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Paleoneurological Studies in Honor of Ralph L. Holloway
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THE HUMAN BRAIN EVOLVING:

Paleoneurological Studies
in Honor of Ralph L. Holloway



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FRONT COVER CAPTIONS

Center: Portrait of Ralph L. Holloway.

Upper left: A modern human brain.

Upper right: Ralph measuring landmarks on an endocast ca. 1976.

Lower right: Homo habilis cranium KNM-ER-1813 from Koobi Fora, Kenya (photo by Holloway).

Lower left: Ralph with an endocast of the Flores "hobbit" cranium.

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CHAPTER 4

HUMAN BRAIN ENDOCASTS, TAUNG, AND THE LB1 HOBBIT BRAIN

RALPH L. HOLLOWAY

This Chapter is dedicated to the memory of Dr. Michael S. Yuan, who conceived this Festschrift, and whose untimely death in 2008 robbed many of us of a cherished friend, colleague, and scientist.

INTRODUCTION, LINES OF EVIDENCE

There are really four approaches toward understanding how the human brain evolved:

(1) comparative neuroanatomy, which can compare the brain structures, size differences, pathways, and neurochemistry between living, extant species, each of which is the terminal end product of their own line of evolutionary development. This approach is indispensable for understanding the relationships between behavioral and neural variations. As such this approach is *indirect*, because the animals compared are not evolutionary stages, but end products, each with a separate evolutionary history of variable time depth. For example, anthropologists and neuroscientists are often comparing present day chimpanzee brains with modern monkey and human brains, and the implicit assumption is that the chimpanzee of today is the same as the chimpanzee ancestor which split from the hominid line some 5-7 million years ago. Since we do not have a fossil record for the chimpanzee we cannot be sure that it hasn't undergone significant evolutionary change since 5-7 million years ago (see, for example, the papers of Rilling, 2006; Schoenemann, 2006; Semendeferi, this volume; Holloway, 2009).

(2) The second approach is paleoneurology, or the study of brain endocasts made from the crania of fossil animals, in particular, hominins from about 3-4 million years ago to the present. This is, at present, the only *di-*

rect evidence available for human brain evolution (see Holloway et al., 2004 and associated references).

(3) A newer approach, however, is developing which offers great promise for understanding human brain evolution, and that is the nascent field of molecular neurogenetics, which in time may be able to unravel the actual genetic/target tissue/behavioral changes that took place in the past.

(4) The fourth method is simple speculation, often derided as “just-so stories” that abound in both the scientific and lay press. Examples include cooling of the brain/radiator hypothesis; singing Neandertals, increased senses of humor to whet the selective and receptive appetite of females, throwing, tool-making, the need for high protein sources, the necessity for cooking meat, working memory, etc, etc. All of these, none of these, or some of these could be true, but behavior simply does not fossilize, and testing these ideas against either comparative, or paleoneurological evidence is extremely difficult if not practically impossible. Nevertheless, insofar as such speculations challenge us with more focused attention to variables involved, testable hypotheses can emerge, leading to further testing. Of course the fossil record is limited, but who is to say that we perceive all of what presently is available in all of its details and associations.

PALEONEUROLOGY: THE DIRECT EVIDENCE

What sorts of data can one retrieve from the paleoneurological approach? First, one needs to remember how poor the data is, as each endocast is simply a cast of the interior of a skull, and therefore not a brain, but rather an impression left on the internal table of bone

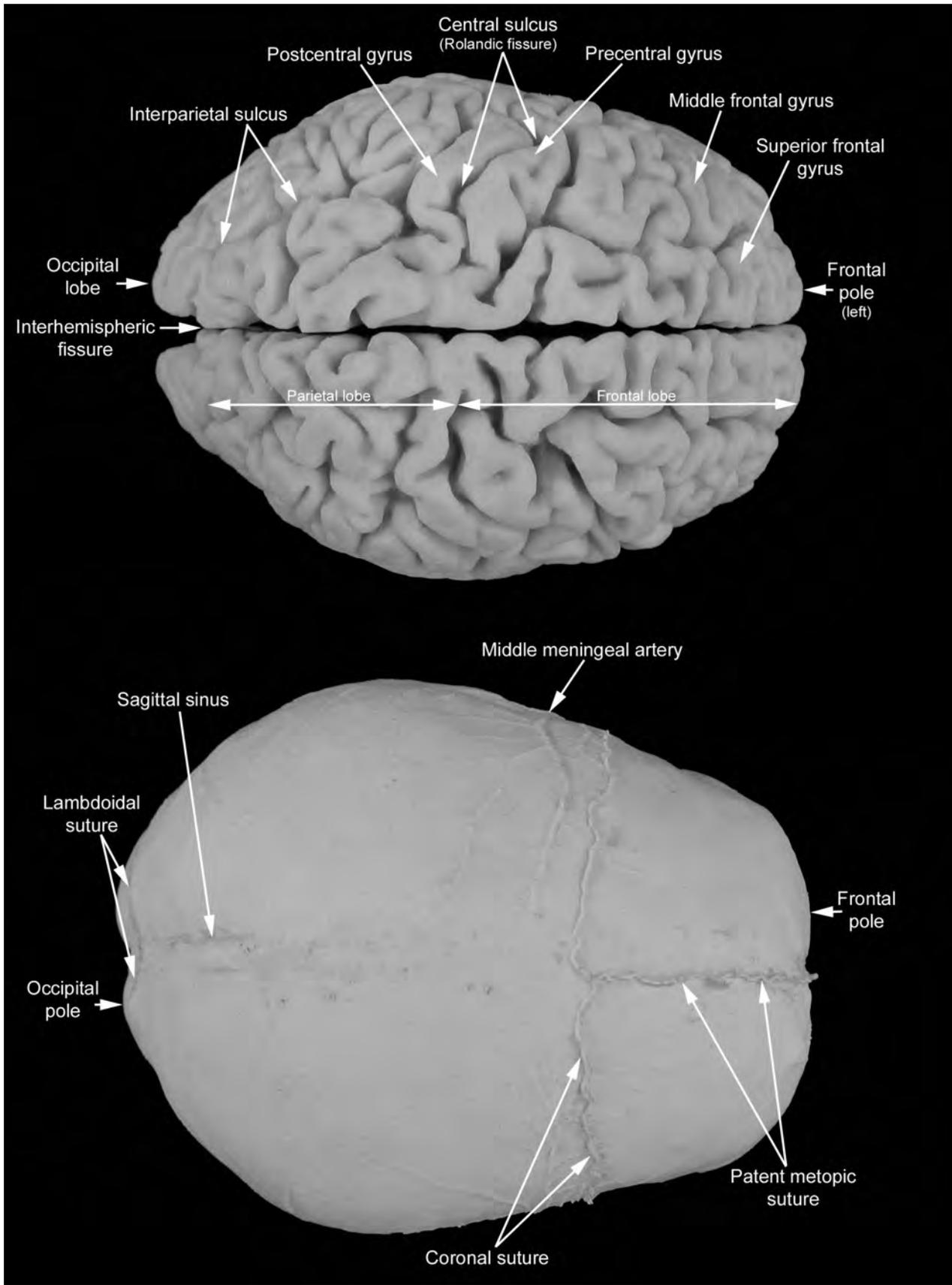


Figure 1. Dorsal view of an actual brain and the endocranium made from its cranium. Note how few, if any, convolucional details are retained on the endocranium.

meaning the outer layer of the dura mater, while the once living brain was covered by two additional menigeal tissues, arachnoid tissue (containing cerebral spinal fluid) and the pia mater, which invests itself on the cortical surface. All three meninges “conspire”, so to speak, against the complete and faithful impressions of the cerebral and cerebellar convolutions on the internal table of the skull.

Four different types of important data can be retrieved from endocasts:

(1) First, and probably most important, is the overall size (volume) of the endocast, which provides a close approximation to actual brain weight of the once throbbing living brain. The accuracy obtained will depend on the completeness of the cranial remains, the amount of distortion, and if based on CT scans, the density profiles used in defining edges and contrasts.

(2) Depending on how well some of the gyri and sulci are impressed through the dura mater, one can get some idea of the extent and form of the various cerebral lobes, i.e., prefrontal, frontal, parietal, temporal, and occipital, however controversial the interpretations. In general, the central sulcus which divides frontal and parietal lobes is seldom visible on hominin endocasts, except possibly in its most superior portion. The precentral sulcus is more frequently visible, but never in its full extent. Similar difficulties exist in defining the boundaries of parietal, temporal and occipital lobes since no cytoarchitectonic data is present, and one must use classical landmarks of neuroanatomical lobar divisions, which in addition to being arbitrary, are not plainly visible on endocasts. On the other hand, one can make out, albeit dimly, possible sulci and gyri such as superior and middle temporal gyri, lunate sulcus and inferior occipital sinus, retrocalcarine sulcus, supramarginal and angular gyri on the parietal lobe (although never completely), and while the Broca’s cap regions of the prefrontal lobe may show a morphology similar to that found in modern humans from *Homo erectus* on, it is rarely the case that the *pars opercularis*, *p. triangularis*, and *p. orbitalis* can be readily visualized.

(3) In humans, and those fossil hominins attributed to the genus *Homo*, one usually finds that the cerebral hemispheres are asymmetrical, and close correlations with handedness have been shown between the petalias (projections of either occipital and/or frontal lobes more to one side than the other.) Indeed, some of the fossils provide evidence of cerebral asymmetries from about 2 million years ago to the present. The prefrontal regions, which include Broca’s caps of the third inferior frontal convolution, including *pars opercularis*, *triangularis*, and *orbitalis*, are sometimes asymmetrical as in modern humans. These asymmetries suggest, through the assumption of homologous structure and function, that the basic human-like organization of the brain was established early in hominin evolution. In other words, if we know from studying modern humans through neuroanatomy, surgical procedures, PET, MRI, fMRI, and dissection, that handedness involves cerebral asymmetry and

specialization, and that Broca’s regions are involved in an important manner with language production, and we find these same appearances on say, Neandertal or *Homo erectus* endocasts, can we reasonably speculate that these hominids also had cerebral dominance and language behaviors similar, if not identical to our own? As to how old such asymmetries are is clouded by the more recent findings of asymmetries in chimpanzees. Asymmetries are of course found in many different animals.

(4) One can take numerous measurements on the endocasts, and using multivariate statistical procedures, attempt to show more objectively how endocast shape patterns vary between different hominin groups. These biometrical approaches are becoming standard in endocast descriptions as seen in the many articles by Bruner (this volume), Bruner and Holloway 2010, Grimaud-Hervé (this volume), and Wu et al (2010).. These approaches are needed to test preliminary qualitative observations regarding endocast morphologies and taxonomic differences, as well as evolutionary behavioral explanations. These are difficult as almost every single measurement taken is allometrically related to overall volume.

MOSAIC BRAIN EVOLUTION IN HOMININS

If both the data for brain size increases through time and key reorganizational features of the brain’s surface, such as petalias, asymmetries in Broca’s regions, a reduction in primary visual striate cortex, or area 17 of Brodmann are accurate, it is clear that the human brain underwent an evolutionary trajectory that **intercalated** size increases with organization changes, and that the evolution of the human brain was a complex mosaic affair, involving more than simple brain size increase and encephalization.

Even the australopithecines, the earliest hominins of 2-4 million years ago, show that despite their ape-sized brain volumes, they had a cortex reorganized toward a more human pattern, as evidenced by the appearance of the lunate sulcus in a more posterior position. However, their frontal lobes do not show Broca’s regions similar to what we find in *Homo*. Indeed, the earliest *Homo* is the famous KNM-ER 1470 specimen, which at a volume of 752 ml, shows clear-cut petalial asymmetries of the human pattern (left occipital/right frontal width) and Broca’s regions that are human-like in external morphology. This occurs at 1.8 to 2.0 million years ago. The size increases through evolutionary time are both allometrical and non-allometrical, the former being related to increased body sizes. But by 1.5 million years ago, as shown by the Nariokotome child skeleton from Turkana, Kenya, *Homo erectus* had a modern human body size, but a brain that appeared to vary between 750 and 900 ml. Any increase in brain size thereafter would be basically, non-allometric, i.e., unrelated to body size increase. Thus, the paleoneurological evidence is suggesting that selection pressures were surely varied over the course of hominin evolution. Selection for increased body size

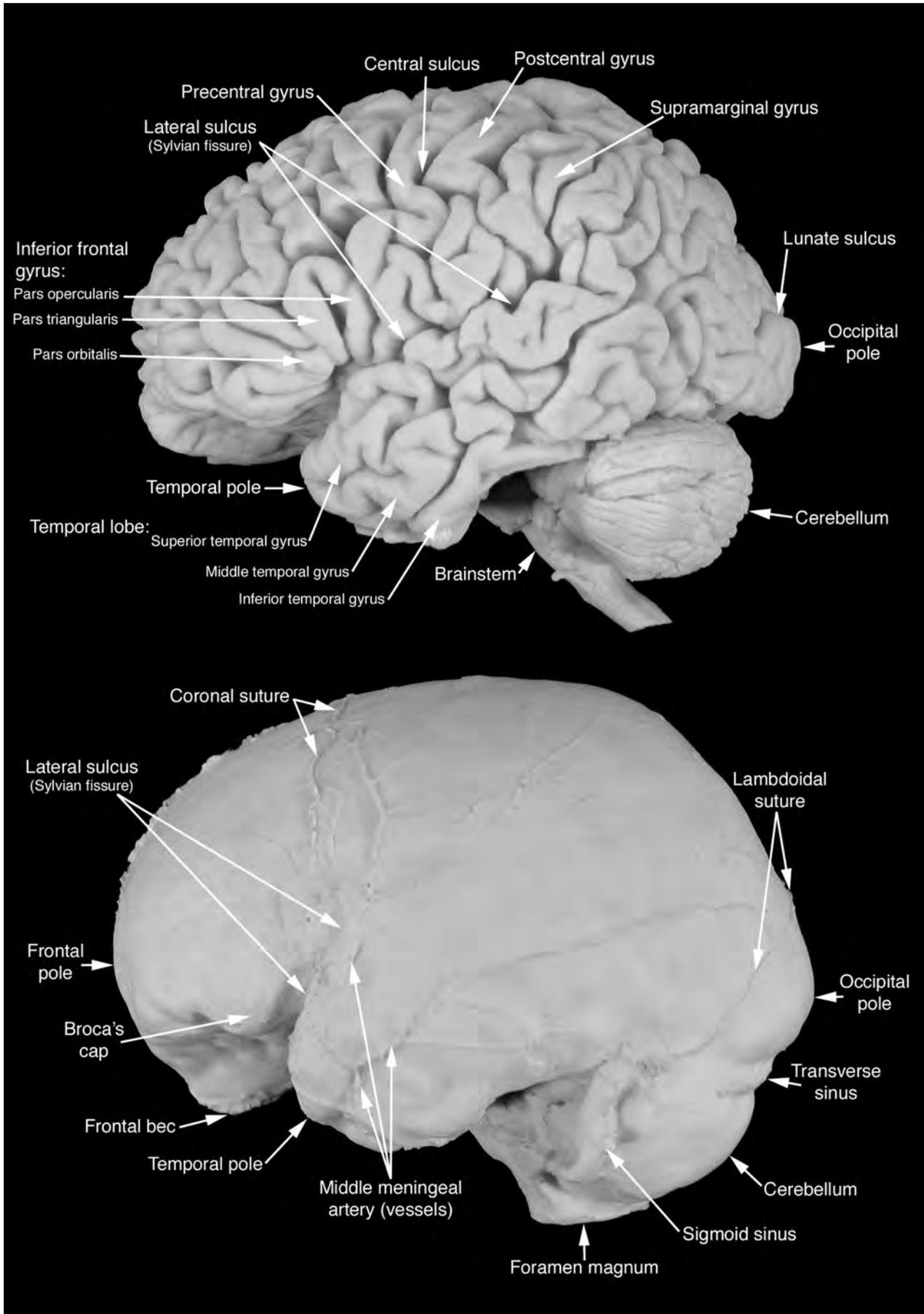


Figure 2. The left lateral surface of the brain and endocast

could have provided part of the increase in brain size in early hominin evolution, i.e., from *Australopithecus* to early *Homo*. Thereafter, and throughout the course of hominin evolution selection pressures for brain size increase, without attending body size increases were occurring, although it is possible that the Neandertals could be an exception, in that their body sizes (lean body mass) and adaptations to cold climates may have necessitated larger bodies, with a concomitant increase in brain volume, as their average slightly surpasses our own volume. (See Bruner, this volume, for biometric analyses showing differential size changes in frontal and parietal lobes; see also Tables 1, 2, & 3 in Chapter 1.)

SOME ONGOING ISSUES IN PALEONEUROLOGY

Seduction by Laser Scanning, or the Demotion of the Taung Endocast's Size

Falk and Clarke (2007) have a recent technical paper in which, by using laser scanning of a replica of the Taung endocast they attempted to place a mirror image of the right side on the left, and came up with a resulting 382 cc endocast volume, considerably less than my previously water displacement 404 cc version (Holloway 1970).

Such a technique of course requires the assumption of perfect symmetry of the two cerebral sides, and the careful definition of a true midline. Neither of these two requisites appears in their paper. Instead, a mirror image of the right side is imposed onto the missing left side with delineating and describing a midline. What is more, their figure of the dorsal surface of the Taung endocast shows that the left and right sides are asymmetrical! (See Fig. 1) As pointed out in the Holloway 1970 paper, a slice of Taung endocast 1 mm in thickness would result in only 7 cc of volume, and it doubtful the definition of the midline in that paper was off by more than a mm.

The main advantages of laser (and CT) scanning of crania, or endocasts as in the above case, is that the methods are non-invasive, and depending on the skills of the investigators, can correct more easily for distortions and missing portions, than one can with plasticene. Still, the results depend heavily on the techniques used and the skill and understanding of brain and cranial anatomy on the part of the investigators. The history of the various volume estimates of Taung, STS 71 (Conroy et al. 1998, 2000; Holloway 1970, 1972, 1973, 1983, 1999; Holloway et al. 2004), and Stw505 as well as the Hobbit LB1, *H. floresiensis* (see below), suggests that my previous volumes were correct after all (see Holloway et al. 2004).

The Hobbit Brain

The major argument existing today is whether or not the brain of the hobbit (based on a single cranium, LB1) is that of a pathological microcephalic (primary, secondary, or yet unknown), or a true non-pathological species

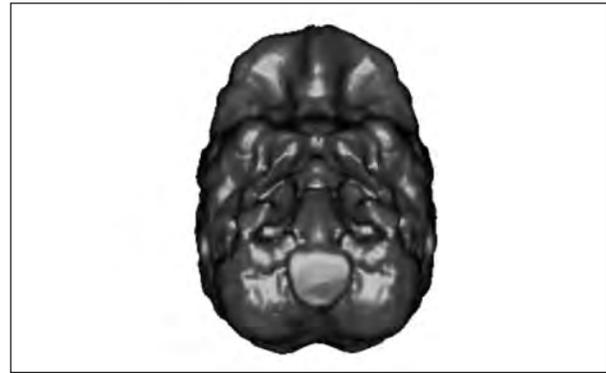


Fig.3 Basal and dorsal views of the Falk and Clarke (2007) mirror image technique applied to Taung. Note that the left and right sides are not symmetrical. (After Falk and Clarke, 2007)

that evolved through some unknown process of island dwarfing. There is a third possibility which is that the brain of the hobbit shows pathology unlike the pathological appearance that one sees in cases of primary or secondary microcephaly, and that these are not recognized because the full range of variation in the broader condition known as “microcephaly” hasn’t been thoroughly studied. Indeed, finding a large sample of these individuals either illustrated or measured hasn’t yet happened. Falk and her colleagues believe the brain is simply that of a new species (Falk et al. 2005, 2007, 2009), probably derived from some earlier *Homo erectus* ancestor (indeed *Australopithecus* is now also in the running) that underwent dwarfing, but was otherwise normal, and not pathological. Martin and his colleagues (Martin et al. 2006), and Henneberg & Thorne (2004) regard the hobbit as severely pathological, the pathology involving not just the brain, but the entire skeleton. A recent entire issue of the *Journal of Human Evolution* has been devoted to showing that this hominin is not pathological.

My own opinion (Holloway et al. 2006) is that more fence straddling is prudent, even if I am only hanging by an ankle. I do agree with Falk and her colleagues that the LB1 endocast does not look like any cases of primary microcephaly found in modern populations that have yet been published or presented, and this includes the Indian microcephalic presented by Martin. I come to this conclusion after having made endocasts of several microcephalics (primary and secondary) from the Pathology collection of the University of Michigan, through the kindness of Dr. Milford Wolpoff, and from Gary Sawyer and Dr. Ian Tattersall from the American Museum of Natural History, two from the Museum of Comparative Zoology, courtesy of Dr. Dan Lieberman, and one intriguing Indian microcephalic from India that Dr. Robert Martin and Dr. Susan MacLarnon sent me. Finally, I have one endocast sent to me by Dr. Dominique Grimaud-Hervé from Paris of a case of Seckel’s (“Bird-headed Dwarf”) microcephaly. Some of these were shown to the audience in Alaska during my AAPA April,

2006 presentation. Aside from the two cases of Seckel's Syndrome and the Indian microcephalic, all of the primary microcephalic endocasts I have seen and studied have relatively enlarged cerebellar lobes compared to their diminutive cerebral cortices. The secondary cases, with larger brain volumes do not show cerebellar protrusion, nor do the overwhelming majority of 198 cases of ape endocasts (Holloway et al. 2010) thus ruling out protruding cerebellar lobes as a derived feature in LB1 (Falk et al. 2009). None, however, show the extreme degree of platycephaly (flattening of the brain) that occurs in LB1. Furthermore, none show the extremely protuberant and narrow prefrontal gyri (recti) which are so striking on LB1, and which I regard as a possible pathology, perhaps akin to microgyria, in which 4 rather than the normal 6 layers of the cortex develop. Additionally, no microcephalic I have seen shows the peculiar spreading of the cerebellar lobes that one sees on the hobbit brain cast, or the peculiar trigonal-shaped eminence on the dorsal surface of the brain stem, which cannot be a blood sinus feature.

Discussions with neurologists, pediatric and otherwise appear to confirm that this trigonal structure doesn't appear in modern human brains, so one is tempted to regard this as an autapomorphy. Much more study is required here (see Figures 4-6, and Table 1 of possible hypotheses). It is best to remember that the full range of variability in external appearances of microcephalic brains (particularly secondary forms) has not been studied, and the possible pathologies I am suggesting remain a possibility in LB1, however unlikely these are viewed at present.

This particular hominin provides also a window on aspects of scientific cooperation in studying these remains. To date, only Falk and her colleagues have provided a study of the endocast using CT scanning where descriptions of exact procedures and smoothing techniques are not available. I have personally tried, since the first description of this find to obtain the CT scan data for an independent assessment of the endocast, and am delighted to have recently obtained the original CT scan data from Dr. Michael Morwood. While this older, now redundant CT scan that has been replaced by a more recent micro-CT scan, the scan data show very clearly that the original endocast required considerable reconstruction, and that the endocast I received from Dr. Peter Brown, and those I made from the stereolith, match exactly the older scan data.

These data show that the right temporal lobe was severely displaced laterally and inferiorly, and that the left temporal lobe was not distorted, and appears relatively small, at least to my eye, which is not in agreement with Falk et al. (2009) claim regarding it as a derived character state in *Homo floresiensis*. Aside from the prominent, but very thin *gyri recti* of the prefrontal lobe, this part of the frontal lobe also appears relatively small to me (see Fig. 7).



Figure 4. Lateral view of a typical case of primary microcephaly. Notice, in particular, the relatively large appearance of the cerebellar lobes relative to the cerebral cortex. (Figures 4-6 are from pictures taken at the 2006 American Association of Physical Anthropologists annual meeting)

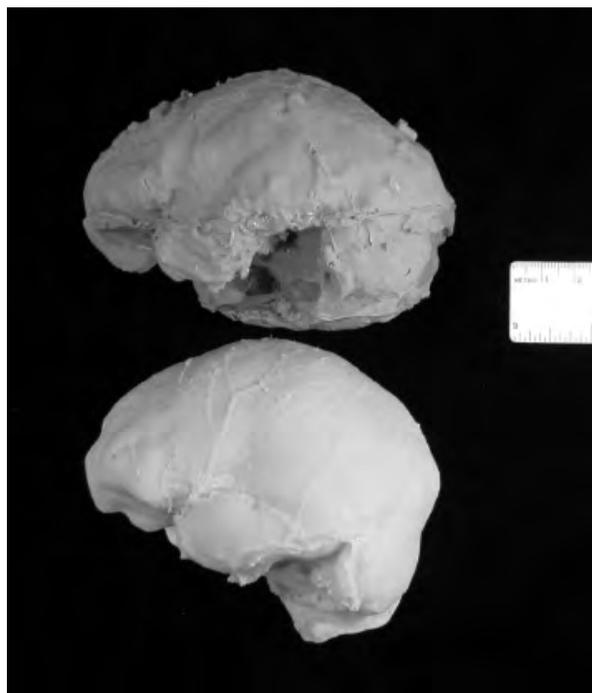


Figure 5. The top endocast is the left lateral view of the LB1 endocast (as resulting from original CT scan data), and the bottom picture is that of an Indian microcephalic with the same brain size. In this case the cerebellar lobes of the microcephalic appear almost normal in relative size, but the height of the endocast is quite different from that of LB1.

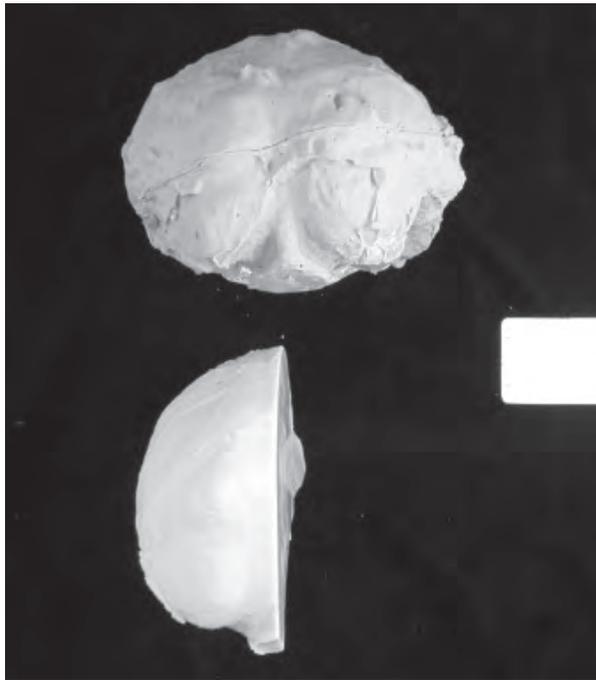


Figure 6. Occipital views of both endocasts. Note that the platycephaly so evident on the LB1 (top) endocast is not present on the microcephalic endocast. Notice also the trigonal eminence between the cerebellar lobes of LB1.

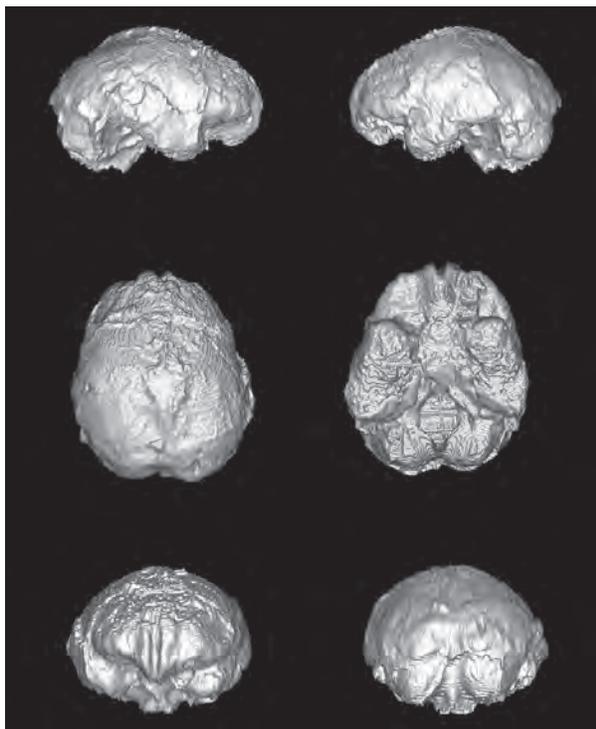


Figure 7. Six standard views of the LB1 endocast segmented using ITK-SNAP, Version 2.0, from the CT scan data, which I received from Michael Morwood and his Indonesian colleagues. These are un-smoothed, and show in particular, the damage to the right temporal lobe.

Table 1 below provides a humorous summary of the possible interpretations of the LB1 hobbit.

Table 1.

IDENTITY CRISIS

- If it's Monday, LB1 must be: **a microcephalic**
- If it's Tuesday, LB1 must be: **a new species, *Homo floresiensis***
- If it's Wednesday, LB1 must be: **a sex slave...**
- If it's Thursday, LB1 must be: **all of the above...**
- If it's Friday, LB1 must be: **an alien from another galaxy**
- If it's Saturday, LB1 must be: **a derived form of australopithecine**
- If it's Sunday, LB1 must be: **an endemic dwarfed form derived from *Homo erectus***
- (Fortunately the "intelligent designer" only had 7 days)

The Political Correctness Angle or the 800-pound gorilla in the room...

Political correctness within biological anthropology, at least as far as the nervous system is concerned, involves the notion that the human species may very well vary from the top of the head down to the toes, but not in the brain, or if the latter is true, the variations are without any behavioral importance. To realize otherwise might lead down the slippery slope of racist history and racism. We know that this is very unlikely, that human groups do have variability in terms of brain size, although we know very little if anything about whether biological populations differ in how their brains are organized (However, see Klekamp et al. 1994 regarding Australian Aboriginal striate cortex volumes). It would surely be an amazing instance of genetic conservatism if all of the thousands of regulatory and structural genes related to the brain and its growth and development were the same in every population. We know considerably more about sex differences in the brain, and to suppose that these differences did not arise through evolutionary selection pressures for aspects of social behavior, or have no genetic basis is just silly in my opinion. It is strange to read so many accounts of how we became smarter and smarter during our evolution when our brains became larger, but such variation in modern human groups has absolutely no behavioral significance today. It is equally strange to talk about how the human sexes are complementary to each other in terms of child care, learning, and subsistence, but then insist that no hard-wired differences in the brain exist between the sexes, when dozens of articles in neuroscience journals indicate otherwise. How else could they have arisen? It would be more accurate to say that the differences in brain size among human populations today, while perhaps statistically significant, are a rather small difference compared to the 1000 ml increase that occurred during hominid evolution over the last 2-3 million years. As to whether or not there are significant behavioral differences, such as IQ, or other cognitive tests,

raises many difficult methodological and moral issues, which combined with an almost species-specific bent toward PC discourages most, if not all investigations into modern human brain variation, despite excellent studies showing maturational, white fiber matter differences throughout the brain (see for example, Rushton and Ankney, 2007, 2009, for a review that might receive rebuke from many social scientists, but yet remains disproven). Perhaps, in the future, as molecular neurogenetics becomes more advanced, we might know more about how the human brain varies, and how such variation relates to behavior, within a cultural context (in particular, nutrition and diet, disease and parasite vectors), and how and why such differences, however minor, evolved. In my opinion, without a fuller knowledge of how the human species' brain varies, it is extremely difficult, if not impossible, to know how the human brain really evolved. I believe we can only benefit, both medically and scientifically, from knowing more about how we vary as a species.

As I have said to my classes many times, human variation is one of the best things we possess as a species, and should be treasured and celebrated, not feared. (Holloway 2008).

ACKNOWLEDGEMENTS

Needless to say, I am very grateful to the Editors of this volume, and to all of the authors who have honored me with their chapters, friendship, and collegiality. I hope our collaboration toward understanding how the human brain evolved will continue well into the future!

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