PART TWO

METHODS AND MATERIALS OF ENDOCAST ANALYSIS

The methods employed to study endocasts will naturally vary depending on the nature of the fossil remains. In the most general terms we attempt to bring the hominid specimen's brain cast back to a state that would be essentially an immediate postmortem one, namely to correct for any distortion and/or missing parts of the endocast. As the degree of completeness and distortion of the original natural or human-made endocasts vary, so do the methods for attempting to obtain the most accurate and reliable reconstruction. This chapter discusses some of the possible ways of achieving these ends.

TOTAL ENDOCRANIAL BRAIN VOLUME

Natural endocasts, for example, those known from South Africa, are seldom distorted, except for the obvious cases of type II and III from Sterkfontein. Taung, Sts 60, and SK 1585 are relatively complete. They were first molded using either latex rubber or silicone-based polymer substances, so that casts, usually of plaster of paris or dental stone, could be used to either add missing parts or carve away projecting adherent matrix (e.g., in the cerebellar-temporal cleft in the Taung specimen). The parts to be added are usually done with modeling clay or plasticene, and the worker tries to follow the missing regions as best as one can. If one side is complete, the requisite amount of plasticene can be added to the missing portions of the other side. When this is done, one must assume complete symmetry in the reconstructed portions.

In the case of cranial portions without natural endocasts, the internal table of bone is first usually carefully cleaned and then treated with a penetrant/coating substance, such as Butvar (polyvinyl butyral) or polyvinyl acetate. A mold is next usually made from the cleaned cranial portion. This may be done in pieces because of undercut problems, or as one section that must somehow be stabilized dimensionally. This mold may itself be used as a working cast, usually of plaster, and provide the base for the reconstruction. Alternatively, the reconstruction can proceed directly from the first mold. It stands to reason that the closer the cast is to the original, the more accurate the final product. (See Holloway et al., 2002 regarding the problems of using multiple generations of casts on the omo 3384-6 specimen.)

The resulting reconstruction is often sprayed with a waterproofing substance to prevent a potential misreading when the reconstruction is submerged in water from water penetrating the little cracks and fissures in the plaster surface. We are currently using polyurethane for this purpose, though other methods may be used. In addition, if the reconstruction is fitted onto the rubber or silicone cast, it is recommended that the inside of the cast be heavy enough so that the resulting reconstruction will readily sink when submerged in water.

The actual measurement of volume relies mostly on Archimedes' principle, which states that when a body is completely submerged in a fluid, the fluid exerts an upward force on the body equal in magnitude to the weight of the fluid displaced by the body. Given that water has a specific gravity of 1.0, the weight of the water displaced will be the same as the volume of the object submerged. When RLH first started working in South Africa, Kenya, and Indonesia, graduated beakers or cylinders were most often available, and these were often calibrated in intervals of roughly 10 to 20 ml. Thus a beaker would be filled to a certain level with water, the endocast submerged, and the old level subtracted from the new level. We personally find this method not only cumbersome but potentially inaccurate, as one must accept whatever intervals are available and constantly worry about water tension causing the meniscus to adhere to the inside of the beaker or cylinder.

Another way of measuring the displaced water is to fill a beaker at least twice as large as the endocast, and catch the run-off water through a spout into another beaker while the endocast is submerged. This run-off water is then weighed, and the beaker's weight subtracted from the total weight (Fig. 11). Alternatively, one can pour the displaced water into another cylinder calibrated in small intervals of 1 to 10 ml.

Most of our measurements are done using a balance scale to weigh the displaced water. We have modified a variety of different size beakers with a run-off spout that is inserted into the neck of the beaker through a drilled hole. The spout is then flexed so that it runs down the inside of the beaker to the base of the container. The modified beakers are filled to capacity, the excess water is allowed to run off until the final drip through the spout, and the endocast is slowly submerged, at the same time collecting the displaced water into a pre-weighed dry beaker. This procedure is repeated three to five times, and the mean weight is used to give a mean volume. Another method directly using Archimedes' principle is to weigh the reconstructed endocast in air and then

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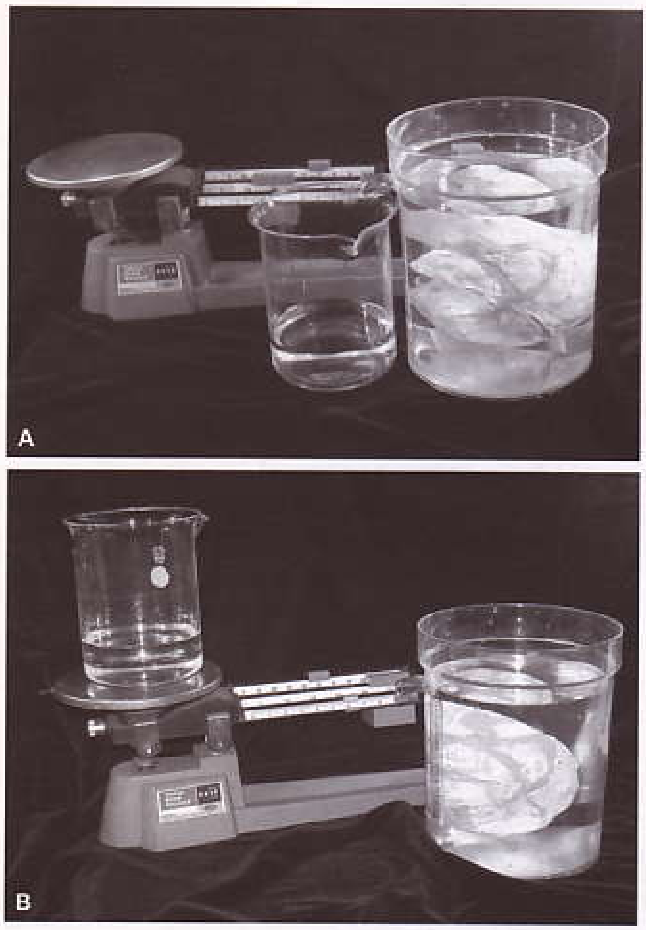


Figure 11. Demonstration of endocast volumetric estimation method, using water displacement. **A**: Endocast is submerged in a large beaker filled to the overflow outlet, and the displaced water is captured in a beaker of known weight. **B**: The beaker holding the displaced water is weighed, giving the weight/volume of the endocast.

weigh it in water. The difference should be the volume of the endocast.

Accurate and reliable measurements require nonporous endocast materials, clean glassware, clean (preferably distilled) water, and accurate balances and weights. It is always distressing to watch bubbles arise due to improper or incomplete coating of the more porous portions of the endocast, but such are the dangers inherent in paleoneurology.

Partial Brain Endocast Volumes

It is often the case that the available cranial portions are too incomplete to allow a reliable total reconstruction of the missing parts, as the missing parts exceed what is present. Tobias and Hughes (see, in particular, Tobias, 1991) ran into this problem when attempting to find the endocranial volume of OH 7, and Holloway (1972) had similar problems in attempting to find total endocranial volumes for the Makapansgat specimens of the MLD 1 occipital portion and the Sts 19 cranial base portion. In these situations one tries to ascertain what percentage of the total volume is represented in a portion of an endocast. In doing this with a variety of taxa, one hopes to arrive at a percentage figure that is fairly tightly distributed. Tobias's (1991) discussions regarding the biparietal tunnel of OH 7 provide a detailed description of how this done. *(We wish to add, parenthetically, that more useful work could be done in this area, both to expand the available databases for future discoveries and to re-check earlier estimates.)*

Endocast Volume Reliability

In the Volume and Method section of each entry in this volume we give our assessment of the reliability of a given endocast volume. The reliability is scored according to method (letter designation) and our evaluation of the given volume (numerical designation). The endocast volumes given here were obtained via one of four methods: (1) direct water displacement of either a full or a hemiendocast with minimal distortion and plasticene reconstruction, (2) determination using a partial endocast as described by Tobias (1967, 1971) and Holloway (1970), (3) extensive plasticene reconstruction amounting to half of the total endocast, and (4) volume calculated from regression formula or estimated on the basis of a few measurements, which are then plugged into formulas such that offered by MacKinnon et al. (1956):

$$V = f[0.5(LWB + LWH)]$$

Here L is maximum length, W is width, B is length from bregma to the posterior limit of the cerebellum, H is the height from the vertex to the deepest part of the temporal lobe, and f is the taxon specific coefficient; X refers to previously published values that have either been confirmed by us or, in certain cases, not. In addition to the endocast method scores, each endocast is scored numerically to indicate our assessment of the reliability of the given volume. These reliability values are evaluated on a scale of 1 to 3 where 1 indicates the highest reliability, 2 that the given volume is generally reliable, and 3 that the given volume has low reliability and should be reassessed.

Brain Endocast Volumes by Formula

As with any physical object, there are relationships between the volume and the linear measurements that describe the object. Brain endocasts are largely ovoid in shape, sometimes approaching an almost spherical shape, and these relationships can be expressed mathematically, the most obvious being through the radius, diameter, or circumference of the object. Physical anthropology has a long history of using measurements to calculate brain weights and volumes (Pearl, 1905; Isserlis, 1914; MacKinnon et al., 1956; Buda et al., 1975; Sgouros et al., 1999). With the development of multivariate techniques, particularly multiple regressions, one hopes that the volume of an object with a somewhat irregular shape such as a hominid brain endocast can be approximated by a few measurements.

RLH (Holloway 1975, 1976, 1978) made a number of attempts to secure formulas that might allow for accurate predictions of endocranial volumes using a few linear chord and arc measurements over the endocast surface. Indeed, the Holloway (1986) description of the Hadar AL 162-28 specimen relied on a prediction made from the biasterionic breadth, based on an extensive collection of ape and hominid (including modern humans) endocasts that RLH made in his laboratory. The proper use of such statistics, however, depends on the sample size and on previous testing for residual values. Considerably more analyses of endocranial measurements should be carried out in the future, and we are providing as many measurements as seem feasible for researchers wishing to explore the predictive merits of our measurements.

ASYMMETRY OBSERVATIONS AND MEASURES

Left-Right Petalias

With the publications of LeMay (1976; Galaburda et al., 1978), it became known that there are high correlations between handedness and different patterns of petalias in human brains. The relationship is clearly correlational and not obligate. The petalias most likely represent slightly different velocities of growth of the two cerebral hemispheres, with two regions in particular appearing to be affected: (1) the occipital lobe in both its posterior projection and width and (2) the frontal lobe in terms of its width (Fig. 12). In general, when there is a combination of both left-occipital projection and right frontal width, the growth torque is correlated highly (ca. 90%) with right-handedness (LeMay, 1976).

In our study of over 100 pongid brain endocasts, Holloway and de Lacoste (1982) did not find this growth torque pattern of petalias to be present in apes, but the pattern did appear in hominids and modern *Homo sapiens*. To be sure, some individual pongid brain endocasts show asymmetries. Particularly endocasts of *Gorilla* are well known for their cranial asymmetries (Groves and Humphrey, 1973), but these asymmetries are seldom if ever in combination as in humans. Since we know that human cerebral hemispheres are somewhat specialized for different tasks, we must consider the possibility that petalias in hominids might reflect similar cognitive specializations/organizations as in modern humans. This is where uniformitarianism leads one. Needless to say, only time machines and behavioral testing aboard them of willing hominids can prove such assertions.

The petalial asymmetries mentioned are most readily observable from the dorsal view of the endocast, and to date the data have been ordinal in value (i.e., whether or not there is a right or left occipital petalia, and a right or left frontal one). These judgments can, on rare occasions, be somewhat difficult to make, depending on the orientation and placement of the occipital pole on the endocast. In one dorsal orientation there may be a petalia on one side that changes when the endocast is rotated up or down. This sometimes occurs because the true occipital pole on one side is shifted or forced downward by the sagittal sinus leading into the transverse sinus or other mechanical agency. Usually, however, the greater width of the occipital region on one side (most frequently the left) helps resolve this problem.

The frontal width is also an ordinal observation, and is often less obvious and thus more difficult to score, than for the occipital petalias. Furthermore it is made taking the frontal lobe as a whole into consideration, and not simply the region of the third inferior frontal convolution or the Broca's cap region (see below). We have not yet finished our analyses of quantifying these petalias, but the work is in progress. It is also sometimes the case that the right frontal *pole* is more anteriorly protruding, and thus any measurement of the frontal-occipital poles' length will not really reflect the petalial pattern. More work in this area is clearly needed.

Asymmetries of the Broca's Cap Region

The literature on asymmetries of the Broca's cap region, namely the *pars triangularis*, *pars orbitalis*, and *pars opercularis* (Brodmann's areas 45, 44, and 47) in modern human brains (Amunts, 1999, 2003; Foundas et al., 1995, 1996), suggests that in right-handed subjects the left Broca's cap region, particularly in area 45, is larger than the right, this based on both histological sectioning and MRI studies. It is, of course, very true that language behavior, and even motor control of vocalization,

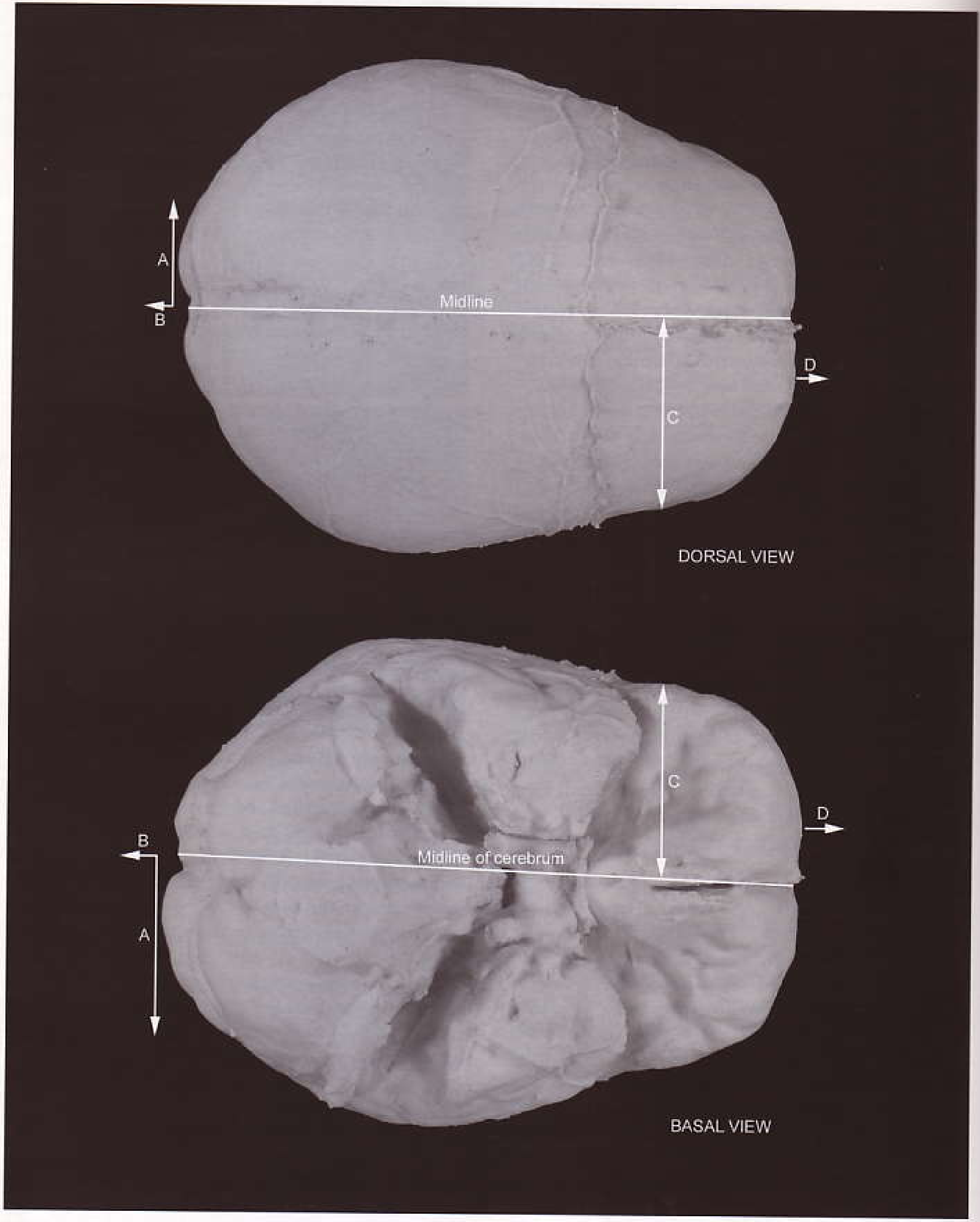


Figure 12. Modern human endocast demonstrating petalias. An occipital petalia is indicated by one occipital lobe being (**A**) wider and/or (**B**) protruding posteriorly beyond the contralateral lobe. A frontal petalia is determined by one frontal lobe being (**C**) wider and/or (**D**) protruding anteriorly beyond the contralateral lobe.

are complex functions, and other brain regions, such as the cerebellum, and striatum, have involvement in complex cognitive processes such as the use of symbol systems for verbal communication. No one believes that "language" can be strictly localized to the left Brocas's cap region, but few would deny the involvement of that region in such behavior, as Paul Broca demonstrated more than a century ago.

It is therefore interesting to observe that the brain endocasts of our sample of modern humans shows a consistent pattern whereby the left Broca's cap region appears more laterally projecting than the right. We also note asymmetries of this region in some of our fossil hominid ancestors, and describe them here. We are prone to believe that these signal possible functional attributes relative to language processing in the hominids displaying these asymmetries. Again, we need that time machine to resolve this issue.

REGIONAL CONVOLUTIONAL DETAILS

Detailed convolutional patterns are by far the most difficult part of endocast studies, given the conspiracies of nature and dural tissues which "hide" the gyri and sulci of the once-pulsating cerebral cortex. In addition the sheer degree of variability that exists in higher primates with regard to sulcal morphology, which varies from one hemisphere to another and between individuals, makes the process more difficult. Even monozygotic twins show some degree of variation (Thompson et al., 2001). The secondary and tertiary convolutions are often impossible to discern without ambiguity, and the difficulties are compounded by the fact that different workers have used different terminologies throughout the history of neurological studies. We rely heavily on two publications in particular: Connolly's (1950) *External Morphology of the Primate Brain*, and Shantha and Manocha's (1969) contribution to the first volume of *The Chimpanzee*, edited by G. H. Bourne. There is no good objective way of following these almost hidden morphologies, but to sit with endocast in hand and compare the slight indentations to the illustrations of convolutions of modern human brains or that of the chimpanzee and try to find the most anatomically reasonable identification. This has been likened to "paleophrenology" by Jerison (1976), and that sometimes is not too far off the mark, except that it IS the morphology we seek and not the functions first! We doubt that our procedures are any different than those used by Schepers (1946, 1950), Smith (1928), Keith (1931), Symington (1916), or Clark et al. (1936) to mention but a few examples.

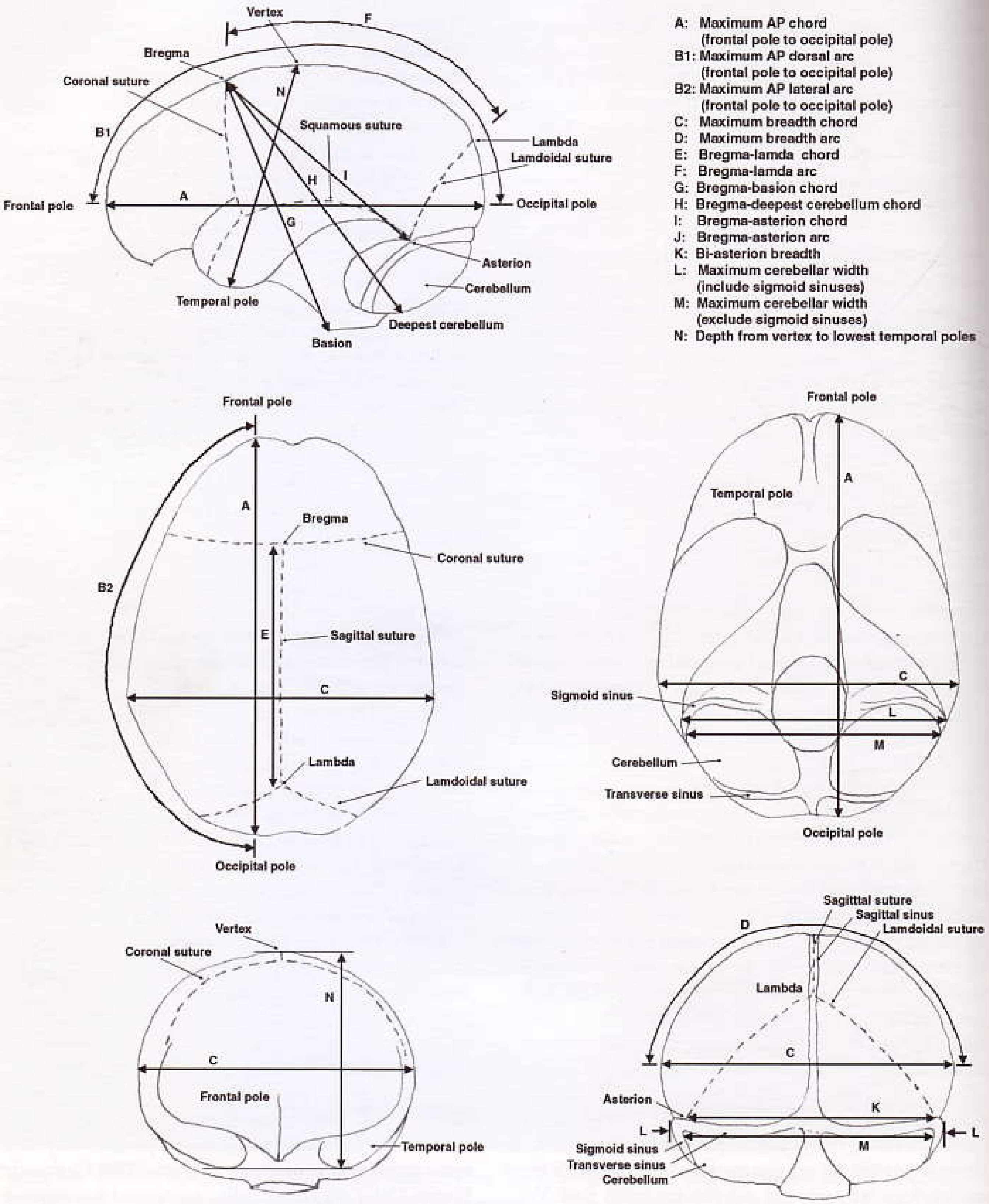
There are two regions, in particular, that we examine closely, as these have important relationship to matters of reorganization of the hominid brain: (1) the primary visual striate cortex (PVC) with the reduction of its lateral and dorsal extent on the occipital lobe and (2) the third inferior frontal convolution containing Broca's region with its developing complexity.

With regard to the former, we know from comparative primate quantitative volumetric data that the human PVC is some 121% less than expected for a primate of its brain weight (Holloway, 1997, 2000; Holloway et al., 2001), and we also know that in all pongids yet studied the PVC is anteriorly constrained by the lunate sulcus (Holloway et al., 2003; see also Holloway, 1985, for the history of these arguments). This landmark, when present in humans, is in a very posterior position, and even when not present, the PVC is a small portion of the occipital lobe. The contrast with pongids is indisputable. The question then becomes, When in evolutionary time and history did the PVC become reduced into a more human pattern? This controversy rests at the very base of our understanding of how hominid brains evolved.

Similarly, given the importance of Broca's cap regions to the motor aspects of language, we look at this region with the goal of trying to understand the homologies between hominid brain endocasts and the brains modern humans. To that end, we use the standard terminology of Brodmann's (1909) cytoarchitectonic areas as ordinal numbers to describe particular brain surface regions of the once underlying cerebral cortex, such as areas 44, 45, and 47 of the third inferior frontal convolution that make up Broca's areas. When we refer to Broca's cap, a term introduced by Anthony back in 1913 when describing the La Quina brain endocast, we are referring to the lateral and inferior bulging of that region in general. The "cap" includes areas 45 and 47, and a portion of area 44.

MENINGEAL PATTERNS

Meningeal patterns have no particular behavioral functional significance, except as servicing the dura mater and internal table of bone. Since their patterns may have some taxonomic consistency (Saban, 1984; Grimaud-Hervé, 1997), we are including meningeal descriptions in this volume. Our descriptions are short, and we are grateful that Dr. Grimaud-Hervé has provided a



A: Maximum AP chord (frontal pole to occipital pole)
B1: Maximum AP dorsal arc (frontal pole to occipital pole)
B2: Maximum AP lateral arc (frontal pole to occipital pole)
C: Maximum breadth chord
D: Maximum breadth arc
E: Bregma-lamda chord
F: Bregma-lamda arc
G: Bregma-basion chord
H: Bregma-deepest cerebellum chord
I: Bregma-asterion chord
J: Bregma-asterion arc
K: Bi-asterion breadth
L: Maximum cerebellar width (include sigmoid sinuses)
M: Maximum cerebellar width (exclude sigmoid sinuses)
N: Depth from vertex to lowest temporal poles

Figure 13. Endocast measurements.

chapter (see Part 5) on this topic using from her monograph the line drawn by her husband, Dr. Pascal Hervé.

MORPHOMETRIC ANALYSES

We employ both chord and arc measurements of the endocast's surface in our descriptions (Fig. 13). Whenever possible, we report both left and right sides. For regression analyses, we use the average of left and right sides, or whichever side is most reliable. When we report a measurement preceded by a *ca* (circa), it represents an approximation. We use this convention for those measurements that span regions of Plasticine reconstruction.

Length, breadth (width), bregma-basion, and height measurements are taken with spreading calipers. The height measurement is the maximum height from vertex to the lowest projection of the temporal lobes in the midsagittal plane. This measurement is taken by stretching the tape over the deepest temporal lobe region, and simultaneously placing the spreading caliper ends on the tape and the vertex of the endocast when oriented in a plane through frontal and occipital poles. The bregma-lambda, biasterionic, and bregma-asterion measures are taken with sliding calipers. All arc measurements are taken with calibrated tape. The frontal and occipital poles, as well as points of maximum breadth, are first marked on the endocast surface with pencil and the measurement taken between the appropriate points. The lateral and dorsal length arcs, between the frontal and occipital poles, are placed over whatever regions of maximum convexity are located between the poles, but in a straight manner. The maximum width, almost always on the posterior part of the superior temporal gyrus, is also marked with pencil, and measured with spreading calipers; the arc width is taken with flexible tape between those points over the vertex. The biasterionic breadth is taken as a chord measurement between left and right asterion, when available. We also have included a lateral arc between these points for which the tape is placed across the transverse sinuses or superior cerebellar lobes. The dorsal arc generally follows the dorsal curvature in the region of the lambdoid suture but is, at best, an approximation only. The maximum cerebellar width is taken medially to the widest part of the sigmoid sinuses when present, while sigmoid sinus width measures the breadth across the widest lateral portions of the sigmoid sinus.

Many other measurements can be taken, as one can see from Weidenreich's (e.g., 1943) papers, Kochetkova's (1978) book, or Grimaud-Herve's (1997) monograph, based on chords and arcs from scaled drawings and projected drawings and tracings. All of our measurements are from the original endocasts and have been selected to pursue the possibility of generating predictive equations that might be useful in studying future partial endocasts. The hope is that combinations of arc and chord measurements will provide rough measures of shape and size relationships useful for prediction of endocranial volumes, either from complete or incomplete endocasts. In order to do so, we have a comparative database of approximately 120+ brain endocasts of pongids (approximately 30–40 brain endocasts each for *Pan paniscus*, *P. troglodytes*, and *Gorilla gorilla*). In addition we have approximately 10 to 15 brain endocasts of modern *Homo sapiens* made by RLH from the crania in his osteological collection at the Department of Anthropology of Columbia University.

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PART THREE

ENDOCASTS OF EARLY HOMINIDS

PART SIX

HOMINID ENDOCASTS: SOME GENERAL NOTES

MOSAIC EVOLUTION

Clearly, the evolution of the hominid brain has been a mosaic affair, at times punctuated, at other times gradual, with allometric and nonallometric brain size increases, interspersed (or interdigitated) with episodes of reorganization of the brain's nuclei, fiber tracts and lobes (see Tables 1–2, Part I for a summary). We cannot know directly about much of the latter changes, particularly when they occur at the subcortical level. We must assume that the changes occurred during the evolution from an ape-like precursor, whose neuroanatomical relationships were somewhat similar to those of extant chimpanzees and gorillas. However, it is always imperative to remember that extant apes have their own individual lines of evolutionary development from time periods most probably situated within the last 5 to 10 million years. And while it is certainly true that the major external phenotypic effect we can witness from the treasures of the fossil record is an increase in brain size, the actual processes must surely have been much richer.

The earliest evidence bearing on this mosaic evolution comes from the australopithecines from 3 to 4 MYA and, in particular, from *A. afarensis*. As fascinating as recent finds such as *Sahelanthropus tchadensis, Kenyanthropus platyops, Ardipithecus ramidus, Australopithecus anamensis*, or *Orrorin tugenensis* might be, these discoveries simply do not provide enough cranial material to allow an accurate determination of relationships with each other to ascertain which was the true stem ancestor to the hominid line eventually giving rise to *Australopithecus* and later *Homo*. We assume that the cranial capacity of such an ancestral group was in the size range of 300 to 400 ml, while the brain itself probably showed no lateral expansion or broadening of either prefrontal lobes nor any significant cerebral asymmetry in either occipital or frontal regions. That ancestral group most probably retained the sympleisomorphic condition of an enlarged primary visual striate cortex, with an anteriorly placed lunate sulcus, a condition clearly shown in *Proconsul africanus* by Radinsky (1974, 1975) and later by Falk (1983). Perhaps these predictions will be borne out with future discoveries. At a minimum, a well-preserved occipital bone might decide this issue once and for all, as we have seen from the Stw 505 specimen.

Australopithecus afarensis, by contrast to the earliest taxa, possessed a somewhat larger brain, ranging from perhaps 385 ml to more than 550 ml (the latter in large males), with considerable sexual dimorphism in body size and thus brain size as well. While we cannot be certain regarding the full anatomy of the frontal lobe, it is unlikely that the Broca's cap region was developed much beyond that of earlier apes. The present specimens, such as Hadar AL 444-2 or the child AL 333-105, simply do not have a *Homo*-like disposition of this region. Nor can we be certain that cerebral asymmetries, perhaps reflecting handedness and possibly other hemispheric specializations underlying more complex cognitive processes, existed in this hominid. We are certain, however, based on the parietal and occipital fragments of the Hadar AL 162-28 specimen with excellent preservation of the internal table of bone that the lunate sulcus was in a more posterior position, thus reflecting a relative reduction of primary visual cortex, or area 17 of Brodmann (see Hadar, Figs. 1–2; Holloway, 1983a). Indeed, based on a comparison with over 70 chimpanzee brain hemispheres of roughly the same volume, the Hadar AL 162-28 fossil shows a distance between the posterior end of the interparietal sulcus and the occipital pole of 15.5 mm, which is roughly one-half the distance found in chimpanzee brains often smaller in brain volume. This distance is roughly 4 SD's less than in chimpanzees (Holloway et al., 2003).

This reduction most probably signifies a *relative increase* of posterior association cortex and is the first evidence of an important reorganization of the cerebral cortex toward a human-like pattern. The associated postcranial materials from both Hadar and Laetoli in Tanzania indicate an upright, striding gait, which, in turn, suggests existence in an adaptive mixed ecological niche of feeding and other behaviors different from that of any forest-dwelling ape. This adds to our conviction that if the hominid was operating in a different behavioral manner, it is more than likely that the brain was reorganized differently than in apes. These conclusions were voiced earlier by Holloway (1967, 1972a, 1975, 1983b, 1995, 1996) and Holloway and Post (1982). We can answer the question as to whether the increase of cranial capacity over an earlier ape-like volume of less than 400 ml preceded the reorganizational event that led to the relative increase in posterior association cortex: AL 162-28, Stw505, possibly AL 288-1, and most likely Taung and SK 1585, strongly suggest that reorganization did precede brain expansion. Admittedly, the

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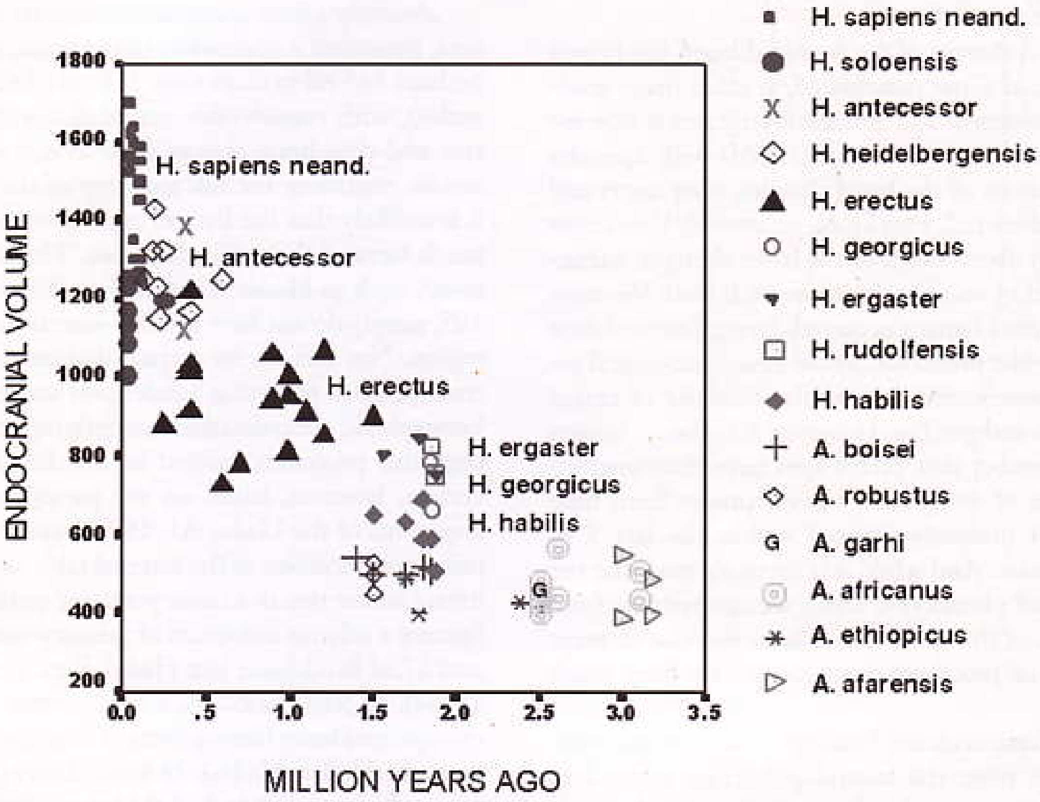

Figure 140. Brain size by age and species.

Stw 505 brain volume (greater than 550 ml) is larger than most chimpanzees, but it would be reasonable to expect that the Stw 505 body size was also greater. We can quibble about these absolute and relative brain sizes, but the major point seems clearly proved: the hominid brain underwent reorganization before it underwent any major expansion in size.

As Figure 140 shows, early hominid brain volumes are mostly static throughout the evolutionary life span from the Hadar specimens through the Pliocene gracile South African specimens (e.g., Taung), although the latter probably shows a slight nonallometric increase in brain size over the earlier AL 444 condition. More specimens will be necessary to demonstrate this. Included in this apparent stasis of brain size is the one incomplete brain endocast available for *A. garhi*, reconstructed to 450 ml. The robust australopithecines, a side branch not leading or contributing to the *Homo* line, are clearly larger-brained than their *A. africanus* cousins, but this increase was likely an allometric one related to a larger body size. This stasis was perhaps some two million years in duration, during which it is likely, but as yet unproved, that our ancestral *Homo* lineage was beginning to branch off from either *A. africanus* or *A. garhi*, most likely the latter, given the remaining dental and cranial evidence (Asfaw et al., 1999). The robust australopithecine represented at Swartkrans by SK 1585 (Holloway, 1972b) shows a clear left occipital asymmetry and a puckering in the posterior occipital lobe, suggesting a reduction of primary visual cortex. This can hardly be taken as proof, however. Perhaps the earliest *Homo* line had brains not only leading to a dramatic size increase but also showing the petalial patterns associated with true handedness and also cerebral hemispheric specialization. Yet the *A. boisei* forms, such as OH 5, Konso, or KNM-ER 406, do not appear to show such clear asymmetries. Nor do the earlier West Lake Turkana specimens unambiguously indicate either enlarged or reorganized brains. We tentatively agree with Falk et al. (2000) that the *A. africanus* prefrontal lobe appears less pointed than in earlier australopithecine specimens, but we also believe that caution is necessary because this feature is quite variable even for *Pan troglodytes* and *P. paniscus*. Their Broca's cap regions do not appear human-like on the specimens currently available. This suggests that with increasing adaptations to mixed environments, and a gradual desiccation of forests, natural selection favored a brain organization capable of appreciating spatial relationships and object properties more advanced than those we know for *Pan* (see Holloway, 1996).

At roughly 2 MYA there must have been important environmental changes that led, in part, to the evolutionary branching of hominids that were more advanced both brainwise and postcranially. These have been referred to as the habilines, based on the earliest finds, designated as *Homo habilis* from Olduvai Gorge, Tanzania, made by the Leakey family. These fossils show an enlarged cranial capacity ranging from roughly 590 ml (OH 24) to close to 700 ml (OH 7). The KNM-ER 1470 and KNM-ER 1590 specimens at roughly 1.8 MYA are clearly larger brained and larger bodied than those from Olduvai Gorge. The more recent taxonomic assignment of these specimens to *Homo rudolfensis*, and the later split of KNM-ER 3733 and KNM-ER 3883 from the KNM-WT 15000 specimen reflected by the division between *Homo ergaster* and *Homo erectus*, is not particularly convincing to us, though we accept the designations as convenient identities. The latter specimens range from 752 ml in KNM-ER 1470 to roughly 900 ml in the Nariokotome youth, KNM-WT 15000. The picture is further complicated by other hominid specimens such as KNM-ER 1813 and KNM-ER 1805, as well as the diminutive OH 62. Added to this complex picture is the recent announcement of the Dmanisi Georgian finds as *Homo georgicus* (Gabounia et al., 2002), although it clearly establishes that there was a very early "out-of-Africa" migration that was a tremendously important event in the evolution of more modern *Homo erectus* groups in both Europe and Asia.

The remains of the Olduvai specimens are either distorted (as in OH 24) or very incomplete (as in OH 7, 13, and 16). The reorganizational patterns are not apparent, although Tobias (1987) has claimed a left parietal petalial pattern for OH 7, an observation we find difficult to accept given the crushed condition of the original fragments. It is important to point out that none of these specimens, except for the extremely fragmented OH 16 and the highly distorted OH 24 specimens, possesses a frontal lobe. There is not enough material available to discuss cerebral asymmetries, reduction of area 17, PVC, or the Broca's cap regions of the third inferior frontal convolution. The OH 12 endocast shows a clear posteriorly oriented lunate sulcus. However, with KNM-ER 1470, there is clearly a left occipital–right frontal petalial pattern, and Broca's cap regions that are definitely more like those of *Homo* than *Pan* or early australopithecines from the *A. africanus* group. The Broca's cap regions were noticed by Holloway in 1974, reported by Leakey in his two books (1978, 1992), and independently reported by Falk (1983). The Broca's cap region of KNM-WT 15000, the Nariokotome youth, is not available in that specimen, or in OH 9, but subsequent *Homo erectus* specimens from Indonesia do show a *Homo*-like pattern of both enlargement and morphology. The Dmanisi fossils from Georgia, Eastern Europe, while not fully described, apparently have brain endocast values in the 650 to 750 ml range (Vekua et al., 2002).

Unfortunately, the postcranial elements from Olduvai Gorge are too few and too fragmentary to provide useful estimates of body size. From the tiny foot from OH 8, and the smallish elements of OH 62, however, it would appear that these early habilines were anything but big bodied. This leads us to speculate that perhaps the increase in brain size was a nonallometric process, reflecting real selection pressures for a more advanced behavioral adaptation based on cerebral enlargement. As for KNM-ER 1470, we simply do not know its body size, but we regard it as unlikely that the increase in brain volume to between 750 and 800 ml was a purely allometric increase based on an increase in body size alone. We are certain, however, that *Homo erectus* (and here we include *H. ergaster*) had a body size nearly indistinguishable from modern *Homo sapiens*. There was a significant enlargement of brain volume that was not allometrically related to body size increase in much of *Homo erectus*, to archaic *Homo* (*H. heidelbergensis*) as represented by Steinheim, Swanscombe, Atapuerca, Ceprano, Petralona, Reilingen, and so on, through to the Neanderthals, where there indeed might have been an increase in skeletal robusticity with an attendant allometric increase in brain size (see for example Holloway, 1985). *Homo erectus* and subsequent fossil hominids clearly show cerebral asymmetries and Broca's cap regions of modern human form. Nevertheless, we cannot be sure that there were not slight changes in the latter leading to modern human behavior. It is important to remember that we are dealing with tiny sample sizes when we talk about brain endocast features such as asymmetries in Broca's caps, or left-right petalial patterns associated with both handedness and cerebral specializations between analytical and more gestalt-like cognitive processes. The record is intriguing, but not ironclad. *We see absolutely nothing, however, in these later forms of* Homo *that would, based on neuroanatomical evidence alone, lead us to conclude that language behavior was not possible.*

Other fossil hominids, such as KNM-ER 1813 and 1805, are frankly puzzling, and perhaps can be viewed as advanced australopithecines or as examples of a mini-adaptive radiation of early *Homo* hominids. While it is common to view KNM-ER 1813 as simply a female KNM-ER 1470 (Stringer 1986; Wolpoff, 1999), we feel that the degree of dimorphism of brain volume (510–752 ml) and brain endocast morphology does not support the suggestion that they are the same species. KNM-ER 1805 is a particularly difficult specimen to place. We would be more willing to entertain the speculative possibility that KNM-ER 1805 and KNM-ER 1813 are sexually dimorphic forms of a different early *Homo* (or advanced australopithecine) line, at least from the viewpoint of brain volume, although the ectocranial morphologies are quite different (Holloway, 1978, 1983b).

If these conclusions, drawn from the paleoneurological and other cranial and postcranial evidence, are correct, most of the important reorganizational changes were complete by between 1.5 and 2.0 MYA. It may be that further changes both in cerebral asymmetries, Broca's and Wernicke's regions, and other cerebral, cerebellar (see Weaver 2001), and subcortical regions such as the limbic system took place, but aside from the cerebellum, we cannot detect these with our present methods.

This leaves us with a considerable hiatus in Europe in large part because the Atapuerca and Dmanisi endocasts are not yet described (aside from estimates of brain volume). It also leaves us with the Neanderthals (as represented at least in Western Europe) showing enlarged cranial capacities and no evidence of cerebral primitiveness, except in the platycephalic shape of the crania. Most emphatically, we see no differences in the morphology of the prefrontal portion of the frontal lobe, a finding congruent with the morphometric analysis of Bookstein et al. (1999). While the Neanderthals might have been a separate species (in the sense of a morphospecies and not a biological species in the modern "Mayrian" sense), we do not see how either the behavioral or underlying neurological morphological evidence from brain endocasts contributes to such a view. We prefer to regard Neanderthals as separate from modern *Homo sapiens* at only the subspecific level (Holloway, 1985), but of course remain open to more convincing evidence on this issue. The 160,000 year-old Herto *Homo sapiens idaltu* crania (White et al., 2003) will eventually yield endocranial remains that are essentially the same as in modern *Homo sapiens* (e.g., size, asymmetries, lobar patterns, and perhaps meningeal vessels).

BEHAVIORAL DYNAMICS

While much has been (and is) made of the near-quantum-like cultural advances beginning in the Upper Paleolithic with "true" *Homo sapiens*—such as blade tool traditions, carvings, parietal art, jewelry, sewing, and religious rites (e.g., see Klein, 1999; Klein and Edgar, 2002; and several papers in Crow, 2002)—we regard cultural dynamics as the most likely explanation for these advances, rather than neurological/behavioral changes in cognitive capacities based on a single or multiple mutations or the acquisition of neural modules (i.e., Ducheine et al., 2001). It is, though, theoretically possible that advances in our understanding of the genetic elements that relate to brain development might illuminate how the human brain evolved at this level (see Preuss et al., 2003). The findings of Paabo (2003), showing far greater genetic differences in brain genomic material for *Homo* than chimpanzee, clearly suggest that natural selection has operated on the neurogenetics of human brain evolution. If one thinks about the differences in cultural behavior from the time of, say, Edison to the present with the use of computers and our dependence on rapid exchanges of information, Satillites and the like, one should be a little skeptical about underlying mutations subserving cognitive abilities that conveniently sprang into being some 50,000 years ago. We believe that we have remained the same species, and were perhaps the same species 150,000 to 200,000 years before that. If one were to only think of the nonperishable remains (i.e., stone tools) of the Australian Aborigines, we would still be having difficulty understanding the complexity of their social structural systems. Would not our great-grandfathers, indeed, grandfathers, be amazed at the obvious differences in intellectual, material, and spiritual lifestyles that have "evolved" from their lifetimes to ours without any empirical demonstration of genetic mutations underlying such behaviors?

The earliest phases of hominid existence are particularly open to speculative embroidery. But when all is said and done, it remains the stone tool industries or traditions that can inform us the most about hominid cognitive abilities. This does not mean that we disregard archaeological contexts such as the faunal remains, home bases, the evidence (or lack of it) for fire, importation over long distances of stones used in making tools, de-fleshing carcasses, or even cannibalism. Holloway (1967, 1969, 1981) suggested that stone tool making and language might have had similar cognitive underpinnings, particularly if the stone tools showed clear evidence of standardization of form from elements (e.g., cobbles) that had very different initial shapes. We appreciate that different stone materials can lead to a certain constraint in final form, but we still regard standardization as most likely culturally driven. We are, however, also intrigued by Weaver's (2001) thesis that shifts in absolute and relative cerebellar size during hominid evolution might have had important correlations with both sensorimotor and cognitive processing.

Since hominids were surely no less vocal and no less noisy than their ape cousins, we find it difficult to assert that there was a gestural stage in early hominids of the genus *Homo* (e.g., Hewes, 1973; Corballis, 2002). With *Homo erectus*, stone tools are clearly highly standardized in form. There is clear evidence of hunting and very likely scavenging and home bases. Brain sizes are within that for modern *Homo sapiens*, and the endocasts indicate modern *Homo*-like asymmetries in the hemispheres and even in the Broca's cap regions. Of course, these associations cannot *prove* language, but the correlations are surely suggestive. We thus fall clearly into an early language camp for the genus *Homo*, however primitive it might have been. Still we do not believe that any species of *Australopithecus* possessed language abilities, although we can certainly accept that their communicative social skills and manipulation of the environment—in terms of collecting, scavenging, perhaps some hunting, and rudimentary tool making and use—were greater than those for extant chimpanzees, which themselves are beginning to appear more complex than previously thought. Language, of course, involves more than the brain, and much speculation has been presented suggesting that the descent of larynx has been an important if not absolutely essential ingredient in the development of hominid language. We are intrigued by recent reports that show laryngeal descent in chimpanzees (Nishimura et al., 2003) and even red deer (Fitch and Reby, 2001), for this clouds the picture as to how important laryngeal descent and cranial base flexion might have been in the evolution of hominid capacity for language. We rather feel that it was the neural elements that were most critical, with laryngeal position being important only in the phonation of modern human speech.

Recently Heim et al. (2002) have suggested that the vocal tract of Neanderthals was morphologically similar to modern humans and that their larynx was situated at the same level as in modern humans. This conclusion is based on a newer reconstruction of the cranial base. They say: "... we do feel safe in saying that Neanderthals were not morphologically handicapped for speech" (p. 130), and they claim that Neanderthals could pronounce vowels "as differentiated" as those of ourselves. We concur that combined with any lack of primitive features in the Neanderthal brain, at least as evidenced by the endocasts, we see no reason why Neanderthals were not fully capable of human speech.

We regard heterochronic changes, based on evolving regulatory-gene controlled endocrine-target tissue interactions, as the most probable explanation for changes in allometric and nonallometric evolution of the brain as suggested by Holloway (1967, 1975, 1979, 1995). In essence, we suggest at least three stages.

Stage 1

Early australopithecine phase, leading to early Homo, *emphasizing social and behavioral adaptations, endocrine-targeted tissue and brain reorganization; beginning development of cerebral asymmetries, suggesting cognitive specializations in different hemispheres; and relative enlargement of posterior parietal association cortex, with possible changes in prefrontal cortex, but not necessarily including Broca's cap regions.*

The early australopithecine phase includes the development of a more cooperative, dimorphic sex-role social grouping than in apes. These social changes were based on genetic changes involving hormones and target tissues that affected the developmental schedules of the brain and body. Earlier this was described as the "initial kick" in what was called "deviation-amplification" (i.e., the continuing action of positive feedback between such changes as in the "initial kick" and enlargement of brain and body size) (see Holloway, 1967, for a description). There was probably a concomitant reduction of sexual dimorphism in tooth and body size but an increase in epigamic features of secondary sexual characteristics, such as permanent enlarged breasts and different distributions of adipose tissue in females. There were probably also behavioral changes that led to a schedule of sexual receptivity different from that in apes, at least as characterized by *Pan troglodytes*. These changes probably meant a set of closer and more cooperative complemental relationships between males, females, and offspring. This set of correlated behavioral, physiological, and anatomical adaptations led to more efficient mating strategies that were essential for the prolonged periods of postnatal dependence and learning, and the delay of sexual maturation—a set of potentially risky adaptations in an evolutionary sense. Changes in the interactions between hormonal and target tissue milieus might have led to a reduction in aggressive behavior, or a heightened threshold to within-group aggression, permitting groups to live more densely with more cooperative behavior as better protection against both predators and other hominid groups. Concomitantly, hormonal-target tissue changes affected growth rates (longer durations of growth and prolonged dependency), possibly with some allometric increase in brain growth that would have been reflected in slightly higher EQs than in apes. Their bipedalism most probably allowed for greater ranges of econiche diversity and exploration, and their growing sophistication about objects and spatial relationships was probably instrumental in selection for a relative reduction in PVC and a relative expansion of posterior parietal lobe. Extension of foresight and memory would obviously have been advantageous, and appear to us to be nascent in these hominids given their somewhat broader prefrontal lobes and expanded temporal lobes.

Later australopithecines probably were using tools but were not showing clear standardization of form either in their choice of tools or their manufacture, the earliest evidence for stone tools going back to approximately 2.6 MYA. If social communicatory skills were greater at this stage than what we witness in extant chimpanzees, this would most likely have been associated with social affect and control than with hunting behavior.

Stage 2

Later early Homo*–early* Homo erectus *phase, emphasizing consolidation of stage 1 and the development of language capacities; clear-cut and modern-human-like cerebral asymmetries, including Broca's cap regions of the prefrontal cortex, and both allometric and nonallometric increases of brain volume, with attending increases in EQ.*

This stage included elaboration and augmentation of the changes in social behavior mentioned in stage 1. More important, it involved a growing dependence on social cohesion, cooperation, and sex-role complementation in all economic tasks, involving beginning language based on arbitrary symbols, however primitive, and the manufacturing of stone tools to standardized patterns with clear cognitive associations between different tools and tasks. Bipedal locomotion was fully human. The brain expanded in size both absolutely and relatively, reflecting more hormonal-target-tissue interactions in the modern human direction. These changes led to further reductions in size dimorphism between the sexes with a possible increase in secondary sexual dimorphism, physiologically, anatomically, and behaviorally. These in turn provided the basis for increasing postnatal dependency and learning, increasing age toward parturition, and the increased duration of childhood to sexual maturity. Social learning of tool making, hunting, collecting, scavenging, and reproductive strategies were all in a positive feedback system between cultural complexity and brain enlargement, but only to the extent that basic obstetrical constraints were not broached. As Holloway noted in this regard (1975: 40):

> Language behavior became more strongly developed and cognitive behavior of a more nearly human type developed, where language and tool-making arose from the same psychological structuring. There were true stone tool "cultures" at this stage, and language had prime importance in maintaining social cohesion and control and in "programming" offspring. Dependence on hunting increased and there was more success in stalking and hunting larger game. There was a selection for increased body size, bipedal agility and predictive abilities for more successful hunting (meaning the full food quest in which women and children are important contributors). The social behavioral changes outlined in stages 1 and 2 permitted longer male-male associations for persistent hunting and for protection of a more secure home base for females and young, who were providing smaller game and vegetables. The "initial kick" or "human revolution" is fully set and leads to stage 3.

Stage 3

Growing elaboration of cultural skills, based certainly on language, using arbitrary symbol systems, and developing through an on-going positive feedback relationship between behavioral complexity and brain enlargement; also continuing refinements in hemispheric asymmetries, and hemispheric specialization for visuospatial, verbal, and sociality skills developed in stage 2.

Stage 3 is us and, we believe, characteristic of Neanderthals. It seems to us unlikely that major changes in postnatal dependency time, gestation, parturition, or reproductive age occurred during this stage, having been for the most part completed in archaic *Homo sapiens* (*H. heidelbergensis*) and pre-Neanderthalien times, as seen at least in Western European Neanderthals of the "classic" sort. We also believe that it was a stage during which increased learning would have been extremely important and under fairly stringent social control, as cultural complexities were occurring in more complex and stimulating material and social environments. The major neurological changes were probably minor increases of size and refinement of the already reorganized brain, in sensorimotor, associative, and extrapyramidal (striatum) modulation, as well as cerebellar involvement in manual dexterity, language, and artistic development such as song, dance, and tool making.

A fourth stage might be suggested, when there occurred a gradual and small decrease in our absolute brain size from the Upper Paleolithic to today's time period, as suggested by Henneberg (1998). This would most surely be explained as an allometric decrease based on a loss of bony/muscular robusticity, without any significant behavioral associations.

We expressly disagree with our colleagues who believe that somewhere in this third stage, a single mutational event made language and art possible, and that one had to witness what many appear to regard as an Upper Paleolithic "revolution" before the brain was adequate to the tasks of full symbolic language and art. We also regard these stages as fairly continuous, but we do not rule out the possibility of mosaics within the mosaic, so to speak. These temporal changes were probably not gradual but "punctuated" within space, frames of thousands of years.

In the human mind's natural desire for closure, it is particularly difficult to accept that our fossil record is so extraordinarily limited. It is a simple task to assume a generation span of, say, 20 years and a constant essential population (N_e) size of 500 reproducing souls during any generational span. Over the course of the past 1,000,000 years (to select an easily calculable figure), how many individuals would have lived during that time? 50,000 generations times 500 souls per generation comes out to be 25,000,000 individual hominids. What, however, is our present-day sample of endocranial casts that reveal something about how the brain evolved? Just to simplify our calculations, assume we have a sample of 100 endocasts. The percentage of possible hominid remains that we have sampled is 0.000004, or .0.004%! An order of magnitude difference in any our assumptions would make little difference. On the one hand, it is remarkable how much scientists can make from so little, but we prefer to be humble in our assessment of how closely we can describe hominid evolution, and in particular, our brains. Even with a time machine, how long would it take one or some of us to observe and measure the brains and behavior of some 25 million hominids?

We have attempted to show in these pages that the evolution of the human brain has always been an important integral aspect of hominid evolution and not just something that took place following changes in other morphological components of the hominids, such as bipedal locomotion, the refinement of precision grip, carrying objects, or language. None of these components can operate (nor did they) in neurological vacuums. A change in locomotory pattern signals not simply a change in musculoskeletal relationships but also in innervations, and motor control, and these newer constellations of musculoskeletal patterns themselves operate within different ecological and thus behavioral contexts.

Endocasts are not alone, at this juncture of their study, a sufficient basis for delineating the exact neurological changes that accompanied behavioral adaptations such as throwing, bipedal locomotion, precision gripping, stone tool making, artistic appreciation and rendition, song, dance, humming, or whatever other behavioral attributes we consider as part and parcel of humanness. Our study of endocasts does convince us, however, that human behavior is a long-standing evolutionary development, possibly three million years old, and not a late invention dependent on a few salutary mutations. Regulatory genes can probably explain much of the progression. The human brain is both the product and cause of our evolutionary pathway, and certainly is the instrument and product of our sociality, wonderful and/or frightening as that may be.

ENDOCASTS YET TO BE STUDIED

Listing all of the endocasts, actual and potential, is not to be taken to mean that those described in this volume have been sufficiently or completely studied. Indeed, we have voiced our honest hope that other researchers might regard these objects as worthy of further study. The fact remains that there some glaring hiatuses in our attempt to be thorough, and we mention them below in the hope of encouraging those in charge of the fossils, or those desiring to work on them, to endocast the fossils and permit access for further study.

Among the South African australopithecines, we underline the desirability of further study on Sts 58, the dorsal calva portion associated with Sts 19, described herein. We have not seen any mention of the newer Dremolin Cave finds, and possible endocasts or portions of endocasts that could be made. The debates between one of us (RLH) and Dean Falk should encourage independent study of both the volumes and morphology of the endocasts of these hominids. In particular, independent study of SK 1585 should be initiated given the wide disagreement between Falk et al. (2000) and Holloway (1972b), and Holloway et al. (2000) regarding its volume.

While all of the considerations above apply to both Kenyan and Ethiopian endocasts, we believe we have described most of them, as has Tobias (1991). On the other hand, hominids such as KNM-ER 406, KNM-ER 407, and KNM-ER 732 should be re-studied (and re-cast), since RLH's original endocasts were left in Nairobi and have long since deteriorated. The descriptions in this volume are based on plastic replicas of often poor quality. KNM-ER 406 is filled with extremely hard matrix and requires much more study through modern scanning techniques, as it is very unlikely that the matrix can ever be removed without seriously damaging the original cranium. An accurate volume estimate would be most welcome.

Newer finds, such as *Kenyanthropus platyops*, and other fragments from Lomekwi, should yield, through modern scanning techniques, a good opportunity to find an accurate volume, particularly in lieu of White's (2003) assessment of possible distortion to the holotype, KNM-WT 40000. Naturally recent discoveries such as *Orrorin, Sahelanthropus* and *Ardipithecus* will yield both volumetric and morphological features that will assist in understanding the earliest phases of hominid brain evolution. To our current understanding, the fragments of these crania are too incomplete to provide such information, but the future always holds promise!

The earliest *Homo* specimens from Tanzania (OH 7, 12, 13, 16, and 24) are particularly in need of further study, building on Tobias's scholarly treatise (1991). The originals that RLH made in the early 1970s have surely disintegrated, and the plastic replicas in his collection are of poor quality. Similarly KNM-ER 1470 and KNM-ER 1590 should be recast and independently studied, particularly with regard to petalial asymmetry patterns and the possibility of cerebral hemispheric specialization, as well as the Broca's cap region. The former is of key importance regarding questions about brain reorganization in the *Homo* line. Indeed, the same applies to KNM-ER 1805 and KNM-ER 1813. These two endocast portions are particularly difficult to assign with any taxonomic closure given their unusual morphology, although we stand confident regarding our volume determinations, whether they are truly early *Homo* or advanced australopithecines.

The Dmanisi specimens of 1.8 MYA are extremely important, both with respect to accurate volumes and possible morphological features. We look forward to reading studies on their paleoneurological information. From our examination of the various photographs of these specimens, we are certain that they can be safely endocast, and would be willing to do so.

As far as we are aware, the Atapuerca crania from Spain (4 and 5) have yielded accurate volumes, and their morphological characteristics are under study by Arsuaga's team. Our attempts to gain information about these possible endocasts have not been answered. Given the prospects that their internal tables of bone are perfectly preserved, the paleoneurologists' appetites should indeed be whetted. These represent a major hiatus in our understanding of possible Neanderthal ancestry and the European hominids in general.

The Steinheim hominid (Germany) is yet another hiatus in the domain of paleoneurological study. Although an accurate volume determination will probably result from newer scanning devices and restorative techniques, it is preferable to have an actual endocast of silicon rubber to palpate. Indeed, even a distorted version is preferred to nothing, which is our current situation. Similar comments can be made for the well-preserved Petralona (Greece) and Ceprano (Italy) specimens. All of these are important for a better understanding of European hominid evolution and their variability.

Newer Indonesian finds such as Sm 4 (Baba et al., 2003) are important additions to our increasing sample of Indonesian specimens of *Homo erectus*, which to date show little in the way of either volumetric or morphological variation, an evolutionary potentially interesting facet of the evolution of the genus *Homo*, and OOA (out of Africa) and MRE (multiregional evolution) controversies. We are very fortunate to have had the opportunity to describe Sm 3, the Poloyo hominid of NYC boutique fame.

Several Chinese hominid crania (aside from the older Zhoukoudian discoveries originally named *Sinanthropus pekinensis*), such as Lantian, Maba, Yunxian 2, Nanjing, Hexian, Shandong, Dali, and Jinniushan, have not been endocast to our knowledge, and a few may be particularly difficult to endocast given their fragmentary and deformed condition. Hopefully these will be added to our paleoneurological sample in the future.

Finally we note that there are several important gaps in our studies of Neanderthal endocasts. In particular, the Italian Saccopastore hominid cranial portions could be endocast, adding very important volumetric and morphological details to the abundant controversies over these hominids. Furthermore the Middle Eastern Neanderthals of the Mount Carmel and Shanidar caves have not been studied by us given problems of access and their fragmentary nature. They are likely to be an important pivotal point in our understanding of Neanderthal evolutionary dynamics, whether or not one agrees with different species designations for these and modern anatomical *Homo sapiens*.

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APPENDIX 1

ENDOCRANIAL VOLUMES OF THE FOSSIL HOMINIDS

NOTES FOR APPENDIX 1

The endocranial volumes for this table are listed by taxonomic group as currently expressed in the literature, and arranged alphabetically within broad geographic regions. Our use of these taxa in this Table does not mean that we concur with all of these designations.

Where the "source" indicates an "**RLH**" that means the endocranial capacities were either determined by RLH or published RLH as in Holloway, RL. 2000. Brain. In: E. Delson, I. Tattersall, J. Van Couvering, and AS Brooks (Eds). **Encyclopedia of Human Evolution and Prehistory.** 2nd Edition. NY: Garland Publ., Inc. pps. 141–149. If the "Source" is "**OTHER**", the volumes reported were taken from the recent literature as found in our Bibliography, and mostly from Ruff, CB, Trinkaus, E., and Holiday, TW. 1997. Body mass and encephalization in Pleistocene Homo. **Nature** 387:173–176 (Supplementary Data). The SM 1 and SM 4 volumes are from Baba *et al.* 2003. Homo erectus Calvarium from the Pleistocene of Java. **Science** 299: 1384–1388.

We have decided to provide a chronological age for each endocranial volume to permit regressing endocranial volume against time. The range of MYA's for many of the hominids are too wide to accept anything but a middle value, and we hope that these dates will become more accurate as new dating techniques become available. Missing, in particular, is any endocranial estimate for the Maba (China) cranium. We could not find a citation anywhere in the literature that we have seen.

APPENDIX 1 **Part 1: Endocranial volumes and data**

Specimen	Source	Volume	Taxon	MYA
AL 162-28	RLH	400	*A. afarensis*	3.18
AL 288-1	RLH	387	*A. afarensis*	3
AL 333-105	RLH	400	*A. afarensis*	3.18
AL 333-45	RLH	492	*A. afarensis*	3.18
AL 444-2	RLH	550	*A. afarensis*	3
KNM-WT 17000	RLH	410	*A. ethiopicus*	2.5
KNM-WT 17400	RLH	400	*A. ethiopicus*	1.77
KNM-ER 23000	RLH	490	*A. ethiopicus*	1.7
Omo L338y-6	RLH	427	*A. ethiopicus*	2.39
KNM-ER 406	RLH	500	*A. boisei*	1.5
KNM-ER 407	RLH	510	*A. boisei*	1.85
KNM-ER 732	RLH	500	*A. boisei*	1.7
KNM-WT 13750	RLH	475	*A. boisei*	1.7
Konso (KGA-10-525)	RLH	545	*A. boisei*	1.4
OH 5	RLH	520	*A. boisei*	1.8
SK 54	RLH	500	*A. robustus*	1.5
SK 859	RLH	450	*A. robustus*	1.5
SK 1585	RLH	530	*A. robustus*	1.5
MLD 1	RLH	510	*A. africanus*	3.1
MLD 37/38	RLH	435	*A. africanus*	3.1
Sts 5	RLH	485	*A. africanus*	2.5
Sts 19/58	RLH	436	*A. africanus*	2.5
Sts 60	RLH	400	*A. africanus*	2.5
Sts 71	RLH	428	*A. africanus*	2.5
Stw 505	RLH	560	*A. africanus*	2.6
Taung	RLH	440	*A. africanus*	2.6
Type 2	RLH	457	*A. africanus*	2.5
Bouri (Bou-VP-12/130)	RLH	450	*A. garhi*	2.5
KNM-ER 1805	RLH	582	*H. habilis*	1.85
KNM-ER 1813	RLH	509	*H. habilis*	1.88
OH 7	RLH	687	*H. habilis*	1.8
OH 13	RLH	650	*H. habilis*	1.5
OH 16	RLH	638	*H. habilis*	1.7
OH 24	RLH	590	*H. habilis*	1.8
KNM-ER 3732	RLH	750	*H. ergaster*	1.88
KNM-ER 3733	RLH	848	*H. ergaster*	1.78
KNM-ER 3883	RLH	804	*H. ergaster*	1.57
KNM-ER 1470	RLH	752	*H. rudolfensis*	1.88
KNM-ER 1590	RLH	825	*H. rudolfensis*	1.85
Dmanisi D2280	Other	650	*H. georgicus*	1.7
Dmanisi D2282	Other	780	*H. georgicus*	1.7
Daka, Ethiopia	Other	995	*H. erectus*	1
Hexian	Other	1025	*H. erectus*	0.412
Jinniushan	Other	1390	*H. erectus*	0.28

(Cont.)

APPENDIX 1 **Part 1:** (*Continued*)

Specimen	Source	Volume	Taxon	MYA
KNM-WT 15000	Other	900	*H. erectus*	1.5
Lantian (Gongwang 1)	Other	780	*H. erectus*	0.7
Narmada	Other	1260	*H. erectus*	0.236
Ngawi	Other	870	*H. erectus*	na
OH 9	RLH	1067	*H. erectus*	1.2
OH 12	RLH	727	*H. erectus*	0.6
Sale	RLH	880	*H. erectus*	0.24
Sambungmacan 1	Other	1035	*H. erectus*	0.8
Sambungmacan 3	RLH	917	*H. erectus*	0.4
Sambungmacan 4	Other	1006	*H. erectus*	0.8
Sangiran 2	RLH	813	*H. erectus*	0.98
Sangiran 3	RLH	950	*H. erectus*	1
Sangiran 4	RLH	908	*H. erectus*	1.1
Sangiran 10	RLH	855	*H. erectus*	1.2
Sangiran 12	RLH	1059	*H. erectus*	0.9
Sangiran 17	RLH	1004	*H. erectus*	1
Trinil 2	RLH	940	*H. erectus*	0.9
Yunxian (1 and 2)	Other	1200	*H. erectus*	0.4
Zhoukodian III, E (Z 2)	RLH	915	*H. erectus*	0.4
Zhoukoudian (Z11)	RLH	1015	*H. erectus*	0.4
Zhoukoudian I, L (Z 10)	RLH	1225	*H. erectus*	0.4
Zhoukoudian III, L (Z 12)	RLH	1030	*H. erectus*	0.4
Atapuerca 4	Other	1390	*H. antecessor*	0.35
Atapuerca 5	Other	1125	*H. antecessor*	0.35
Atapuerca 6	Other	1140	*H. antecessor*	0.35
Dali 1	Other	1120	*H. soloensis*	0.209
Ngandong 1 (Solo I)	RLH	1172	*H. soloensis*	0.031
Ngandong 6 (Solo V)	RLH	1251	*H. soloensis*	0.031
Ngandong 7 (Solo VI)	RLH	1013	*H. soloensis*	0.031
Ngandong (Solo IX)	RLH	1135	*H. soloensis*	0.031
Ngandong 13 (Solo X)	RLH	1231	*H. soloensis*	0.031
Ngandong 14 (Solo XI)	RLH	1090	*H. soloensis*	0.031
Arago	RLH	1166	*H. heidelbergensis*	0.4
Biache	Other	1200	*H. heidelbergensis*	na
Bodo	RLH	1250	*H. heidelbergensis*	0.6
Ceprano	Other	1165	*H. heidelbergensis*	0.8
Ehringsdorf	Other	1450	*H. heidelbergensis*	0.23
Kabwe	RLH	1325	*H. heidelbergensis*	0.18
Lazaret	RLH	1250	*H. heidelbergensis*	0.13
Petralona	Other	1230	*H. heidelbergensis*	0.21
Reilingen	RLH	1430	*H. heidelbergensis*	0.2
Saldanha	Other	1225	*H. heidelbergensis*	0.5
Steinheim	Other	1200	*H. heidelbergensis*	0.225
Swanscombe	RLH	1325	*H. heidelbergensis*	0.25
Amud	Other	1740	*H. sapiens neanderthalen*	0.041
Engis 2	Other	1362	*H. sapiens neanderthalen*	0.06
Ganovce	RLH	1320	*H. sapiens neanderthalen*	0.09

(*Cont.*)

APPENDIX 1 **Part 1:** (*Continued*)

Specimen	Source	Volume	Taxon	MYA
Gibralter (Devil's)	Other	1400	*H. sapiens neanderthalen*	0.05
Gibralter (Forbe's)	Other	1200	*H. sapiens neanderthalen*	0.05
Jebel Irhoud 1	RLH	1305	*H. sapiens neanderthalen*	0.1
Jebel Irhoud 2	RLH	1400	*H. sapiens neanderthalen*	0.1
Krapina B	Other	1450	*H. sapiens neanderthalen*	0.13
Krapina 3 (Cranium C)	RLH	1255	*H. sapiens neanderthalen*	0.13
Krapina 6 (Cranium E)	RLH	1205	*H. sapiens neanderthalen*	0.13
La Chapelle	Other	1625	*H. sapiens neanderthalen*	0.05
La Ferrassie	Other	1640	*H. sapiens neanderthalen*	0.07
La Quina 5	Other	1172	*H. sapiens neanderthalen*	0.065
La Quina 18	Other	1200	*H. sapiens neanderthalen*	0.06
Le Moustier	Other	1565	*H. sapiens neanderthalen*	0.041
Monte Circeo (Guat1)	RLH	1360	*H. sapiens neanderthalen*	0.052
Neanderthal	Other	1525	*H. sapiens neanderthalen*	0.04
Saccopastore 1	Other	1245	*H. sapiens neanderthalen*	0.125
Saccopastore 2	Other	1300	*H. sapiens neanderthalen*	0.125
Shanidar 1	Other	1600	*H. sapiens neanderthalen*	0.06
Shanidar 5	Other	1550	*H. sapiens neanderthalen*	0.06
Skhul 1	Other	1450	*H. sapiens neanderthalen*	0.1
Skhul 4	Other	1554	*H. sapiens neanderthalen*	0.1
Skhul 5	Other	1520	*H. sapiens neanderthalen*	0.1
Skhul 9	Other	1590	*H. sapiens neanderthalen*	0.1
Spy I	RLH	1305	*H. sapiens neanderthalen*	0.068
Spy II	RLH	1553	*H. sapiens neanderthalen*	0.068
Tabun 1	Other	1271	*H. sapiens neanderthalen*	0.11
Teshik-Tash	Other	1525	*H. sapiens neanderthalen*	0.07
Herto 1/16	Other	1450	*H. sapiens idaltu*	0.16
Brno I	Other	1600	*H. sapiens sapiens*	0.026
Brno II	Other	1500	*H. sapiens sapiens*	0.026
Brno III	Other	1304	*H. sapiens sapiens*	0.026
Border Cave	Other	1510	*H. sapiens sapiens*	0.07
Bruniquel 2	Other	1555	*H. sapiens sapiens*	na
Cap Blanc 1	Other	1434	*H. sapiens sapiens*	na
Chancelade	Other	1530	*H. sapiens sapiens*	na
Combe Capelle	Other	1570	*H. sapiens sapiens*	0.028
Cro-Magnon 1	Other	1730	*H. sapiens sapiens*	0.03
Cro-Magnon 3	Other	1590	*H. sapiens sapiens*	0.03
Dolni Vestonice 3	Other	1285	*H. sapiens sapiens*	0.0275
Dolni Vestonice 14	Other	1538	*H. sapiens sapiens*	0.0275
Dolni Vestonice 18	Other	1481	*H. sapiens sapiens*	0.0275
Dolni Vestonice 20	Other	1378	*H. sapiens sapiens*	0.0275
Dolni Vestonice 21	Other	1547	*H. sapiens sapiens*	0.0275
Grotte des Infants 4	Other	1775	*H. sapiens sapiens*	na
Grotte des Infants 5	Other	1375	*H. sapiens sapiens*	na
Grotte des Infants 6	Other	1580	*H. sapiens sapiens*	na
Kostenki 2	Other	1605	*H. sapiens sapiens*	0.02
Kostenki 14	Other	1222	*H. sapiens sapiens*	na
Laetoli 18	Other	1367	*H. sapiens sapiens*	0.12

(*Cont.*)

APPENDIX 1 **Part 1: (*Continued*)**

Specimen	Source	Volume	Taxon	MYA
Liujiang	Other	1480	*H. sapiens sapiens*	0.04
Minatogawa 1	Other	1390	*H. sapiens sapiens*	0.018
Minatogawa 2	Other	1170	*H. sapiens sapiens*	na
Minatogawa 4	Other	1090	*H. sapiens sapiens*	na
Mladec 1	Other	1540	*H. sapiens sapiens*	0.03
Mladec 2	Other	1390	*H. sapiens sapiens*	na
Mladec 5	Other	1650	*H. sapiens sapiens*	na
Nazlet Khater 2	Other	1420	*H. sapiens sapiens*	0.037
Obercassel 1	Other	1500	*H. sapiens sapiens*	na
Obercassel 2	Other	1370	*H. sapiens sapiens*	na
Omo 2 (Kibbish)	Other	1435	*H. sapiens sapiens*	0.12
Pataud 1	Other	1380	*H. sapiens sapiens*	na
Pavlov1	Other	1472	*H. sapiens sapiens*	0.026
Predmosti 3	Other	1580	*H. sapiens sapiens*	0.026
Predmosti 4	Other	1250	*H. sapiens sapiens*	0.026
Predmosti 9	Other	1555	*H. sapiens sapiens*	0.026
Predmosti 10	Other	1452	*H. sapiens sapiens*	0.026
Qafzeh 6	Other	1568	*H. sapiens sapiens*	0.09
Qafzeh 9	Other	1531	*H. sapiens sapiens*	na
Qafzeh 11	Other	1280	*H. sapiens sapiens*	na
San Teodoro 1	Other	1565	*H. sapiens sapiens*	na
San Teodoro 2	Other	1569	*H. sapiens sapiens*	na
San Teodoro 3	Other	1560	*H. sapiens sapiens*	na
San Teodoro 5	Other	1484	*H. sapiens sapiens*	na
Singa 1	Other	1550	*H. sapiens sapiens*	0.133
St. Germain-la-Rivie	Other	1354	*H. sapiens sapiens*	na
Sungir 1	Other	1464	*H. sapiens sapiens*	0.024
Sungir 2	Other	1267	*H. sapiens sapiens*	na
Sungir 3	Other	1361	*H. sapiens sapiens*	na
Sungir 5	Other	1453	*H. sapiens sapiens*	na
Veyrier 1	Other	1430	*H. sapiens sapiens*	na
Yinkou	Other	1390	*H. sapiens sapiens*	0.13
Zhoukoudian (Upper Cave) 1	Other	1500	*H. sapiens sapiens*	0.015
Zhoukoudian (Upper Cave) 2	Other	1380	*H. sapiens sapiens*	na
Zhoukoudian (Upper Cave) 3	Other	1290	*H. sapiens sapiens*	na

APPENDIX 1 **Part II: Average endocranial volumes and EQs**

TAXA	Mean Volume (ml)	Mean MYA	BODYMASS	EQMARTIN	EQHOMO
A. afarensis	445.80	3.11	37.00	4.87	42.79
A. africanus	462.33	2.66	35.50	5.21	45.58
A. ethiopicus	431.75	2.09	37.60	4.66	41.01
A. garhi	450.00	2.50			
H. erectus	941.44	0.81	57.80	7.32	67.64
H. ergaster	800.67	1.74	57.50	6.25	57.72
H. habilis	610.00	1.76	34.30	7.06	61.50
H. heidelbergensis	1,265.75	0.27	68.70	8.64	81.30
H. rudolfensis	788.50	1.87	45.60	7.35	66.08
H. neanderthalensis	1,487.50	0.08	64.90	10.60	99.14
H. sapiens	1,330.00	0.01	63.50	9.63	89.90
H. soloensis	1,155.86	0.06			
A. robustus	493.33	1.50	36.10	5.49	48.11
A. boisei	515.00	1.65	41.30	5.17	46.02
P. troglodytes	405.00	0.01	46.00	3.75	33.75
G. gorilla	500.00	0.01	105.00	2.47	24.39

APPENDIX 2

STATISTICAL ANALYSES OF ENDOCRANIAL VOLUMES BY TAXA

Provided herein are the initial basic statistics for all the hominid endocranial samples we described in this book. These statistics can be arranged differently, but we chose these various combinations because, by relying on consensual taxonomic placements, we were able to increase sample sizes within taxa. In addition to mean and standard deviation, we include minimum and maximum values, the coefficient of variation (CV), skewness, and kurtosis. If we assume that all hominid populations' endocranial capacities were basically of a normal Gaussian nature, the strong deviations from such normality might signal clues regarding sampling and taxonomic placements.

For example, populations with very large or very small CVs (i.e., departing strongly either way from about 10%) suggest caution is advisable. The CV for *A. afarensis* of 16.1% suggests a fairly dimorphic sample, or a combination of taxa. We believe the former to be the case despite the recent findings of Reno et al. (2003) regarding modern *Homo*-like sexual dimorphism of the femoral head in *A. afarensis*. On the other hand, the CVs for "all *Homo erectus*" are 16.2%, and 14.9% for early *Homo*, because these samples contain multiple taxa rather than strong sexual dimorphism in endocranial capacity. However, we are not claiming that CVs trump morphology, only that they might have a use in sensitizing us to question the basis for the high or low values. More sampling will of course resolve these questions. Similarly the low CVs for *A. robustus/A. boisei* probably signal a combination of low sample size and bias in both discovery and methodological issues when reconstructing incomplete endocasts. Similarly the relatively low CVs for the Ngandong (Solo) and *H. heidelbergensis* groups suggest either sampling or reconstruction bias, whereas the *A. africanus* and *H. habilis* groups have CVs that are more in line with expectations for early hominid sexual dimorphism and population variation. We believe the same applies to *H. erectus* without *H. ergaster, H. rudolfensis,* and *H. georgicus*.

Mostly from our findings, but including those of several other workers, on the accumulation of endocranial capacities, we propose an average endocranial capacity for *H. sapiens neanderthalensis* that is lower than that for modern *Homo sapiens* of the Upper Pleistocene. The addition of two smallish Krapina (3 and 6) specimens, less than 1275 ml, both probably females, could change our bias regarding the old paleanthropological "chestnut" that Neanderthal had brains larger than our own. As the modern *Homo* sample is unquestionably mostly male, this supposition requires more analysis than we can provide here.

Similarly the skewness and kurtosis figures are only approximate due to imperfect sampling or clustering of taxa. In general, values greater or lesser than ±1.0 signal significant departures. We do not suggest any use of these statistics to determine either the correctness or wrongness of taxa. In general, these figures for skewness and kurtosis appear to be suggesting over-all Gaussian normality within taxa.

Statistical Analysis of Endocranial Volumes by Taxa

Taxa	N	Mean	SD	CV	Skewness	Kurtosis	Maximum	Minimum
A. afarensis	5	445.8	71.84	16.1	0.938	−1.28	550	387
A. aethiopicus	4	431.7	40.4	9.3	1.569	2.45	490	400
A. robustus & A.boisei	9	503.3	28.39	5.6	−0.55	0.51	545	450
A. boisei	6	508.3	23.38	4.6	0.298	0.94	545	475
A. garhi	1	450	na	na	na	na	na	na
A. africanus	9	461.2	49.17	10.6	1.059	0.81	560	400
H. habilis (includes 1813, 1805)	6	610.3	62.03	10.2	−0.624	0.34	687	510
H. erectus *(no ergaster, rudolfensis, georgicus)*	20	951.8	113.5	11.9	0.131	0.62	1220	727
H. soloensis	7	1155.8	83.56	7.2	−0.744	−0.14	1250	1013
H. heidelbergensis	12	1262.8	99.62	7.9	0.856	−0.25	1450	1150
H. sapiens neanderthalensis	28	1427.2	150.55	10.5	−0.005	−1.27	1700	1200
H. sapiens sapiens (includes *idaltu*)	23	1496.5	111.09	7.4	−0.336	0.46	1730	1250
All Australopithecines	28	467.4	51.29	11	0.104	−1.14	560	387
All *Homo erectus* (includes Atapuerca, *heidelbergensis, and soloensis)*	41	1092.9	177.6	16.2	−0.585	0.72	1450	727
Early Homo (includes *habilis, rudolfensis, georgicus*)	13	697.8	104.03	14.9	−0.189	−0.97	848	510
H. rudolfensis	2	788.5	51.6	6.6	na	na	825	752
H. georgicus	2	715	91.9	12.8	na	na	780	650
H. ergaster	3	800.7	49.1	6.1	−0.304	na	848	750

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