal patterns (Holloway, 1983, 1984, 1985, 1988, 1991; Holloway and Kimbel, 1986; Holloway et al., 2001, 2004; Falk, 1983, 1985a,b, 1986, 1989, 1991; Falk et al., 1989).

The reader may wonder why so much attention has been given to the lunate sulcus. Determining the location of *L* for Taung and other small-brained early hominins is highly relevant for understanding human brain evolution. On the one hand, a caudally located *L* would provide fossil evidence for the long-held view that as brains evolved, the lunate sulcus was displaced caudally due to expansion of the bordering parieto-occipital association cortex (Smith, 1904a). It would also imply that changes in the arrangement of sulci preceded brain size increase (Holloway, 1983). On the other hand, a rostral apelike position of *L* in australopithecines would suggest that changes in sulcal patterns did not precede brain

enlargement (Falk, 1985b). As will become clear, the difference between these two views has profound implications for unraveling the evolutionary dynamics between changes in brain shape and altered sulcal patterns.

Since Dart's initial description of the Taung endocast, new information has come to light including identification of its enlarged occipital-marginal (O/M) sinus (Tobias and Falk, 1988), restoration of its missing right temporal pole (Fig. 2b) (Falk and Clarke, 2007), identification of bony morphology adhering to its basal surface (Falk and Clarke, 2007; Fig. 1), and a revised (reduced) cranial capacity estimate of 382 cm³ with an estimated adult value of 406 cm³ (Falk and Clarke, 2007) in place of earlier juvenile and adult estimates of 405 cm³ and 440 cm³ (Holloway, 1970).

In July–August, 2008, I visited the University of Witwatersrand Archives in Johannesburg, South Africa, and gained access to a long unpublished manuscript of Dart's that was completed in 1929, in which he provided extensive details about Taung's endocast (Dart, unpublished

material). Tobias (1993) had reported on his recovery and rescue of this manuscript in 1951. I also studied unpublished drafts of other manuscripts, personal correspondence, and notes written by Dart, and obtained copies of four unpublished illustrations of the Taung endocast that were prepared under his direction, and on which he labeled numerous sulci. Because Dart had identified only two sulci in his 1925 figure of the Taung endocast (Fig. 2a), these historical materials reveal new, detailed, and surprising information about his assessment of Taung's entire sulcal pattern. Below, I revisit the sulcal pattern reproduced on the Taung endocast in light of these previously unpublished materials and their historical context, and discuss the general implications for hominin brain evolution.

Historical background

It is clear from materials in the University of Witwatersrand Archives that Dart was stung by his colleagues' skepticism about his interpretation of the Taung endocast. He prepared a detailed defense of his analysis of the entire Taung fossil in three drafts of a 269-page unpublished manuscript, "*Australopithecus africanus: And His Place in Human Nature*," which was completed in 1929 and submitted on his behalf to the Royal Society, London, for consideration for publication by his mentor and Fellow of the Royal Society, Elliot Smith. This remarkable manuscript contained detailed sections on the geology, bones, teeth, and endocast, as well as thorough discussions about the "cradle of mankind," and "Africa as the cradle of pre-man." The manuscript was rejected by the Royal Society in a letter to Elliot Smith dated July 4, 1930 (Atowle, July 4, 1930; Unpublished letter from Secretary of the Royal Society, London, to G. Elliot Smith), with the suggestion that only the section about teeth be revised and resubmitted. Elliot Smith offered advice about revising the section on dentition in a letter to Dart dated February 25, 1931 (Smith, February 25, 1931; Unpublished letter to Raymond Dart from Grafton Elliot Smith). However, the only specific comment Elliot Smith offered about Dart's analysis of

Taung's endocast was, "You refer to the 'failure of the endocranial cast to meet the middle line in the cerebellar region.' This has been criticized both as a statement of fact and on the matter of style; on the matter of fact because less than half of the cerebellar region is present so that the statement with reference to the midline is not valid, and you attribute an active volition to the endocranial cast in failing to meet the mid line." Dart later recalled:

Sir Arthur Keith had already told me that he had written an exhaustive description of the cranial material [of Taung] for his forthcoming book on recent anthropological discoveries, so I took my manuscript back to South Africa in the hope that a more propitious occasion would present itself in the future. The thorough analysis but adverse conclusions concerning the fossil which I knew was soon to appear in Sir Arthur Keith's new book reflected the British attitude. (Dart and Craig, 1959, p 52).

As Dart had anticipated, Keith questioned his interpretation of the Taung fossil in his book, which was published in 1931. Contrary to Dart's illustration (Fig. 2a), Keith illustrated and labeled the lambdoid suture and illustrated a crescentic depression caudal to it (*L?* in Fig. 3a) that was meant to indicate the feature that Dart had identified as *L* (Fig. 2a). Keith stated that he doubted that this "slight crescentic depression" (Keith, 1931, p 84) was the lunate sulcus, and suggested, instead, that it was more probable that a series of slight depressions that were located rostral to that feature indicated this sulcus (*LK* in Fig. 3a,b). Keith concluded, "If my interpretation is right, then this area of the Taungs brain... falls into the [nonhuman] anthropoid category" (Keith, 1931, p 85).

Dart was so discouraged that he declined to submit the suggested revision about australopithecine dentition to the Royal Society. Instead, approximately 2 years after receiving Elliot Smith's letter, Dart wrote to a colleague in Japan asking if he would like to publish a paper on the dentition of *Australopithecus* in a Japanese journal (Dart, April 26, 1933; Unpublished letter from Raymond Dart to Professor Okajima). The answer was affirmative, so Dart's paper on australopithecine teeth appeared in Japan rather than England (Dart, 1934). (Although it is beyond the scope of this paper, the

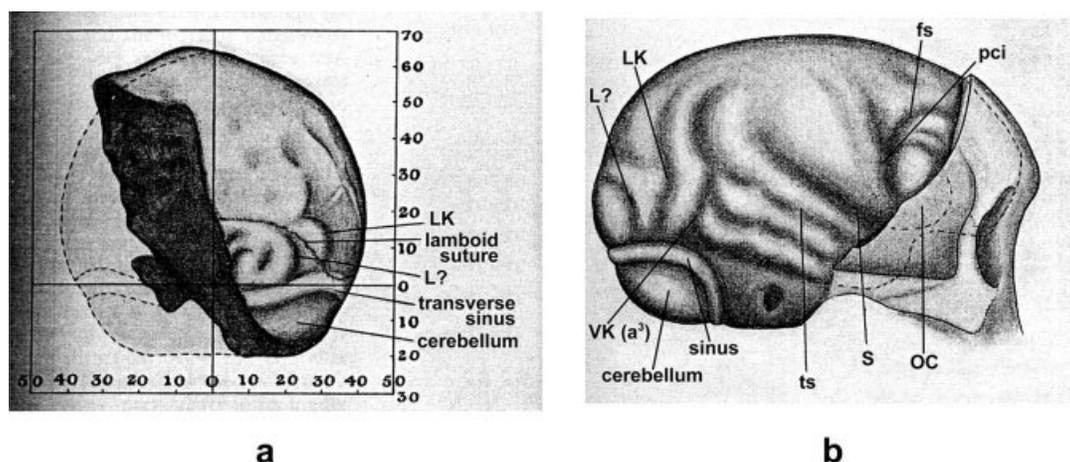


Fig. 3. Arthur Keith's occipital (a) and lateral (b) views of the Taung endocast illustrating two possible positions for the lunate sulcus (*L*). *fs*, "part of the upper frontal sulcus" (Keith, 1931:82); *L?*, slight crescentic depression that Keith doubted was the lunate sulcus; *LK*, depression that Keith suggested was part of *L*; *OC*, orbital cap; *pci*, precentral inferior sulcus; *VK*, vertical sulcus (=a³, occipitalis anterior ramus of the superior temporal sulcus of Connolly, 1950). Modified from Keith (1931, Figs. 14 and 18).

academic politics between the British scientific establishment and Dart are discussed elsewhere [Falk, in preparation; Tobias, 1984, 1996].)

Meanwhile, the concerns about Dart's description of Taung's endocast deepened. In 1936, the *Journal of the Royal Anthropological Institute of Great Britain* published a paper by Clark, Cooper, and Zuckerman that compared brains and corresponding endocasts from six chimpanzee skulls and applied the results to an assessment of Dart's description of the Taung endocast:

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. Situated 22 mm in front of this lambdoid impression in *Australopithecus* is a depression extending a little way out from the midline . . . This corresponds very well with the depression related to the upper end of the lunate sulcus in [chimpanzee] Cast No. 1. This suggests that the lunate sulcus in *Australopithecus* may have occupied a position similar to that found commonly in the chimpanzee . . . Apart from the general contour and proportions of the endocranial cast (which would repay a detailed comparative study), there is nothing to suggest that *Australopithecus* possessed in its cerebral anatomy any features indicative of an approach to a human status. (Clark et al., 1936, p 268) (Clark's 1947 reassessment of the Taung endocast is discussed below).

Dart was deeply upset by Clark et al.'s 1936 paper, as revealed in a preliminary handwritten draft of a chapter (Chapter 13, "Putting *Australopithecus* in his place") (Dart, unpublished material) that Dart had intended for his book, *Adventures With The Missing Link*, but which, ultimately, was not included (Dart and Craig, 1959). (The University of Witwatersrand Archives also contains an unpublished typed and revised version of this chapter.) Regarding the paper by Clark et al., Dart observed:

In this innocent looking paper these three British anatomists were striving to follow up Sir Arthur Keith's (1931) thesis of discrediting the neurological basis upon which my interpretation of the significance of the Taungs discovering [discovery] had originally rested. Their reputation locally in England was such that, had no further australopithecine remains been coming to light simultaneously, their views might well have prevailed. (Dart, unpublished material, p 6a)

As we will see, Dart went far beyond the lunate sulcus in his 1929 unpublished manuscript, in which he meticulously documented his identifications for most of the sulci on the Taung endocast. He also argued that the endocast was derived toward a human condition in certain shape features. Why, then, did he not publish his observations and illustrations of the Taung endocast that are only now coming to light 80 years after his manuscript was completed? The reason, Dart explained, is that he was influenced by Earnest Hooton's suggestion that discoverers should not be the ones to describe their specimens (Hooton, 1938). According to Dart:

E. A. Hooton ('38) says: "The tendency toward aggrandizement of a rare or unique specimen on the part of its finder or the person to whom its initial scientific description has been entrusted, springs naturally from human egoism, and is almost ineradicable" (p 112). He points out that the errors in interpretation that can arise through enthusiasm, ignorance, isolation, and "the psychological conflict in which the discoverer or describer is torn between his desire to find primitive, unique, or anthropoidal features which will enable him to place his specimen nearer to the apes than any previously recorded, and his equally powerful urge to demonstrate the direct and central position of his new type in the ancestry of modern man" (p 113). He concludes that "a dispassionate interpretation of new fossil evi-

dence is usually obtainable only when one awaits the reworking of the material by persons not emotionally identified with the specimen" (p 114). (Dart, 1940, p 167).

In somewhat more colorful terms, Dart continued:

I feel that Hooton's observations have justified my reserve. The object that had been hidden for perhaps a million years could well await a further few score in being recognized for what it was. Like criminals in certain countries, advocates of the unexpected are naturally suspect until others appear who can prove their dependability. (Dart, 1940, p 168).

Dart later filled in other details:

In addition to the Taungs endocranial cast, three of the specimens recovered at Sterkfontein had been natural brain casts. As Broom had no experience in interpreting endocranial casts he asked me to undertake this on his behalf. I willingly agreed but decided to withdraw after reading certain remarks by E. A. Hooton . . . I felt duty-bound to hand over the material to another uncommitted investigator. Hooton's attitude was sufficiently general for me to feel that it was best also to hand over the Taungs specimen to Broom and my description of its endocranial cast to G. W. H. Schepers, the newly appointed professor of anatomy at the University [of Pretoria] (Dart and Craig, 1959, p 78-79).

Aided by access to Dart's 1929 manuscript and the original Taung endocast, Schepers published a detailed description of its sulcal pattern (and those of several other australopithecines) in 1946 (Schepers, 1946). After studying the original specimen and obtaining a copy of its endocast, I published an independent analysis of Taung's entire sulcal pattern in 1980 (Falk, 1980), in which I compared my sulcal identifications to those of Schepers (see Fig. 4). I suggested that both Dart (Dart, 1925) and Schepers (Schepers, 1946) had misidentified the lambdoid suture as *L* and (as noted) concluded that, contrary to the literature, in my opinion all of the australopithecine endocasts reproduced sulcal patterns that were pongidlike rather than humanlike.

Shortly after Schepers published his description of australopithecine endocasts, Clark had an opportunity for the first time to study the original Taung endocast (and those of other australopithecines), which caused him to capitulate from some of his earlier views about Taung's endocast that were based on a comparative study of ape brains and their corresponding endocasts (Clark et al., 1936; Clark, 1947). Based on his observations of the original endocast, he noted (correctly) that "the convolutional markings" that were preserved on australopithecine natural endocasts were "much more distinct and sharply defined than in the endocranial casts of the recent anthropoid apes or modern man" (Clark, 1947, p 311). Clark also observed (correctly) that "it seems certain that the identity of some of the sulci which Schepers has described and figured (particularly those in the parietal and occipital areas) are open to question, since the corresponding impressions on the casts are rather too vague and indefinite for certain identification" (Clark, 1947, p 311). Critical examinations of Schepers' identifications of individual sulci are available elsewhere (Falk, 1980; Holloway, 1981).

However, Clark did not capitulate on his earlier suggestion that Dart had mistaken *lb* for *L* (Clark et al., 1936). Rather, he observed:

Dart's interpretation has been criticized by other anatomists who claim that the sulcus lunatus must have been placed much

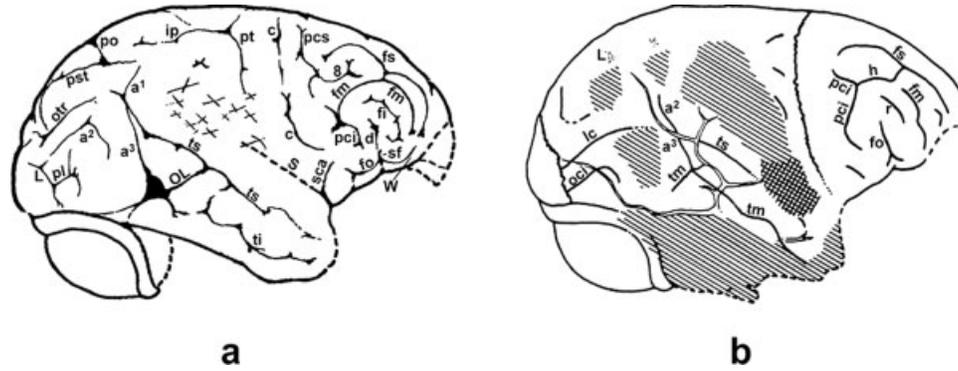


Fig. 4. Identifications of sulci reproduced on the Taung endocranial cast by (a) Schepers in 1946 and (b) Falk in 1980. Falk's illustration also shows coronal and lambdoid sutures, meningeal vessels, damaged areas (hatching), and the adhering bony fragments (crossed hatching) (compare with Fig. 2b). Reproduced with permission from Falk, *Am J Phys Anthropol*, 1980, 53, 525–539, © Wiley-Blackwell. See Table 1 for abbreviations of sulci (Connolly, 1950). Additional abbreviations used by Schepers: *OL*, occipitalis lateralis; *pt*, postcentralis; *ti*, temporalis inferior; 8, intermediate fossit (Schepers, 1946, p 193).

more anteriorly, i.e. in the position of the typical simian sulcus of a chimpanzee or gorilla 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 (*L* in Fig. 4a), it must be at least as far anterior as the depression marked 26 (*a*³ in Fig. 4a) (for between [these two] the convolutions are disposed in an approximately anterior–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 (relatively to the distance between the frontal and occipital poles) than in any modern ape 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.* (Clark, 1947, p 312; emphasis mine)

Below, questions about the identities of *L*, certain other sulci, and *lb* on the Taung endocranial cast are revisited in light of previously unpublished observations and illustrations that were prepared by Raymond Dart between 1925 and 1929.

MATERIALS AND METHODS

The Taung natural endocranial cast and Dart's previously unpublished analyses of it are the foci of this paper. The original specimen was reexamined by the author in the School of Anatomical Sciences at the University of Witwatersrand in August, 2008. Ron Clarke prepared a copy of the Taung endocranial cast (Fig. 2b), on which he restored the right temporal pole by casting its negative impression from the back of the fossilized face (Falk and Clarke, 2007). The endocranial cast represents most of the right hemisphere. Because mirroring a hemisphere around a rigid midsagittal plane (Holloway, 2008) is likely to encompass error due to shape asymmetries (petalias), Falk and Clarke used commercially available software (Raindrop Geomagic, Research Triangle Park, NC) to increase "tension on the clear midline that courses along the endocranial's dorsal surface and continues ventrally midway between the orbits and medial to the fragment of the left pterygoid process that adheres to the endocranial's ventral surface, creating a smooth midline along which the right hemisphere was electronically mirrored"

(Falk and Clarke, 2007, p 530). The copy of the Taung endocranial cast used for this paper is more complete than endocranial casts in other collections, and our revised cranial capacity estimate of 382 cm³ with an estimated adult value of 406 cm³ is smaller than other estimates (Holloway, 1970) that were published before virtual imaging technology became available for reconstructing endocranial casts (Tobias, 2001; Falk, 2004), including Dart's estimate of 520 cm³ that was uncorrected for age (Dart and Craig, 1959, p 11).

Naturally formed endocranial casts of South African australopithecines reproduce a surprising amount of cortical detail including sulcal patterns (Clark, 1947; Falk, 1980) compared with artificially prepared endocranial casts (often made with latex) from skulls of apes and humans, as revealed by comparisons of actual brains and their corresponding artificial endocranial casts (Symington, 1916; Clark et al., 1936; Connolly, 1950). Possible reasons for this are discussed elsewhere (Falk, 1980). The natural endocranial cast of Taung reproduces excellent detail of the external morphology of the right hemisphere of the brain, and may well have been formed through a process envisioned by Dart in 1929:

I should, however, say, in modification, of what I stated in 1925, that the hindmost part of the cast, that is the cerebellum, does not quite reach the midline of the occipital bone. Unfortunately the left side of the endocranial cavity was not filled with the sand and lime This misfortune nevertheless has its instructive side. It demonstrates that in death the infant lay on its right side, the head drooped in the breccia and sand, and reposed near its right hand. As the soft tissues disappeared, and access was provided to the endocranial cavity for the sand at the foramen magnum, it filled mainly the front of the head and the right side. Later by the percolating lime this access of sand was cut off at the margin of the foramen magnum and only pure lime was deposited on the interior. It clothed the sand inside entirely with a crystalline deposit. (Dart, unpublished material, p 153–154).

Paleoneurologists traditionally used relatively simple methods to study endocranial casts. The volume of Taung's endocranial cast was initially estimated by comparing surface measurements with those from ape endocranial casts of known volume (Dart, 1925). Early researchers including Dart and, later, Schepers recognized surface features by direct inspection (including palpation), measured the lengths and relationships of sulci, and graphically recorded the

details in dioptographic tracings and sketches (Schepers, 1946). Additional surface features were sometimes revealed by photographing endocasts under oblique illumination or applying carbon to them to highlight morphological features. Shapes of horizontal and coronal contour tracings were also recorded from endocasts. The data collected from Taung's endocast were compared with similar data from apes and humans, and the results were interpreted in light of what was then known about functional neuroanatomy (often referring to Brodmann's areas). Schepers observed more detail on Taung's endocast than previous researchers, which he attributed to his having removed a thin layer of inner table bone that obscured some of the sulci. This is unlikely, however, because more recent workers have not been able to detect numerous details that Schepers illustrated (see below). Although the above techniques are still used, they are now supplemented with more precise methods for measuring and comparing features on endocasts, such as production of electronic (virtual) endocasts using three-dimensional computed tomography (3D-CT) (Tobias, 2001; Falk, 2004; Falk and Clarke, 2007).

Sulci identified by Dart on four previously unpublished illustrations of Taung's natural endocast that are reposed in the University of Witwatersrand Archives are compared with those identified and illustrated by Keith (1931), Schepers (1946), and Falk (1980). Dart's identification and illustration of sutures reproduced on the Taung endocast are also compared with Keith's and Falk's. (Schepers did not illustrate the sutures.)

Although Holloway declined to publish an illustration of Taung's entire sulcal pattern (Holloway, 1984, p 287), some of his written descriptions (Holloway, 1981) of certain sulci identified by Falk (1980) and Schepers (1946) are included in this discussion. Arthur Keith's, Grafton Elliot Smith's, and Clark's published views about Taung's endocast are also discussed. New insights about Dart's reaction to the controversy that surrounded his 1925 identification of *L* on Taung's endocast are provided from his unpublished manuscript, notes, personal correspondence, and preliminary drafts of papers that are reposed in the University of Witwatersrand Archives.

The hypothetical locations of *L* and other sulci on the Taung endocast that have been proposed by several scientists are assessed in light of sulcal patterns of great apes described and illustrated by John Connolly (1950), as well as the location of *L* on a highly detailed latex endocast prepared from a skull of a juvenile bonobo (*Pan paniscus*, accession number R.g. 29006) at the Koninklijk Museum voor Midden-Afrika in Tervuren, Belgium.

The terminology used in this paper is after Connolly (1950), unless otherwise indicated. Table 1 provides a key for Connolly's names and abbreviations for sulci.

RESULTS

Figure 19 of Dart's 1929 manuscript, with the legend "Dioptographic tracing of skull & endocranial cast of *Australopithecus* to illustrate the main morphological features," is reproduced below (Fig. 5a). Although Dart identified only two sulci on his 1925 dioptographic tracing of Taung (Dart, 1925) (Fig. 2a), this illustration contains the same two plus fourteen additional sulcal identifications. Dart also indicated sutures that were not included in his original illustration (Dart, 1925) with dashed lines. Another unpublished illustration (Fig. 5b) appears to have been a preliminary draft for Figure 19,

TABLE 1. Abbreviations for sulci (after Connolly, 1950, p ix) and other features reproduced on endocasts

Sutures
<i>co</i> , coronal suture
<i>lb</i> , lambdoid suture
Other
<i>chip</i> , bony fragment
<i>m</i> , meningeal blood vessel
<i>tp</i> , temporal pole
Sulci/fissures that separate lobes
<i>c</i> , centralis (=Rolando)
<i>ipo</i> , incisura parieto-occipitalis
<i>po</i> , parieto-occipitalis
<i>S</i> , fissure Sylvii (=lateralis)
Frontal lobe sulci
<i>d</i> , diagonalis
<i>fi</i> , frontalis inferior
<i>fm</i> , frontalis medius
<i>fo</i> , fronto-orbitalis
<i>fs</i> , frontalis superior
<i>pci</i> , praecentralis inferior
<i>h</i> , horizontal ramus <i>pci</i>
<i>pcs</i> , praecentralis superior
<i>r</i> , rectus
<i>sca</i> , subcentralis anterior
<i>sf</i> , subfrontalis
<i>W</i> , fronto-marginalis
Temporal lobe sulci
<i>tm</i> , temporalis medius;
<i>ts</i> , temporalis superior (=parallel sulcus)
<i>a</i> ¹ , parallelus superior ramus of <i>ts</i>
<i>a</i> ² , angularis ramus of <i>ts</i>
<i>a</i> ³ , occipitalis anterior ramus of <i>ts</i>
Parietal lobe sulci
<i>ip</i> , intraparietalis
<i>pst</i> , parietalis superior transversus
<i>pts</i> , postcentralis superior
Occipital lobe sulci
<i>L</i> , lunate
<i>lc</i> , calcarinus lateralis
<i>u</i> , ramus superior of <i>lc</i>
<i>oci</i> , occipitalis inferior
<i>oct</i> , occipito-temporalis (=ti, temporalis inferior)
<i>otr</i> , occipitalis transversus
<i>pl</i> , praelunatus

since it did not illustrate sutures or contain labels for some of the sulci that were included in Fig. 5a (namely, *a*², *a*³, *c*, *pci*, *pl*, *S*, *tm*; see Table 1). Dart also mislabeled a sulcus in the frontal lobe as the "upper limb prefrontal" in the preliminary illustration, which was corrected to sulcus "precentralis" in Figure 19 of the manuscript, and included an identification for *oci* in Fig. 5b that did not appear in the finished illustration.

Dart recognized what he thought was a visible part of the lambdoid suture (*lb*) on Taung's endocast for the first time in his 1929 manuscript, which he depicted as a short dashed segment slightly caudal to his identification of *L* (Fig. 5a). This is of particular interest for several reasons. First, it suggests that Dart was sensitive to criticism that he had misidentified *lb* as *L* years before Clark et al. (1936) published their study of corresponding brains and endocasts from chimpanzees that bolstered this criticism. Second, in his unpublished manuscript, Dart stated that the courses of *L* and *lb* partly coincided on Taung's endocast: "[in all apes] the sulcus lunatus ... lies before the lambda suture while it lies behind it, in Men ... in *Australopithecus*, on the right side of the cast, it coincides in position with the lambdoid suture in portion of its extent" (Dart, unpublished

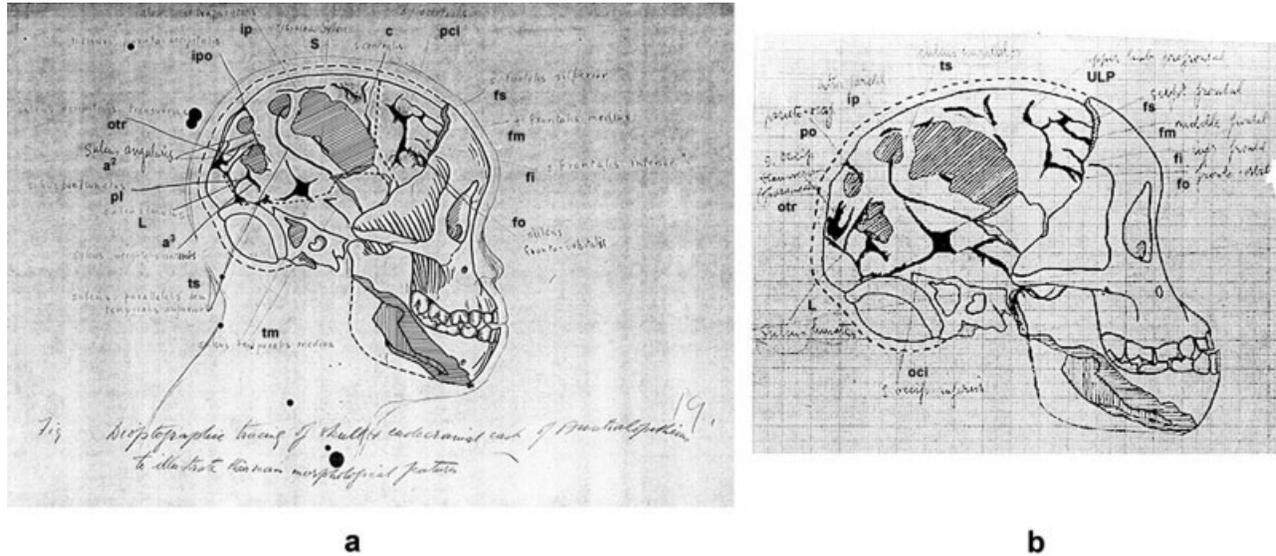


Fig. 5. Two previously unpublished illustrations of the Taung fossil by Raymond Dart. (a) Figure 19 from Dart's unpublished manuscript (Dart, unpublished manuscript), with the legend "Dioptrographic tracing of skull and endocranial cast of *Australopithecus* to illustrate their main morphological features." Dart indicated sutures with dashed lines. (b) A previously unpublished illustration that appears to have been a preliminary draft for (a). For both illustrations, sulcal identifications are in Dart's handwriting, and abbreviations of Connolly (Table 1) have been added to clarify Dart's written labels. Additional abbreviation: ULP, upper limb prefrontal. Note that (b) lacks many of the identifications included in (a), and that it also contains a tentative identification for an occipital inferior sulcus (*oci*) that was excluded from the final illustration. Figures reproduced with permission of the University of Witwatersrand.

material, p 168). Third, in additional unpublished notes, Dart stated that the portion of coincidence between *L* and *lb* was "large" and, further, provided an estimate of the length of *L*: "Lunate sulcus is present as an arc-like depression about 25 mm. in length The lunate depression is almost coincident throughout a large portion of its course with the lambdoidal suture."

The shortest distance between the point where *lb* intersects the sagittal suture and the point where it intersects the medial border of the transverse sinus measures approximately 37 mm on my copy of the Taung endocranial cast (Fig. 2b), most of which Dart labeled as *L* in 1925 (Fig. 2a). Although Dart failed to identify *lb* at that time, the above shows that by 1929 he recognized that at least a short portion of *lb* was visible, although, as noted, he illustrated it as caudal to the actual *lb*, which he persisted in identifying as *L*. His estimate of 25 mm for the total length of *L* was considerably shorter than the length of *lb* measured on my copy of the endocranial cast (37 mm).

Fig. 5a reveals that Dart identified a segment of *L* as separate from and rostral to the feature he identified as *lb*. Referring to landmarks on Fig. 5a and measuring my copy of the Taung endocranial cast with calipers, I estimate that the dashed line medial to the transverse sinus that Dart drew to represent *lb* (and, thus, approximately the length of the portion of *L* rostral to it) would have been less than 14 mm long. If so, and if Dart was right about *L* being about 25 mm long, that leaves at least 11 mm of *L* coursing medially that is coincident with *lb*, a continuation that Dart depicted with a solid line (Fig. 5a). Because reproduction of sutures are superficial to those for cortical sulci on endocranial casts due to the fact that skulls enclose brains (and not vice versa) (see Fig. 2b), Dart's 1929 illustration (Fig. 5a) would have been more realistic if the entire length of *lb* had been represented with a dashed line, leaving only the portion of *L* that Dart thought coursed rostral to it as a solid line. In any event, it appears that Dart continued to misidentify the actual *lb*

as *L* in 1929, and added a short dashed segment to represent *lb* caudal to the actual *lb* in Figure 19 (Fig. 5a).

It is noteworthy that Keith commented later that "Professor Dart believes that the lunate sulcus of *Australopithecus* is in the human position. There is a slight crescentic depression at the site indicated by him" (Keith, 1931, p 84). Interestingly, Keith located the depression that he thought Dart had identified as *L* (Fig. 2a) caudal to *lb* (*L*? in Fig. 3a), rather than rostral to it as Dart indicated in his 1929 illustration (Fig. 5a). (It is unclear whether or not Keith had read Dart's 1929 manuscript, although he could have been one of its anonymous reviewers [Falk, in preparation]).

Although Dart turned his unpublished manuscript over to Schepers (Dart and Craig, 1959, p 78–79; Schepers, 1946, p 157), Schepers failed to illustrate sutures on his 1946 lateral view of the Taung endocranial cast (Fig. 4a). He did, however, incorporate Dart's idea about the relationship between *lb* and *L* into his discussion:

The identification of the lunate sulcus ... in *Australopithecus africanus*, originally made by Dart, provoked a great deal of adverse criticism on the part of many scientists, notably Keith (1929) the suggestion that it may be represented by the curved sulcus near the tip of the occipital lobe, which lay almost opposite the lambdoidal (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 remain but 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, p, 192).

Dart's memoirs suggest that Schepers was incorrect about critics not having access to the original fossil. Dart visited London in 1930, where he "immediately got in touch with Elliot Smith, Keith, and Smith Woodward" (Dart and Craig, 1959, p 57). Elliot Smith invited him

to a meeting of the Zoological Society of London on February 17th, and asked him to bring the original Taung fossil with him, which Dart did. Elliot Smith also invited Dart to a dinner at the Royal Society Club the next night and “everyone there had an opportunity of examining the skull and endocranial cast” (Dart and Craig, 1959, p 58). When he departed England to return to South Africa, Dart left the original Taung specimen with Elliot Smith so that copies could be made of it for distribution throughout the world.

In light of the new information reported here, I have made two nominal revisions to my original observations on the Taung endocast (see Fig. 6). [Identifications are indicated on a photograph of my copy of the endocast rather than in a drawing, as was done in 1980 (compare Fig. 6a with Fig. 4b)]. First, with respect to the branches

of *ts*, my original identification of a^2 on Taung was questionable, and I failed to identify a^1 , as Holloway correctly observed (Holloway, 1981, p, 52). Dart illustrated the terminal end of *ts* curving rostrally and entering a damaged area on the endocast (Fig. 5a,b), which he described in unpublished notes: “Parallel sulcus is very clearly marked running back from under cover of the lozenge-shaped piece of adherent bone (temporal and parietal) in the Sylvian region for a distance of 25 mm and then curves upwards and forwards for a distance of 15 mm, and is lost in a fracture of the cast surface.” Careful examination of the endocast (the reader may wish to enlarge Fig. 2b) suggests that the superior parallel ramus of *ts* (a^1) is, indeed, visible as recognized and labeled by Schepers (Fig. 4a), and that it is located in the rostral part of the damaged area to which Dart referred.

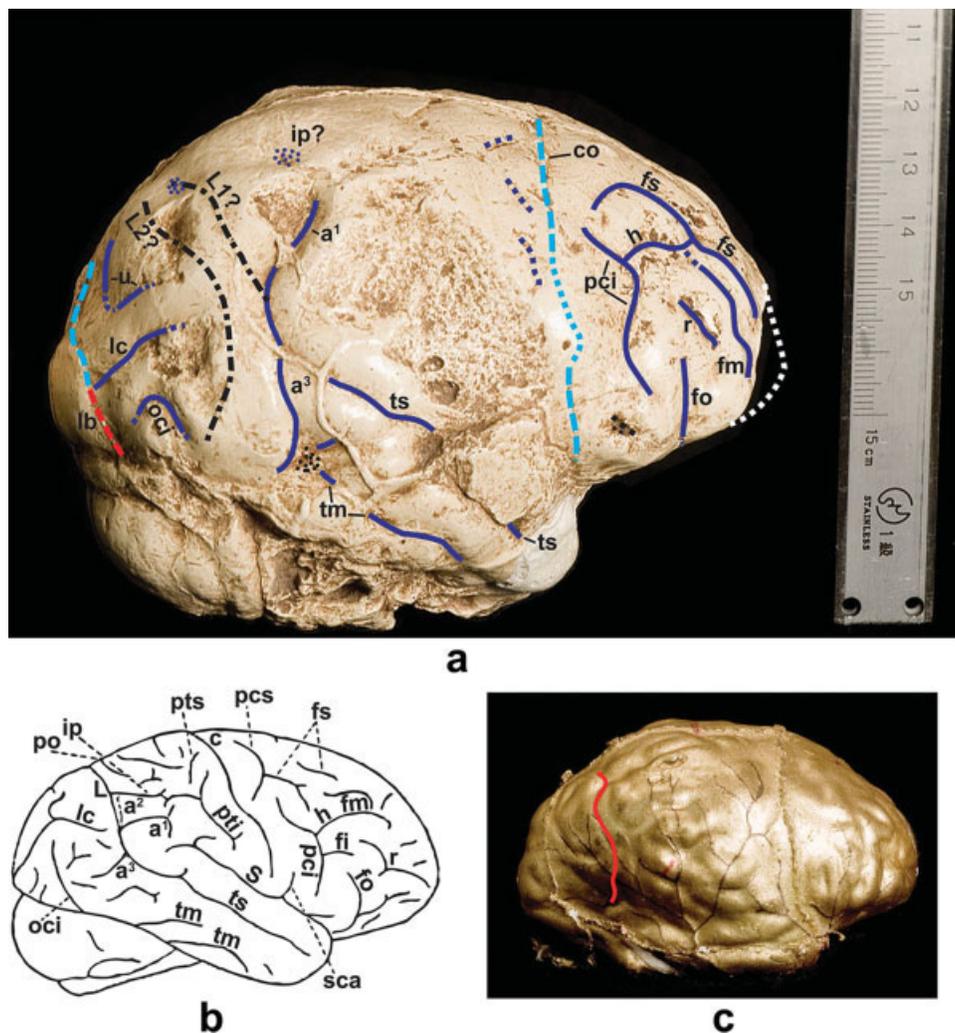


Fig. 6. Right lateral views of the Taung endocast, a brain of a young male chimpanzee, and an endocast from a juvenile bonobo. See Table 1 for abbreviations of sulci. (a) The author's identifications for features indicated directly on a copy of the Taung endocast (compare with Fig. 2b). Clear sulci are indicated with solid lines; less clear sulci and continuations of sulci and sutures are indicated with short dashes; pits and depressions are speckled. Two hypothetical lines ($L1?$, $L2?$) form rostral and caudal boundaries of an area that could have contained a lunette sulcus on the corresponding brain that would not have interrupted other sulci or convolutions. If so, L was not reproduced on the endocast, as is the case for most ape and human endocasts; or it may have been partially reproduced as a superficial concurrence (i.e., an occipital operculum) with a short segment of *ts* and the sulcus identified here as a^3 (see text for discussion). (b) Sulcal pattern of young male chimpanzee, reversed from left to right to facilitate comparison with the Taung endocast. Notice that a^3 appears to form the lateral part of L and that a^2 is covered by the lunette sulcus. Modified from Conolly (1950, p 108, Fig. 80). (c) Endocast from a juvenile bonobo (*Pan paniscus*, accession number R.g. 29006), with L highlighted. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

I have therefore extended *ts* to include a^1 and, thus, no longer identify its termination as a^2 (compare Fig. 4b and 6a). The latter may have been opercularized by *L* as Connolly illustrated and described for a young male chimpanzee (Fig. 6b): "The temporal superior ... is superficially concurrent in this specimen of the chimpanzee with part of the lunate sulcus, a submerged gyrus separating the two. The anterior branch (a^1) runs sagittally ... the middle branch (a^2 dotted line) runs dorsally under cover of the occipital operculum" (Connolly, 1950, p 110). Alternatively, a^2 could have originated medial to the point where the meningeal vessel crossed over *ts* (Fig. 6a) and coursed in a dorsomedial direction, and simply not been reproduced on the endocast (Clark et al., 1936).

The second change in my illustration of Taung's endocast pertains to a pit (speckled) just rostral to the lateral end of a^3 (Fig. 6a) that both Schepers and Dart illustrated (Figs. 4a and 5a,b), but which I neglected to indicate in my initial illustration of the Taung endocast (Fig. 4b) (Holloway, 1981). Accordingly, I no longer identify the lateral end of a^3 as *tm* [although one of Connolly's figures for an adult male chimpanzee illustrates that the lateral end of a^3 sometimes converges with the caudal end of *tm* (Connolly, 1950, p 114)] (compare Figs. 4b and 6a). It is striking that, with these two modifications to my earlier illustration, Dart's and my *visual observations* of sulci and sutures are very similar, despite whether or what we each named them (compare Figs. 5a,b and 6a).

The main difference between our illustrations is in the *identifications* of features that we both perceived at the caudal end of the endocast, although Dart identified a feature that I did not (and do not) perceive in that part of the endocast—namely, the sulcus angularis (a^2 ramus of *ts*) (compare Figs. 4b and 5a). Dart identified the feature that I recognize as the inferior occipital sulcus (*oci*) as a confluent *pl* and a^3 (compare Figs. 5a and 6a), which he illustrated but did not label in his preliminary figure (Fig. 5b).

Oci is a highly variable sulcus in pongids (Connolly, 1950), and Connolly illustrated it in a location and configuration on brains of orangutans (p 69, 71), a gorilla (p 93), and a chimpanzee (p 113) that is similar to the feature I identify as *oci* on the Taung endocast (Fig. 6a). (In his preliminary figure [Fig. 5b], Dart labeled a lateral continuation of my a^3 [Fig. 6a] as *oci*, but did not include this identification in his final version [Figs 5a].) Regarding his 1929 identifications of a^2 and a^3 , Dart wrote, "there are distinct traces in the cast of another sulcal system running dorso-medially in the district between the *parallel sulcus* [*ts*] and the *anterior occipital sulcus* [a^3], whose only homologue ... can be the human *angular sulcus* [a^2]" (Dart, unpublished material, p 190). Accordingly, Dart illustrated and labeled these hypothetical traces of a^2 in Figure 19 just lateral to the damaged area intersected by *ipo* and another lateral to the larger damaged region below that (compare Fig. 5a,b).

Dart also illustrated but did not label the sulcus that I identify as the lateral calcarine (*lc*) (Fig. 6a). *Lc* is highly variable in great apes, in which it may have a y-shaped form or, alternatively, it may be linear with a superior (dorsal) ramus (*u*) that is separated from the main furrow (Connolly, 1950, p 105), as Connolly illustrated for an orangutan (p 71), two chimpanzees (p 108), and noted for 9 of 24 gorilla hemispheres (p 105). A sulcus that I tentatively identified and illustrated in my initial sketch of the Taung endocast but did not label (Falk, 1980,

p 529, 531) is now labeled as *u* that is separate from *lc* (compare Fig. 4b and 6a). Dart, on the other hand, labeled the medial stem of this sulcus as the occipital transverse (*otr*) in his preliminary illustration, but changed the label to indicate its lateral stem in Fig. 19 of his manuscript (compare Fig. 5a,b). In apes, *otr* is frequently formed by a medial fork of the caudal end of *ip*, which may, or may not, merge with *L* (Connolly, 1950, p 112; see illustrations of chimpanzee brains on p 108). In humans, on the other hand, *otr* usually forks off the caudal end of the paroccipitalis sulcus (Connolly's *par*), which is caudal to *ip* (Connolly, 1950: see illustrations on p 215). Dart's Figure 19 showed *otr* as separated and very distant from *ip*; nor was it forking from a *par* (Fig. 5a). For his part, Schepers identified the same sulcus as *otr*, but illustrated it just lateral to a transverse parietal sulcus (*pst*) that intersected *po* (=Dart's *ipo*) rostrally, which was observed by neither Dart nor myself (compare Figs. 4a,b; 5a,b; and 6a).

Where was Taung's lunate sulcus?

As noted above, Clark observed the original Taung endocast in 1947, commented on Schepers' illustration of it (Fig. 4a), and concluded that "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, p 312). He offered two reasons for his conclusion: 1) A lunate sulcus located in the position of a^3 on Schepers' diagram (=Falk's a^3) would be located further forward than in any modern ape, and 2) an alternative location for *L* would have been impossible between a^3 and the feature that Schepers identified as *L* (i.e., in the position of the lambdoid suture). Others have since reiterated Schepers' reasoning. For example, referring to Falk's illustration (Fig. 4b), Holloway observed, "If there is always some distance between the most anterior end of the *lc* and the margin of the lunate sulcus, the only remaining location for the inferior part of the lunate sulcus is Falk's A^3 ! Something is most un-pongid here" (Holloway, 1981, p 52, emphasis his).

There are good reasons, however, to question these assertions. First, the dashed line labeled *L1?* on a photograph of the Taung endocast (Fig. 6a) indicates a hypothetical location for *L* in which a^3 and a short segment of *ts* are superficially concurrent with the lateral arc of *L*, as is the case for a chimpanzee brain described and illustrated by Connolly (Fig. 6b). That the sulcus labeled a^3 in Fig. 6a exists on the Taung endocast is beyond doubt: Although their labels for this sulcus varied, it was recognized on the Taung endocast by Dart, Keith, Schepers, and Clark. Keith illustrated this sulcus on a lateral view of Taung's endocast (Keith, 1931; Fig. 18), which he called a "vertical sulcus" (*VK* in Fig. 3b) and about which he stated, "a vertical sulcus... emerges from the parallel fissure (*ts*) and descends to the lower border of the brain near the temporo-occipital junction ... (it) was well developed in the Taungs brain" (Keith, 1931, p 83–84). [Contrary to Schepers (1946, p 193), however, this is not the sulcus that Keith identified as *L* (compare *LK* in Fig. 3a,b)].

The vertical sulcus of Keith (*VK*, fig. 3b) was independently observed and labeled a^3 (anterior occipital ramus of *ts*) by Schepers (Fig. 4a), and Clark confirmed the presence of the medial portion of the sulcus: "That the groove on the cast which apparently corresponds to

the upper part of the sulcus (a^3) is not an artefact seems to be assured by the fact that it is crossed by an uninterrupted impression of the parietotemporal branch of the middle meningeal vessels" (Clark, 1947, p 311). (See Fig. 2b.) Dart also illustrated the feature recognized visually by Schepers, Keith, Clark, and myself, although he did not label it in Figure 19 of his 1929 manuscript (Fig. 5a). As noted, however, Dart labeled the inferior part of the sulcus as *oci* in his preliminary draft of the figure (Fig. 5b). Only Holloway, referring to Falk's identification of a^3 (Fig. 4b), remarked that " a^3 is purely guess work" (Holloway, 1981, p 54).

But is it true that Falk's a^3 (=Schepers' a^3 = Keith's *VK* = Clark's observed sulcus, the identity of which he was unsure = Dart's illustrated sulcus, the lateral portion of which he at one time considered to be *oci*) was too far forward on Taung's endocast to occupy an apelike position for *L*? Because Taung was estimated to have died at about 3.5 years of age (Bromage and Dean, 1985), it is appropriate to compare its endocast with those of other juveniles, such as that from the skull of a juvenile bonobo (*Pan paniscus*, accession number R.g. 29006) at the Koninklijk Museum voor Midden-Afrika in Tervuren, Belgium (Fig. 6c). The maximum length (frontal pole [fp]-occipital pole [op]) of the bonobo right hemisphere of 111 mm is about 5 mm shorter than that of Taung's reconstructed right hemisphere (116 mm, Falk and Clarke, 2007). Although this is just one ape endocast, the position of the most rostral point of its *L* (and that of the young male chimpanzee in Fig. 6b) does not appear to be as far forward as the most rostral point of a^3 is (i.e., along the horizontal fp-op axis) on the Taung endocast. Thus, despite the fact that the relationship of a^3 to other sulci on Taung (compare Fig. 6a,b) and the crescent shape of its $L1? \rightarrow a^3$ are consistent with the hypothesis that a^3 (Fig. 6a) could be concurrent with the lateral portion of an apelike *L*, such an *L* would be unusually far forward for an ape. (I hasten to add that in my view this does not, in and of itself, rule out the possibility that $L1?$ represents *L*.)

It is important to clarify that the medial (dashed) portion of $L1?$ is hypothetical, although the dimple at its medial end exists on the endocast, and, indeed, was the feature I initially identified as a likely medial end of *L* (Falk, 1980) (compare Figs. 2b and 4b). Despite the fact that natural endocasts reproduce better detail than artificial ones, their reproduction of sulci is far from perfect (Falk, 1980); and ape and human endocasts (in addition to those of early hominins) are notorious for failing to reproduce lunate sulci (Symington, 1916; Clark et al., 1936; Connolly, 1950). It would therefore not be surprising if *L* were reproduced only partially (or only partially concurrent with other visible sulci such as a^3) on the Taung endocast (e.g., the lateral end of $L1?$, Fig. 6a).

Comparative studies of brains and corresponding endocasts indicate that it would also not be surprising if *L* had existed on Taung's brain but failed to be reproduced as a sulcus on the natural endocast. Despite this fact, the endocast reveals that a continuous *L* would not have been precluded from occupying a position between the lambdoid suture and a^3 by intervening convolutions, as Schepers and others asserted (Fig. 6a). There was, in fact, ample space on the Taung endocast for an apelike *L* to be located anywhere between the hypothetical locations $L2?$ (which is more consistent with the position of *L* in Figs. 6b&c) and $L1?$ (Fig. 6a).

One might use the same reasoning, however, to argue that *L* may have occupied a position underneath or caudal to *lb*, although I do not perceive traces of it in a position that is either immediately rostral (Fig. 5a) or caudal (Fig. 3a) to *lb*, as others have suggested. I remain skeptical about this possibility, however, for several reasons. In making the first argument, Dart illustrated but declined to provide identifications for two apelike sulci (a^3 and *lc*, Fig. 6a), and the existence of the feature he identified as a^2 was (as noted) highly questionable. For his part, Schepers identified what appears to have been an obvious *lc* as part of a different highly improbable a^2 (Connolly, 1950, p 295), and added a questionable *pst* that neither Dart nor I perceived (Fig. 4a). It bears reiterating that the sulci and sutures illustrated in Fig. 6a were all perceived by Dart (Fig. 5a), although our identifications differed in some cases—especially for caudally-located features. It should also be noted that I extrapolated less than Dart for some sulci, such as the depression labeled *ip?* in Fig. 6a, which may well have been part of an actual sulcus that Dart illustrated and identified as *ip* (Fig. 5a). Significantly, the entire sulcal pattern illustrated in Fig. 6a is similar to those reproduced on great apes, such as the chimpanzee shown in Fig. 6b. The illustrations of Schepers and Dart, on the other hand, indicate a humanlike sulcal pattern caudally (but with questionable identifications, as noted) on an ape-sized endocast that, elsewhere, reproduces a relatively simple, apelike sulcal pattern (Fig. 6a). The inconsistency of a hypothetically humanlike sulcal pattern caudally in combination with a rostral apelike sulcal pattern becomes apparent when one examines Taung's frontal lobe.

Frontal lobe sulcal pattern on the Taung endocast

Dart prepared two different sketches of the sulcal pattern reproduced on the frontal lobe of Taung's endocast (Fig. 7a,b) that were unpublished and appear to have been preliminary to his, still different, final illustration that was included in Figure 19 of his 1929 manuscript (Figs. 5a and 7c).

Dart's description of the sulcal pattern of Taung's frontal lobe, quoted here at length, is revealing when considered in light of his three sketches in Fig. 7:

The numerical terminology of Kappers [Ariëns Kappers] ... with reference to the frontal lobe sulci is a useful accessory in description and has been followed, in order to permit of comparison with his description of the endocranial cast of *Pithecanthropus*. He denominates the *sulcus fronto-orbitalis* as 1. The area within which sulci are to be found in the frontal lobe of *Australopithecus* is confined anteriorly owing to the fracture; which has separated the most anterior portion (which still lies within the forehead of the skull) at the level of the coronal section passing through the *sulcus fronto-marginalis* or 9, and just anterior to the connection 11c, and 7b, between the *superior frontal sulcus* 11 and the *middle frontal sulcus* 7 ... Insert Figure 19. The most outstanding peculiarities of the sulcal system of the frontal lobe lie in its strong similarity to the same system in *Pithecanthropus*. First there is a marked forward bend of the *inferior precentral-inferior frontal sulcus complex* 5, 4, and 3 ... Secondly the territory between the *middle frontal sulcus* 7, and the superciliary border is not occupied by a "fossette 8", and dorso-ventrally running sulci 7c, and 7d as in *Pithecanthropus* (Dart, unpublished material, p 179–180).

In keeping with Dart's description, the labels (numbers combined with letters) and specific identifications

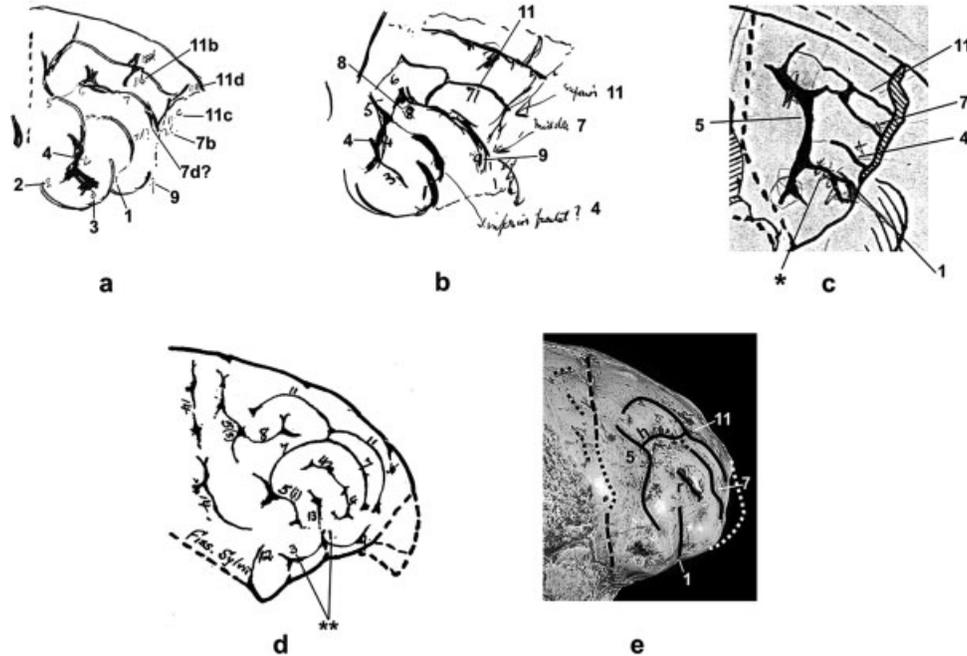


Fig. 7. Illustrations of the sulcal pattern reproduced on the frontal lobe of the Taung endocranium. (a) Dart's previously unpublished drawing of the sulcal pattern that he numbered for comparison with Ariëns Kappers' comparable figure of *Pithecanthropus erectus* (Ariëns Kappers, 1929a, p 226, 1929b). Numbers are keyed to the abbreviations in Table 1: 1, fronto-orbital (*fo*); 2, anterior ramus of Sylvian fissure; 3, axialis operculi orbitalis; 4, inferior frontal (*fi*); 5, precentral inferior (*pci*); 6, junction between 7 (middle frontal, *fm*) and 5; 7*b-d*, rami of *fm*; 8, intermediate fossite; 9, fronto-marginal (*W*); 11, superior frontal (*fs*); 11*b-d*, rami of *fs*. Dart referred to the combination of 5, 4 and 3 as the "inferior precentral-inferior frontal sulcus complex" (Dart, unpublished material, p 180). (b) A second sketch of Dart's using the same numbering system, in which the identifications of sulci differ somewhat from the first. Some of Dart's numbers have been clarified in the margins; both figures are reproduced with permission of the University of Witwatersrand. (c) Dart's illustration of Taung's frontal lobe as it appeared in Figure 19 of his manuscript (Fig. 5a) differed somewhat from both of his preliminary sketches (a) and (b); *added to indicate Dart's 'arcuate sulcus' discussed in text. (d) Schepers identifications for Taung's frontal lobe (Fig. 4a), which differed somewhat from Dart's: 1, subfrontalis (*sf*); 3, fronto-orbital (*fo*); 5*s*, precentral superior (*pcs*); 5*i*, precentral inferior (*pci*); 12, subcentral anterior (*sca*); 13, diagonal (*d*); 14, Rolandic (*c*). **Identifications differed from Dart's for the same numbers (see text); the other numbers corresponded to Dart's. (e) Falk's identifications for Taung's frontal lobe labeled with the same numbering system (Falk, 1980) (Figs. 4b and 6a). Other sulci: *h*, horizontal ramus of *pci*; *r*, rectus. Dots located caudolaterally indicate a pit that may have contained a short sulcus.

used in Fig. 7a closely resembled those of Ariëns Kappers for the frontal lobe of *Pithecanthropus* (compare Fig. 7a with Fig. 115 of Ariëns Kappers [1929a, p 226, 1929b]). In Fig. 7b, however, the labels were simpler (numbers only), and a feature that was not labeled in Fig. 7a was identified as the inferior frontal sulcus (#4), plus an identification for 'fosette 8' was added. The frontal lobe portion of Dart's final Figure 19 (Fig. 7c) corresponded more closely with Fig. 7b than with Fig. 7a, although it differed from the former because it excluded "fosette 8" (consistent with Dart's written description).

Keith also illustrated the sulcal pattern on Taung's frontal lobe, but not in as much detail as others have. He identified parts of *pci* (#5) and *fs* (#11) and noted that they were linked by a "direct connection" (see Fig. 3b), which I also observed and identified as the horizontal branch (*h*) of *pci* (Fig. 7e). Keith suggested that this configuration reproduced an arcuate fissure similar to those of monkeys but unusual for apes (Keith, 1931). Although the lower end of *pci* and *h* are, indeed, thought to represent the homolog of the arcuate sulcus of monkeys (Connolly, 1950, p 190, 193), their configuration in Taung is not unusual in apes, as Keith suggested (Connolly, 1950). Dart also illustrated but did not label *h* (Fig. 7c), which he labeled as a junction between *pci*

and *fm* (#6) in his preliminary sketches (Fig. 7a,b). Schepers observed the connection too, but simply labeled it 7 (*fm*) (Figs. 4a and 7d).

Although Dart, Keith, Schepers, and I recognized the same sulcus as *pci*, Holloway observed that "Falk's identification of *pci* more than 10 mm anterior to the coronal suture is somewhat a problem . . . *Pci* could very well be just slightly caudal to the coronal suture" (Holloway, 1981, p 53). While this reservation might apply to large-brained humans, it is questionable when applied to hominins with ape-sized brains. In a comparison of sulcal relations in apes and humans, Connolly observed: "In the human brain the precentral inferior sulcus shifts more caudally relative to the temporal pole. This is partly due to the forward growth of the temporal lobe, but also to an actual caudal displacement of the precentral inferior sulcus, as a result of the growth of the frontal lobe. The precentral inferior is likewise more caudal with respect to the coronal suture" (Connolly, 1950, p 325-326).

The reader will recall that Dart turned his unpublished manuscript over to Schepers, and it is interesting to compare their illustrations of Taung's frontal lobe. Schepers' identifications (Fig. 7d) incorporated different aspects of Dart's two preliminary figures (Fig. 7a,b). Although Schepers' identifications for #s 3, 1, and 9

occurred in the same general area as Dart's #s 3, 1, and 9 in Fig. 7a, it is important to note that #3 indicated *fo* for Schepers, but the axialis operculi orbitalis (part of *pci*) for Dart; while #1 indicated the subfrontalis (*sf*) for Schepers, but *fo* for Dart (compare ** in Fig. 7d with Fig. 7a). [Schepers' identifications are confusing because *sf* may be homologous with *fo* (Connolly, 1950, p 184), in which case one would not expect to see the two sulci in the same brain.] Schepers' identification of #4 was the same as Dart's corresponding identification in Figures 7b,c. Although a number of Schepers' identifications agreed with Dart's (#s 5i, 7, 11), his illustrations included features that were not observed by others (a separate configuration of #s 5s and 8 dorsomedially, #12, and misidentification of the coronal suture as the central sulcus [#14]). Schepers also labeled the medial portion of the sulcus identified as *fo* (#1) by both Dart and Falk as the diagonal sulcus (#13), which is unlikely in light of Connolly's discussion and illustrations of *d* in both apes and humans (Connolly, 1950, p 108, 193).

Connolly, who did not have access to Dart's unpublished figures, assessed Schepers' illustration of the Taung endocast and raised serious questions about the identifications and relative configurations of #s 14, 5i (its lateral part), 3, 13, and 4 (Fig. 7d) (which he suggested might better be identified as *r*, as it has been in Fig. 7e), in addition to those for caudally-located features including 18 (*L*) and 25 (a^2) (see Fig. 4a) (Connolly, 1950, p 294–295). He concluded: "Whatever status future investigations may finally assign to *Australopithecus* and the allied fossil genera, one may feel assured that the true interpretation of the sulcal relations of the brain will not show the above noted discrepancies but will be more in harmony with the developmental processes seen in the brain of ape and man" (Connolly, 1950, p 295).

Dart's and Falk's independent perceptions and identifications of frontal lobe sulci were very similar (compare Fig. 7c,e). The main exception is the sulcus that Dart (and Schepers) labeled as the inferior frontal (#4), which Falk identified as the rectus (*r*). For reasons discussed by Connolly in specific reference to the Taung endocast (Connolly, 1950, p 294), I continue to think *r* is the correct identification. The most significant similarity between Dart's and Falk's identifications is the sulcus they identified as *fo*. Dart was clear about his identification: "There is the customary *sulcus fronto-orbitalis*, incising the superciliary border of the cast, 20 mm. in front of the Sylvian depression" (Dart, unpublished material, p 179). Keith also appeared to perceive *fo*, although he did not specifically name it. However, he illustrated and commented on the apelike morphology of the "orbital cap" of the Taung endocast (Fig. 3b), which he illustrated as bounded rostrally by *fo* in apes (Keith, 1931, p 81–82), as indeed it is (Connolly, 1950, p 325).

Falk identified the same sulcus on Taung's endocast as *fo* that Dart had, and noted that it was apelike, in part because this sulcus does not appear on the lateral surface of human brains (Falk, 1980, p 528–530): "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, p 330). Thus, *fo* is not visible on the lateral surface of the human brain" (Falk, 1980, p 528). Holloway's assessment of the sulcus Dart and Falk identified as *fo* differed from theirs. Instead, he

stated that "What Falk has called *fo* on the Taung specimens (sic) does not show that deeply incised pattern in its inferior aspect . . . Falk's *fo* could well be Connolly's *fi* (frontalis inferior), or [the] . . . subcentralis anterior" (Holloway, 1981, p 53, emphasis his).

Dart seemed to have been unaware that *fo* does not appear on the lateral surface of human brains. He, further, claimed that a sulcus extended from the medial end of *fo* and connected it with the lateral end of *pci* on Taung's endocast (* in Fig. 7c), and argued that such a configuration was dissimilar to that of apes:

A deeply marked longitudinal arcuate sulcus runs from the anterior aspect of the *fronto-orbital sulcus* 1, and curves backwards over it to be lost posteriorly in the *inferior-precentral complex* at its forward bend (see Figure 19) . . . The presence of a distinct arcuate depression in this important region is entirely dissimilar from what is found in the living Apes. (Dart, unpublished material, p 180).

(Note that Dart used the term "arcuate" as a general adjective, rather than as a reference to its homolog [= *pci* + *h*], as Keith did.) Dart's final illustration of Taung's frontal lobe, thus, differed from his preliminary sketches (Fig. 7a,b) because it included a sulcus curving caudally from the medial end of *fo* (#1) to the lateral end of the "inferiorprecentral complex" (* in Fig. 7c). It also differed from the illustrations and discussions of frontal lobes of Keith (Fig. 3b), Schepers (Fig. 7d), and Falk (Fig. 7e), none of whom illustrated or discussed such a pattern, which has not, as far as I know, been described for either apes or humans.

Dart's analysis of brain shape in Taung

Dart devoted 30 pages of his 1929 manuscript to a discussion about the shape of three cortical association areas on the Taung endocast that went far beyond his observations in 1925 (Dart, unpublished material, p 167–197), and two additional pages to a summary of this discussion (Dart, unpublished material, p 208–210). Although a two-paged summary was eventually published (Dart, 1940, p 181–183), to the best of my knowledge the brunt of Dart's analysis remained unpublished. Some of its more interesting aspects are discussed in this section.

Dart claimed that information about expansion in three cortical association areas was the only type of evidence from Taung's endocast that could indicate the evolutionary relationship between *Australopithecus* and humans:

It is important to reiterate that the only type of evidence the cast can yield, which would indicate proximity to Man, is that of *expanded association cortices*; which by their localisation, have profoundly affected the shape of the brains as compared with those of living Apes. Further the particular regions of the lateral brain surface which are especially expanded in Man and have affected its general contour as compared with Apes, are three in number. They are what Elliot-Smith . . . has called the "three significant cortical areas" . . . and are the parietal, the inferior frontal or prefrontal and the inferior temporal. Genuine expansion in these regions, even if the expansions are only relative; nay, because they are rare [they are] relative – constitutes trustworthy evidence in demonstrating the ancestral relationship of this Anthropoid to Man. (Dart, unpublished material, p 165–166).

Although Dart had discussed the first cortical area, the parietal association cortex, to a limited extent in

1925, in 1929 he specified that the increased distance between *ts* and *L* on Taung's endocast indicated that Brodmann's areas (BA) 18, 19, and 39 had proliferated in comparison to apes and, thus, forced the visual cortex (BA 17, bounded rostrally by *L*) to migrate posteriorly "as in Man, instead of its occupying the major area of the post-sylvian brain surface, as in Monkeys and Anthropoids" (Dart, unpublished material, p 168). But Dart went even further: "The sulcal landmarks [*ts*, *L*] ... do not limit the area in which parietal expansion has occurred. They merely serve as a guide to the extent of the expansile changes which had been taking place in the whole district between the post-central cortex - [BA] 1, 2, and 3 - and the visual cortex - [BA] 17" (Dart, unpublished material, p 168).

In addition to sulcal landmarks, Dart specified shape features of the Taung endocast that were correlated with expansion of the parietal cortex, including a relatively "increased length of the parietal arc,"... "dome-like human appearance of the parietal region" (Dart, unpublished material, p 167), and "the forward position of the cerebellum under cover of the temporoparieto-occipital region" (Dart, unpublished material, p 193). Interestingly, Dart viewed Taung's enlarged parietal cortex as a specific correlate of bipedalism:

We are now in a position to understand the true significance of the great parietal enlargement in the fossil cast. It means that *Australopithecus* had made a momentous stride forward beyond living Anthropoids in *stereognostic* ... and *kinaesthetic* ... ability. He had built up an increased knowledge of his bodily parts and their potentialities in movement ... evoked by a revolutionary change in bodily orientation, namely the assumption of the erect posture—with its accompanying differentiation and delimitation of the physiological aims and uses of the fore and hind limbs ... Expansion of this significant cortical area of the brain is one of the main features, which differentiates Man from the Apes. It is a necessary corollary of that thesis that the Ape, which had achieved such an expansion, had made a measurable and distinctive advance towards human status, by assuming the posture of Man and a man-like control of its limbs. He had hands and feet. (Dart, unpublished material, p 175–176).

Significantly, Dart thought that Taung's brain was reorganized globally rather than in a more piecemeal 'mosaic' manner, as some have suggested (Barton and Harvey, 2000; Holloway, 2001):

It would be erroneous to believe that in the assumption of the erect attitude, the only necessary cerebral development, important as it might be, was a fine coordination of visual impressions with those streaming into the cortex from the trunk and lower limbs themselves. On the sensory side it also involved enhanced representation of vestibular sensation in the temporal cortex; in addition to the tactile, muscular and arthroidal delegations in the parietal cortex. On the motor side the phenomenon was even more complex; for the ascendancy of the fore-brain over the brain stem and the cerebellum, as a pliable posture-regulating mechanism, is achieved through descending tracts from the prefrontal, temporal, occipital and probably also the parietal territories (see Elliot Smith ...). The assumption of the erect posture and the ability to display great muscular skill therefore depends upon the orderly expansion of all three of the significant cortices (Dart, unpublished material, p 176).

Dart stated that Taung's prefrontal association cortex (the second area referred to above) was relatively expanded, for the first time in 1929. He credited this observation to Elliot Smith (Smith, 1927), who observed a pronounced orbital margin on the Taung endocast that was as developed as that of *Pithecanthropus*, in contrast to the rounded margin of apes. Elliot Smith attributed

this morphology to "a definite increase in size of the prefrontal area ... in comparison with that of the Gorilla ... This affords very valuable and objective corroboration for Professor Dart's claim (which was based primarily on the contrast in the parietal proportions) that the Taungs Ape reveals evidence of a definite if slight advance towards the human condition" (Smith, 1927, p 167). Dart, therefore, claimed that Elliot Smith "has confirmed my arguments by his independent study of the frontal region in a plaster cast of *Australopithecus*" (Dart, unpublished material, p 177), which he reiterated decades later: "He (Elliot Smith) ... agreed in 1927 with my original interpretation of the Taungs endocranial cast in his *Essays on the Evolution of Man*; and went beyond it in noting additionally the humanoid form of its orbital margin" (Dart, 1972, p 174). It is important to note, however, that although Elliot Smith corroborated Dart's claim that Taung's endocast was, to some degree, advanced toward a human condition, there is no evidence to suggest that he ever accepted Dart's identification of *lb* as *L*.

Dart attributed the "lateral bulging" (Dart, unpublished material, p 177) of Taung's prefrontal cortex to "expansile processes that have taken place in the inferolateral segment of the frontal cortex ... affecting that whole district" (Dart, unpublished material, p 180). He further stated that the sulcus he alone perceived coursing from the medial end of *fo* to *pci* (* in Fig. 7c) illustrated these expansile processes. According to Dart, "the localized growth of the inferolateral portion of the frontal cortex, whose increment is responsible for the production of the 'orbital-margin,' bespeaks an advancement in intelligence—of forethought and skill—such as is encountered in no other Ape whatever, but which is found elsewhere only in Primitive Man" (Dart, unpublished material, p 185).

Dart also described Taung's endocast as advanced toward a human condition in the third significant area referred to above, the inferior temporal association cortex, although his remarks also incorporated information about other parts of the temporal lobe: "There is present simultaneously a marked relative widening of the lower portion of the contour, which corresponds with a relatively increased expansion of the posterior part of the temporal region especially in its inferior part ... The superior temporal gyrus is broad and expanded and not thin and undeveloped in appearance, as is the case in the Chimpanzee and the Orang ... The middle and inferior temporal gyri are also more robust" (Dart, unpublished material, p 187–188). Dart associated this morphology with increased representations of BA 37 and 39 (Dart, unpublished material, p 190).

Functionally, Dart attributed the morphology of Taung's temporal lobe to an improved ability for interpreting social sounds and cries:

The process of widening in the temporal lobe is not restricted to the inferior temporal gyrus. The middle temporal gyrus is full and expanded. While it displays no definitely marked and localised bulging, such as is found in *Pithecanthropus* and *Eoanthropus* [Pitdown Man], the character of the posterior part of the middle temporal gyrus in *Australopithecus*, previously referred to, indicates a general improvement beyond the Chimpanzee in its capacity to recognize the significance of sounds, and to interpret the significance of the cries emitted by his companions and the ideas underlying their employment. (Dart, unpublished material, p 194).

However, Dart did not think Taung's temporal lobe was as advanced as its parietal and prefrontal cortices

because, in his opinion (also expressed in Dart, 1925), *Australopithecus* had not yet evolved speech:

The third significant (inferior temporal) cortex is also expanded, but has lagged in this respect behind the two previously cited. Attention has been drawn to a *temporal margin* to the development of a typical human temporo-occipital lobule, to the contraction of the vallicula between the temporo-sphenoidal lobe, and to the forward position of the cerebellum and to its well-filled character. These features testify to improvement in the understanding of sounds and the interpretation of their significance, to the intelligent control of the bodily musculature and the maintenance of equilibrium in the erect posture. There is no positive evidence of localized expansion in the middle temporal gyrus, such as appears to signify the rhythmical control of articulation in all known types of Man. *Australopithecus* presumably had not acquired the habitual use of articulate speech. (Dart, unpublished material, p 209–210).

Dart concluded that the morphology of the three significant cortical association cortices reproduced on the Taung endocast showed that *Australopithecus* was closer to *Pithecanthropus* than to the living apes:

The endocranial cast as a whole is the physical embodiment of those features, which have been anticipated as necessarily occurring in pre-human evolution and in a corresponding order of emergence. It has long been believed that the upright posture came first, bringing in its train manual, visual and facial control and finally the acquisition of speech. *Australopithecus* stands, as it were, in the midway of this process. His brain reveals the parietal region of a fully-erect, plantigrade Ape, the frontal region of an Ape that has achieved stereoscopic visual perfection and which, by virtue of his acquisition and the liberation of its hands, has made noteworthy progress in an intelligent understanding of objects and the practical, serviceable uses to which they can be put . . . Finally, although significant changes have occurred in the temporal region, these are juttily [justly] attributed to the important part, which this area plays in the acquisition and control of posture, and to an appreciable improvement in acoustic memory and understanding. A profound upheaval in the direction of expansion and differentiation in the temporal cortex waited the progeny of the *Australopithecidae* before they could truly be regarded as having stepped over the fine line of speech that alone separates them from *Pithecanthropus*—an upheaval which unquestionably must have had a repercussive effect upon the all-important prefrontal cortex; by means of which there was translated into sounds the conceptual imagery, whose concrete basis was being laid down in the brain of *Australopithecus*. (Dart, unpublished material, p 200).

Dart's claim that the Taung endocast reproduced a shape that, compared to apes, was advanced toward a human condition in its parietal, prefrontal, and posterior inferior temporal association cortices appears to have been, at least, partially correct. An occipital lobe that extends caudally relative to the cerebellum, which is tucked forward underneath the occipital cortex in Taung, has classically been recognized as a derived feature compared with the usual position for apes, and, indeed, may be correlated to some degree with reorganization of the parieto-occipital association cortices (Smith, 1927; Dart, 1940; Connolly, 1950). With respect to the second significant area, it is now known that the rostral lateral prefrontal cortex in *Australopithecus africanus* endocasts is expanded giving the frontal lobe a squared off shape (in dorsal view) that is derived toward a humanlike condition, compared to the less expanded teardrop shape of the frontal lobes of *Paranthropus* endocasts (Falk et al., 2000). The recently reconstructed frontal lobe of the Taung endocast shares the expanded prefrontal cortex of the other gracile australopithecines (Falk and Clarke,

2007), in keeping with Dart's suggestion (Dart, unpublished material). Dart's claim that the third significant area, the posterior inferior temporal cortex, was relatively expanded in Taung is questionable, however. A number of measurements (and ratios) indicate that Taung's temporal lobe was generally small and that its posterior inferior portion was not relatively enlarged, although this might be due to the juvenile status of the individual (Falk and Clarke, 2007). It is also worth noting that the morphology of the newly-reconstructed temporal pole was shaped similar to the derived shape of *Australopithecus*, rather than *Paranthropus* (Falk and Clarke, 2007).

DISCUSSION

Dart's 1925 claim that Taung represented a human ancestor (*Australopithecus africanus*) that was physically and cognitively advanced compared to living apes was path-breaking (Dart, 1925). However, the weight of his argument for Taung's advanced cognition rested heavily on the mistaken identification of the lambdoid suture as the lunate sulcus, which contributed to the skepticism with which Dart's discovery was greeted by fellow scientists (Falk, in preparation). Dart was stung by the negative reaction to his discovery, which he defended at great length in a manuscript he prepared from 1925 to 1929 that was ultimately rejected for publication. From that manuscript and four of Dart's unpublished illustrations of the Taung endocast, we have previously unavailable insight into Dart's analysis of the Taung endocast that he developed after his initial publication.

Dart's papers indicate that he was sensitive to the suggestion that he had misidentified *lb* for *L* and, further, that he attempted to address it in his unpublished manuscript by identifying a short segment of *lb* caudal to its actual representation on the endocast (Fig. 5a), and by suggesting that *L* and *lb* coincided for much of their lengths. Dart's reanalysis of the caudal end of Taung's endocast was awkward, however, for reasons discussed above. He also added an arced sulcus to the medial end of *fo* on Taung's frontal lobe (* in Fig. 7c), that he had not illustrated in two preliminary drawings (Fig. 7a,b), and which others did not perceive, and argued that it was part of a sulcal pattern that was advanced over an apelike condition.

Dart's interpretation of the Taung endocast was greatly influenced by the training he received from his mentor, Elliot Smith, whom he held in almost worshipful esteem:

There is no greater authority in this matter of interpreting the significance of the cerebral pattern exhibited by the mammalian and particularly the primate brain than Professor G. Elliot Smith. He also, probably more than any single writer, is responsible for placing the study of the endocranial cast on its modern accurate basis. The utmost importance naturally attaches itself in a study of this sort to his statements concerning the primate brain in general, and concerning those cerebral features which separate Man from the Apes in particular. I shall therefore have occasion to quote liberally from the writings of the master, at whose feet I was privileged to sit just a decade ago. (Dart, unpublished material, p 163).

As discussed above, Elliot Smith observed that the prefrontal cortex of Taung was relatively expanded, and stated that this corroborated Dart's claim that the "Taungs Ape" showed "a definite if slight advance

towards the human condition" (Smith, 1927, p 167). Although Elliot Smith had not corroborated Dart's identification of *lb* as *L* (which is what Dart's 1925 interpretation was all about), Dart repeatedly interpreted Elliot Smith's remark as an indication that he agreed with Dart's original interpretation of the Taung endocast (Dart, unpublished material; Dart, 1940). Elliot Smith's 1931 letter to Dart about his rejected manuscript, however, suggests that he did not use his influence to help Dart publish his observations about Taung's endocast, despite the fact that Dart's analyses of *L* and the three significant association cortices were solidly grounded on Elliot Smith's own theories: "All these notes apply to the pages relating to the teeth, because in the case of that part of the paper I did make a desperate effort to see whether I could not secure its publication before you arrived home" (emphasis mine) (Smith, February 25, 1931; Unpublished letter to Raymond Dart from Grafton Elliot Smith). As far as I can tell, the only researcher who defended Dart's identification of *lb* as *L* was Schepers (1946), to whom Dart had turned over his unpublished manuscript along with the responsibility for describing Taung's endocast.

All of the sulci that Falk identified had been perceived earlier by Dart, although some of their names differed (compare Figs. 4b, 5a, and 6a), but the reverse was not true. I, like most earlier workers, do not perceive any trace of *L* near *lb*; nor, like all earlier workers (except Dart), do I perceive a curved sulcus connecting *fo* to *pci*. This is important because *L* and *fo* are the two sulci in which dramatic differences in location, in fact, distinguish ape from human brains: Apes have rostrally located lunate sulci; humans do not (Smith, 1903; Connolly, 1950) and it is now questionable whether humans have lunate sulci at all (Allen et al., 2006; Falk, in press). Apes have fronto-orbital sulci that incise the lateral border of the frontal lobe and course caudally toward the temporal pole; *fo* does not appear on the lateral surface of human frontal lobes (or endocasts), in which it has been displaced caudally to become the anterior limiting sulcus of the insula (Connolly, 1950, p 330).

To me, the entire sulcal pattern on the Taung endocast continues to appear apelike, and I still believe that this was the case for australopithecines in general, despite the claim of a caudally-located *L* on the endocast from Stw 505 (Holloway et al., 2004), which will be addressed elsewhere. Nevertheless, certain shape features discussed above and elsewhere (Falk et al., 2000; Falk and Clarke, 2007) indicate that parts of the brain of Taung and the other gracile australopithecines (occipital lobe, lateral prefrontal cortex) had begun to expand toward a human condition.

It, therefore, seems reasonable to hypothesize that changes in hominin sulcal patterns occurred after certain cortical regions began to expand and alter their connections (Kaas and Preuss, 2008). It is well known that bigger brains have more gyri (bulges) and sulci (valleys between gyri), which is true for primates as well as other animals. Increased gyrification appears to be due partly to mechanical effects in which surface areas of brains buckle in order to keep pace with the volumes as brains enlarge (Jerison, 1973, 1991). According to Van Essen, the pattern of connections within the brain influences the specific locations of gyri and sulci, with tightly interconnected regions forming bulges, while poorly interconnected regions tend to be separated by sulci (Van Essen, 1997, 2007). Although "reorganization prior to

brain enlargement" (Holloway, 1988, p 33) may occur at neocortical, subcortical, and limbic levels, and may involve changes in neural density, neuroglial cells, and dendritic branching (Holloway, 1966), the analysis presented above suggests that, when it came to *sulcal* patterns, reorganization occurred in larger-brained hominins that lived more recently than Taung, and that sulci altered in cortical regions that had begun to expand earlier (e.g., prefrontal, parieto-occipital), perhaps in conjunction with an overall increase in brain size. In other words, dynamically expanding cortical areas eventually triggered sulcal changes in keeping with the processes described by Van Essen and Connolly.

Holloway's belief that Taung's *L* was located caudally indicated to him that "there was a reorganization of the brain involving, minimally, a decrease in primary visual cortex on the convex cerebral surface and an increase in parietal and temporal association cortex, allowing for greater discrimination among complex cues of the environment and for extension of foresight and memory to cope more effectively with the savanna-type environment" (Holloway, 1975, p 39) and, further, that this reorganization predated brain expansion (Holloway et al., 2003). Holloway's hypothesis that there was a relative increase in posterior association cortex that reflected early differential selection on one (caudal) part of the brain is an illustration of the concept of "mosaic brain evolution" (Holloway, 2001). Dart, on the other hand, believed that Taung's endocast suggested a more global reorganization that entailed related changes in cortical areas in all of the brain's lobes (as detailed above), rather than in a mosaic manner (Barton and Harvey, 2000; Holloway, 2001).

These different views reflect, to some degree, classical debates about the relative evolutionary importance of brain size versus cortical reorganization that continue to this day (reviewed in Falk, in press). For example, Barbara Finlay and her colleagues demonstrated a conserved order in how neurons are generated during neurodevelopment across 131 species of primates, bats, and insectivores that accounted for extremely robust (predictable) allometric scaling of different parts of the brain, and concluded that "the most likely brain alteration resulting from selection for any behavioral ability may be a coordinated enlargement of the entire nonolfactory brain" (Finlay and Darlington, 1995, p 1578). Nevertheless, the authors showed that the magnitude of variability (including the limbic factor) left room for species-specific brain adaptations, a fact lost on critics who suggested that brains evolved by selection for sizes of specific but distributed neural systems (modular or mosaic evolution) rather than for more global sizes (Barton and Harvey, 2000; Holloway, 2001; Barton, 2006).

More recently, Finlay and Brodsky (2006) explored the hypothesis that scaled-up cortical modules were significant drivers of brain evolution using computer-simulated experiments on neural net architecture, and found little to support it, or the related hypothesis that relative size or number of cortical areas are related to niche-specific adaptations such as frugivory or folivory. Instead, they propose that much smaller subnets (units of neural wiring that use modularity at a microscopic scale to implement logical computations) may be the fundamental units of brain development and evolution (Finlay and Brodsky, 2006). (See also Kaas and Preuss, 2008). This idea fits well with the observation that "functions may play more freely over the cortical matrix specified early

in development than we have imagined,” and the implication that “the neocortex is not a piecemeal collection of areas, each with its own discrete function, but is a generalized processing device” (Kaskan et al., 2005, p. 98). Finlay’s most recent research is consistent with her earlier findings regarding the conserved nature of neurogenesis (Finlay and Darlington, 1995), the fact that the major predictor of the sizes of various brain structures is whole brain size (Finlay and Darlington, 1995), and observations regarding the remarkable plasticity of the brain (Kaskan et al., 2005). Additional information is rapidly accumulating from comparative neuroanatomical (Semendeferi et al., 2001, 2002; Rilling and Seligman, 2002; Schoenemann et al., 2005; Preuss, 2007a,b; Kaas and Preuss, 2008) and functional imaging (Semendeferi and Damasio, 2000; Semendeferi, 2001; Tobias, 2001; Falk, 2004) studies of the brain. These various analyses mesh well with many of Dart’s views about the evolution of association cortices and their interconnectedness, and I suspect he would have been pleased with the progress that has occurred in paleoneurology.

Dart perceived most of Taung’s sulcal pattern accurately, although he was mistaken in a few crucial identifications. His critics knew this and were tough on him, which wounded him deeply (Falk, in preparation). Perhaps it was in response to them that he wrote the following defense of the study of primate endocasts, with an eloquence that will be appreciated by any paleoneurologist who has been accused of practicing phrenology (an occupational hazard):

If the form of endocranial cast is unintelligible, the comparative neurological studies of the last half century are a mockery, a delusion and a snare. It would be deplorable if, at this stage of neurological history, no tangible conclusions could be drawn from the shape of the simian endocranial cast, which Nature has provided for scrutiny; and dismal indeed, when the gap separating Man from the Apes is so patently cerebral and psychological, rather than structural or bodily. Such an attitude towards the study of endocranial casts today would be obscurantist and disastrous (Dart, unpublished material, p 162).

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