THE HUMAN FOSSIL RECORD

Volume Three

Brain Endocasts—
The Paleoneurological Evidence

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WILEY-LISS
A John Wiley & Sons, Inc., Publication

The Human Fossil Record

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The Human Fossil Record, Volume One: Terminology and Craniodental Morphology of Genus *Homo* (Europe)
by Jeffrey H. Schwartz, Ian Tattersall

The Human Fossil Record, Volume Two: Craniodental Morphology of Genus *Homo* (Africa and Asia)
by Jeffrey H. Schwartz, Ian Tattersall

Forthcoming Volume:

The Human Fossil Record, Volume Four: Craniodental Morphology of Early Hominids
by Jeffrey H. Schwartz, Ian Tattersall

Preface

The evolution of the human brain is surely a hot topic, if the number of articles and books written about the subject is any indication. Claims regarding single mutations, language genes, the relevance of microcephalic genes to encephalization; the role of protein in brain growth (and thus the necessity of hunting and scavenging early in hominid evolution); cooling of the brain, the expansion of the pelvis; selection for humor and good looks as a driving force of brain evolution; and the appearance of art as the only valid evidence for our human symbolic capacity are among the plethora of speculation recently put forward. And, this by no means exhausts the list.

It is curious that in all of the scenarios described and for all the speculation provided (e.g., Crow, 2002) not a single source has bothered to examine the actual fossil evidence for human brain evolution, namely the paleoneurological record composed of the brain casts (endocasts) produced from the actual cranial remains of the fossil hominids from *Australopithecus afarensis* of three to four million years ago (MYA)—and potentially in earlier hominid species—through to modern *Homo sapiens*. Although there are a dozen or more brain endocasts of Neanderthals, none of these appear to have warranted examination beyond the amount of water the endocasts can displace or the amount of seeds that can fill their crania. Size clearly trumps all else in these scenarios.

It is true that we will never fully understand how the human brain evolved. Brains do not fossilize, and even if they did, there is no way to read out their behavioral qualities. Still it is nice to know, for example, the volume of the hippocampus, or whether the amygdala was larger or smaller than expected. For the full story we would need many time machines equipped with video-cameras, PET, and MRI scan paraphenalia, dissection tools and microscopes, as well as the ability and tools necessary to collect DNA. Other scientists would take along the brains of extant primates for comparative analyses, despite the fact that such brains, whether of chimpanzees, Bonobos, gorillas, or orangutans, are not ancestral brains but rather those of extant species that have their own evolutionary lines of development.

We prefer a more empirical approach, and that is what this volume is about. Brain endocasts—the casts made from the inside of the skull—are the only direct evidence we have about hominid brain evolution. The data resulting from analyzing such objects is admittedly limited in quantity and quality, but surely far from worthless. It deserves to be examined in the light of all we know from comparative neurology and modern functional neuroanatomy.

This book is not a treatise regarding how the human brain evolved (indeed, we are purposely eschewing controversy over such speculations), but rather a detailed analysis of the direct evidence—the endocasts—and how these show changes through time, both in terms of brain size and what can be ascertained about the brain's organization from surface features—for example, convolutional patterns, cerebral asymmetries, biometrical comparisons, and, thanks to the included contribution of Dr. Dominique Grimaud-Hervé, meningeal patterns of the endocranial surface. What we are striving for herein is a scenario of hominid brain evolution based

on the direct fossil evidence, which consists of brain size, lobar patterns, shape and morphometric analyses, and asymmetries, as each of these variables has some correlation with behavioral variation.

We do not mean to imply that we alone have made this attempt. We stand on the shoulders of others, namely Grafton Elliot Smith, W. E. LeGros Clark, Raoul and J. Anthony, Raymond Dart, G. H. Schepers, Ariens Kappers, Tilly Edinger, Marjorie LeMay, Veronika Kochekova, Harry Jerison, C. R. Connolly, Franz Weidenreich, Phillip V. Tobias, Len Radinsky, Dean Falk, and Wally Welker, and we are indebted to the crews of hominid searchers who have taken the political risks and suffered the hostile elements in their searches to provide the skeletal discoveries that have eventually led to the production of the brain endocasts that we study. This volume is certainly not free of speculation, but we have tried to frame our speculations on the basis of an amalgam of current neuroscience and the fossil record. We have not discovered any genes for language, asymmetries, or reduction of Brodmann's area 17; nor do we know what the distribution of oxytocin receptors were like in the thalamus of *Homo habilis*. We do not know what drove or produced sexual dimorphism in brain size, and we cannot detect sexually dimorphic neural nuclei or fiber tracts in our paleoneurological record. Indeed, we can only guess as to the sexual identities of most of our fossil cranial remains. We have not discovered or uncovered any modules in the hominid brain that we can plug into the EEA. In time, with the future unraveling of DNA and the stereochemical properties of the proteins they help produce, we might have a better picture of the molecular changes that underlie our more gross neuroanatomical variation. Instead, what we find presently in our paleoneurological remains are the variates of size, overall morphology, asymmetries, regional differences in gyri and sulci, and variations in meningeal patterns. We use these to offer speculations about their interrelatedness and evolution through time, and even here we often feel on shaky ground.

Finally, we have not studied these paleoneurological remains to advance any particular taxonomic viewpoint. We do not regard the generic and specific names used for fossil hominids as necessarily writ in stone, and we are not (nor do we wish to be) involved in taxonomic controversies. Indeed, the authors individually disagree on the taxonomic affinities of many of the specimens presented in this volume. To that end, it is worth noting, outside the general text, the taxonomy that we generally adhere to in this volume. We use a conservative (in the sense of mostly consensual) classification where we recognize the species *afarensis, africanus, garhi, aethiopicus, robustus,* and *boisei* of the genus *Australopithecus* (earlier species do exist, but we have no endocranial remains of them as yet). The last thing we wish to become involved in are "splitter-lumper" controversies. If we use the term *Zinjanthropus* or *Paranthropus,* it is in the hope of distinguishing them from other morphs. We believe that mini-adaptive radiations were probable in the earliest phases of hominid evolution. In addition we believe that adaptive radiations were less frequent within the genus *Homo,* and we believe that the species *habilis, erectus, rudolfensis,* and *sapiens* were true species. We regard *H. ergaster, H. heidelbergensis,* and *H. antecessor* as most probably subspecific or "racial" variants of *Homo erectus,* and we regard *H. neanderthalensis* as a within-species variant of *Homo sapiens.* We trust that the series Editors will forgive us. With more fossil materials and more study, it is certainly possible that what we call early *H. habilis,* as represented by OH 7, OH 13, OH 16, OH 24, and OH 62, will turn out to be simply more advanced australopithecines. Indeed, as this Preface is being written, a newly announced discovery from Olduvai Gorge (Blumenshine et al., 2003) suggests that OH 7 and the new OH 65 are the same taxon, thus bringing into question the sanctity of *Homo rudolfensis* as a taxon. The recent designation of the Dmanisi Georgian finds as *Homo georgicus* seems precipitous to us, but we have not seen the fossils nor had access to their endocranial remains. We can state the same for the Atapuerca materials in Spain, known as *Homo antecessor.* We note that White and his colleagues have labeled the Middle Awash hominids of 160 K years ago as *Homo sapiens idaltu,* the latter word meaning "elder," thus suggesting that it was the earliest member *Homo sapiens* but quite possibly of a different subspecies than our own *Homo sapiens sapiens* (White et al., 2003). We find this wholly acceptable. In sum, if we err it is on the side of restricting both genera and species labels to very distinct morphologies, and accepting subspecific labels for what appear to have been either breeding isolates or populations with some degree of chronological and morphological identity.

Whatever the "true" taxonomic relationships of all the hominids, we regard each of the endocasts we have studied as representing once living, breathing, pulsating human or near-human individuals with cognitive capacities and emotions very similar, albeit not identical, to our own. The skeletal and endocranial remains didn't come out of the deposits waving labels, and it is up to us, the social

constructors, to place them into some taxonomic scheme so that we know whom we are talking about. Naming different species, however, implies genealogical distances that we cannot test by their reproductive abilities, and we remain uncertain that our knowledge of the genetic basis of morphological variations warrants assumptions of reproductive isolation in the modern sense of biological species (e.g., Mayr, 1963). While we appreciate that others (e.g., Tattersall, 1999; Schwartz and Tattersall, 2000) prefer to use a morphological species concept, we are skeptical that such discrimination can be applied to indicate a true biological species. We are certain that the morphological differences of endocasts we detail herein are of little value in making taxonomic distinctions, given the wide range of variability seen in size, asymmetries, shape, and morphology of brain endocasts for our own species. If these are sins, please forgive us.

We present this material largely in alphabetical order so that we can follow the rationale and organization of the previous two volumes of the series. We are grateful that the editors have allowed us to present the australopithecine materials in a separate, but alphabetically arranged, section. The genus *Homo* is presented alphabetically within broad geographical regions, namely Africa, Europe, and Asia.

Contents

Introduction

The brain is the central organ responsible for making humans both dramatically different from and yet very similar to our closest relatives, particularly the chimpanzee and the gorilla. The differences are mostly behavioral, involving the ability to learn and generate symbols, to manipulate symbol systems, to communicate with these systems (i.e., true language), to develop very high levels of intelligence, and to develop a large variety of skills, including artistic expression and perhaps other cognitive domains just beginning to be explored. Thanks to this organ and successive generations of humanly accumulated "culture," the human animal holds the fate of the species, indeed all of the earth's species, in its purview. We are the most dangerous animal going and a genus with a very short paleontological record. It remains to be seen how we use this brain that we have evolved over the past few million years.

The human brain is absolutely the largest among primates, and while its relative brain weight is not the highest, the combination of both large absolute and relative size is testimony to the importance of this organ in human evolution. There is also evidence, beyond size considerations, that the human brain is uniquely organized. However, no new structures, either in terms of brain nuclei or fiber, tracts are evident in our own species.

Differences in the quantitative relationships between brain nuclei and fiber tracts among different primate species are referred to as "reorganization" (as first expressed by Smith, 1924, and Dart, 1925, and particularly his 1956 paper; see also Holloway, 1964, 1966, 1967, 1968, 1969, 1979, 1981, 1983, 1995, 1996, 2002; Holloway et al., 2003). These differences suggest that species-specific patterns of behavior have a neural basis, however difficult it is to specify exactly the causal links between neural structure and behavior. Preuss' (2000, 2001; Preuss et al., 1999) findings regarding different connectivity in certain layers of primary visual striate cortex in *Homo sapiens*, as in Brodmann's area 17 (see Fig. 1 for Brodmann's cytoarchitectural maps, and Table 1 for functional roles of these areas), demonstrates species-specific differences without concomitant volumetric differences in neural nuclei or cortical areas, as does the demonstration of different cortical columns by Buxhoeveden and Casanova (2002). The work on oxytocin receptors in the brains of prairie and mountain voles by Insel and Shapiro (1991) also underlines for us the importance of reorganization at yet another neural level, that of neuroreceptor sites (see Fig. 2 for examples of reorganizational changes possible without volumetric differences in total brain size). In addition the human brain shows different degrees of cerebral asymmetries than known for pongid brains (Holloway and de Lacoste, 1982). Indeed, our difficulty in accepting Jerison's (1973, 2002) view regarding the triviality of the reorganization concept for humans has recently been reinforced by Finlay et al. (2001; see also Holloway, 1974, 1979, 2002, for critique) who showed that there is a large neurogenetic (thus developmental) constraint operating in most of the animal kingdom,

The Human Fossil Record, Volume 3, by Ralph L. Holloway, Douglas C. Broadfield, and Michael S. Yuan.
ISBN 0-471-41823-4

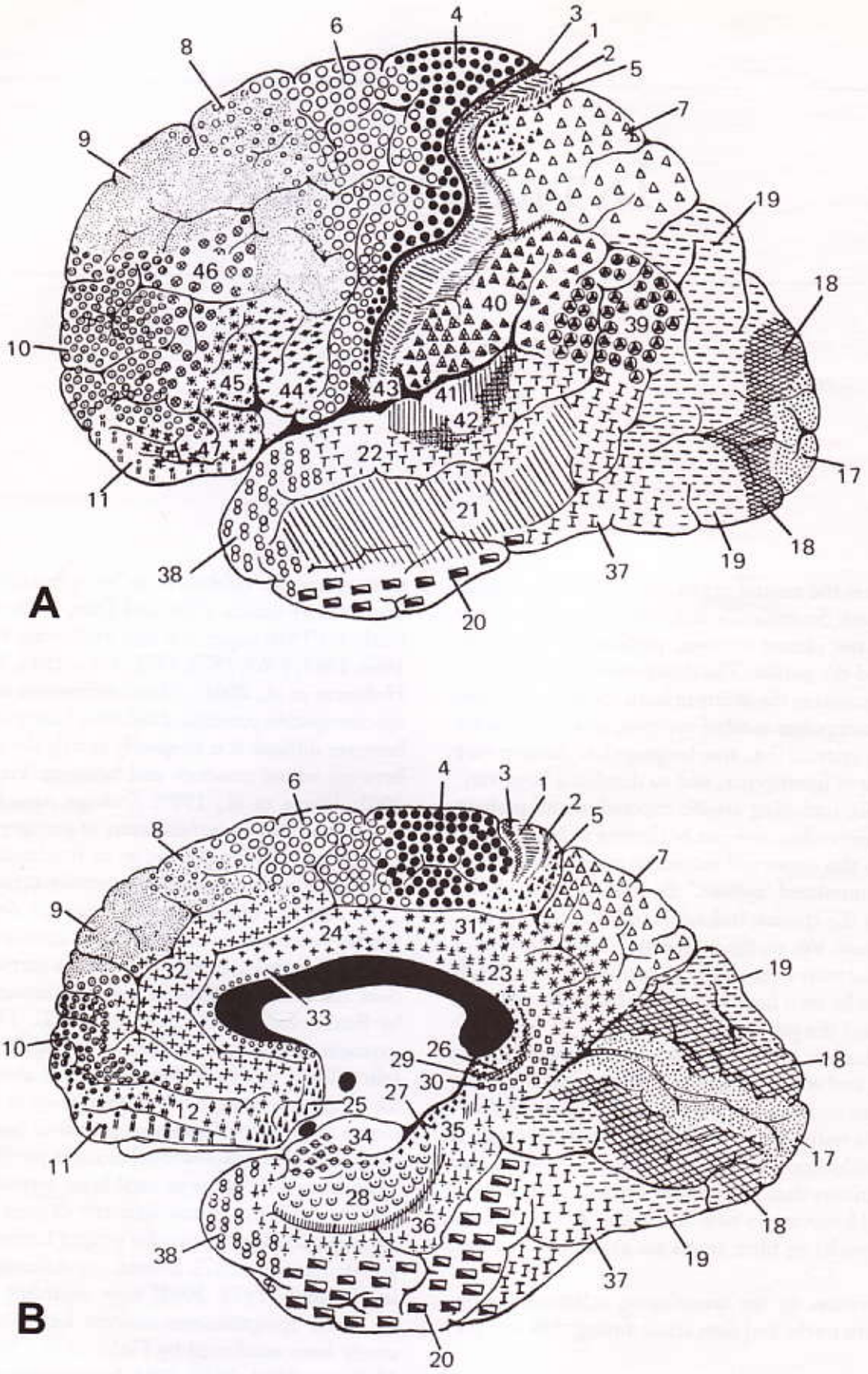

Figure 1. Brodmann's (1909) cytoarchitectural maps of the human brain. **A**: Lateral view; **B**: Medial view.

TABLE 1 **Major cortical regions in early hominid evolution**

Cortical Regions	Brodmann's Areas	Functions
Primary visual striate cortex	17	Primary visual
Posterior parietal and anterior occipital (peri- and parastriate cortex)	18, 19	Secondary and tertiary visual integration with area 17
Posterior parietal, superior lobule	5, 7	Secondary somatosensory
Posterior parietal, inferior lobule (mostly right side; left side processes symbolic-analytical)	39	Angular gyrus; perception of spatial relations among objects; face recognition
Posterior parietal, inferior lobule (mostly right side; holistic, gestalt processing)	40	Supramarginal gyrus, spatial ability
Posterior superior temporal cortex	22	Wernicke's area, posterior superior temporal gyrus; comprehension of language.
Posterior inferior temporal	37	Polymodal integration, visual, auditory; perception and memory of objects' qualities.
Lateral prefrontal cortex	44, 45, 47	Broca's area (Broca's cap), motor control of vocalization, language
	(also 8, 9, 10, 13, 46)	Complex cognitive functioning, memory, inhibiton of impulse, foresight, etc

and in particular, mammals, although they downplayed the very real differences in species-specific behavior patterns that are underlain by small or sometimes large reorganizational shifts in neural nuclei and fiber tracts.

Progress in both field and laboratory studies of chimpanzees, and studies using noninvasive imaging techniques, such as PET, may eventually provide us with a better understanding of how neural structures and processes underlay observable and testable behavioral patterns. In the meantime comparative and paleontological records provide the best available data regarding how the human species evolved from essentially bipedal, small-brained, small-bodied apes some 5 to 7 million years ago (MYA).

Lines of Evidence, *Direct* and *Indirect*

This volume is devoted almost exclusively to one line of evidence regarding human brain evolution, namely paleoneurology. While we also rely on the comparative neurological data that exist for modern primates, such as data regarding their brain and body weights, neural nuclear sizes, and cytoarchitectonic patterns in the cerebral cortex and other structures, only brain size is readily available from the human fossil record (aside from some controversial interpretations of cortical sulcal patterns and cerebral asymmetries), and these data are provided by brain endocasts. As noted (Holloway, 1966, 1968, 1975, 1979, 1983, 1996), we consistently regard the comparative neurological data as *indirect* because it is data for extant species, not ancestral forms. The brain endocasts of our fossil ancestors are the only *direct* evidence from paleontology.

It is important to understand that the *indirect* evidence from extant brains is as rich and as varied as our techniques do or will allow, and that this evidence is indispensable in enlarging our understanding of the relationships between neural and behavioral variation in different living animals, as studied both under natural and laboratory conditions. We particularly recommend the excellent paper by Geary and Huffman (2002), which discusses these issues completely. How the evidence from comparative neuroanatomy is used to infer the evolutionary dynamics in our species' brain is, however, often dependent on what is being viewed in evolutionary terms. For example, the concept of reorganization in human brain evolution might be a trivial concern if one is examining broad genetic and evolutionary conservatism between large numbers of taxa as do Finlay et al. (2001) and Jerison (1973) before them. Indeed, if one is trying to explain species-specific differences in behavior, for *Homo sapiens* or even for all animal species, the constraints become trivial while the reorganizational events rise in importance (Holloway, 1974, 1979, 2001).

We expect the principle of uniformitarianism to operate, allowing us to move from the extant *indirect* evidence to speculations about the *direct* evidence manifested in the brain endocasts of the fossil record. It is no secret, of course, that the *direct* evidence is very limited, since brains do not fossilize, thus rendering forever

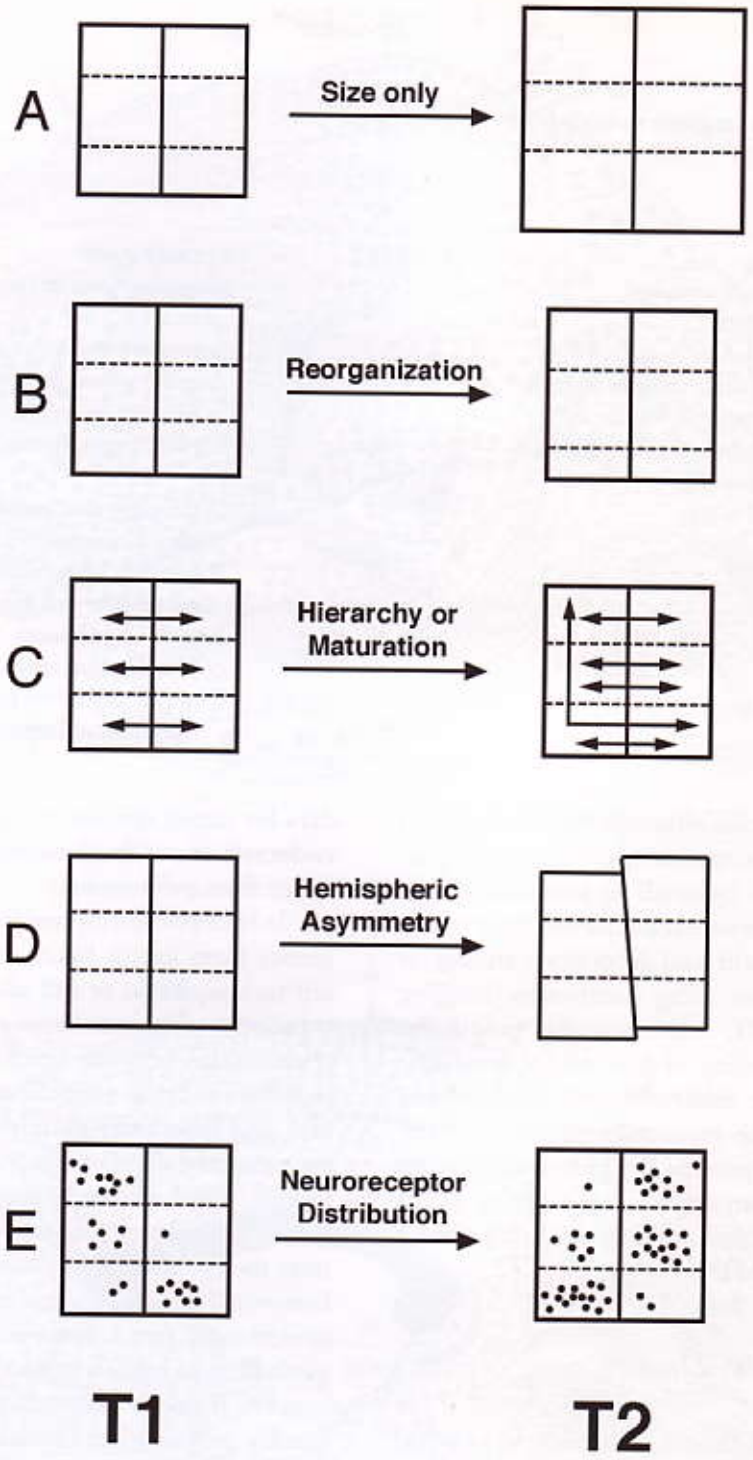

Figure 2. Possible scenarios of brain changes through time (T1 to T2). **A**: The brain, shown with two hemispheres (left and right), and two transverse dotted lines that represent the central and lunate sulci, respectively. The change from T1 to T2 is simply an increase in size (absolute) without any change between the size of components or connections between them. This change could occur isometrically or allometrically. **B**: The change from T1 to T2 does not involve any change in absolute brain size, but rather a change in components, such that the lunate sulcus is placed more posteriorly, thus expanding the posterior portion of parietal association cortex. This is a reorganizational model. **C**: Changes in hierarchical development without any change in absolute brain size from T1 to T2. The arrows represent fiber systems maturing at different rates and/or increasing in number between different cortical regions through the corpus callosum, although other brain structures and fiber systems could be involved. **D**: Absolute brain size remains the same from T1 to T2, but a more human-type of hemispheric asymmetrical petalial pattern emerges (i.e., left occipital, right frontal). **E**: Absolute brain size remains the same from T1 to T2, but there is a redistribution of neuroreceptors.

mute (but we hope not also moot) the actual neural organization that existed in the past.

When considering the interplay between direct and indirect lines of evidence, two important facts should be kept in mind. First, hominid and pongid lines have been separated in their evolutionary development for some 5 to 7 million years, and second, we have no brain endocasts representing fossil pongid evolution from the split of 5 to 7 million years ago to the present, as evidenced by extant species of chimpanzee or gorilla. Therefore one should always view with a modicum of skepticism the tendency to rely on observations from extant primate neuroanatomy and behavior, the latter from both field and laboratory studies, when we extrapolate from these studies to the evolutionary development of our own species.

Brain Endocasts

What Is a Brain Endocast?

A brain endocast is nothing more than a cast that is made of the interior of the neurocranium of a skull, which is that part of the cranium that houses the brain. From here on, we refer to these as simply *endocasts*, the term "brain endocast" actually being redundant. Endocasts may be *natural* or *human-made*. We speak of a *natural* endocast as one that results when, after death, the cranium is infiltrated with fine sediments through the cranial foramina, including the foramen magnum. In time these sediments filling the cranium, or some part of it, become indurated with calcareous water secretions that eventuate in a rock-like cast inside the cranium. This process probably takes hundreds if not thousands of years, although no one really knows how long it takes to make a natural endocast. The famous Taung, Sts 60, SK 1585, types II and III, from South Africa are well-known examples of *natural* endocasts. Some endocasts have an almost gem-like quality to them, and indeed, the medial side of Taung is replete with calcite crystals.

Human-made endocasts (e.g., all of the genus *Homo* from Asia, Africa, and Europe) are casts made by applying a molding material, such as liquid latex rubber or silicon rubber to the inside of the cranium or a portion thereof. After the application of the requisite number of coats and the drying of the molding material, the cast is peeled away from the cranial fragment(s) and is ready for reconstruction, examination, measurement, description, and so on. Often the *human-made* endocast is only partially complete. Cast from incomplete cranial fragments, it is reconstructed by adding modeling clay or plasticene to the missing sections to best effect an accurate approximation of the overall size and shape of the original brain. Endocasts can also be made from either hemisected or whole crania. Many endocasts in other collections, such as at University of the Witwatersrand, have been made simply by pouring plaster-of-Paris into cranial portions.

Endocasts are also made from extant animal species, and animal endocasts have become important components of the comparative collection. At Columbia University alone we have a collection of some 40 *Gorilla gorilla*, 36 *Pan troglodytes*, and 44 *Pan paniscus* whole brain endocasts, just to mention the African apes, with dozens more of *Pongo* and *Hylobates*. These endocasts were made from specimens borrowed from various museums and institutions.

Historically the study of brain casts is relatively old. Tilly Edinger (1949), in her historical paper, mentions Oken's observation in 1819 of some petrified mud in a pterodactyl skull, and similarly references that of a crocodilian by Owen in 1841. By 1929, Tilly Edinger had counted some 280 papers devoted to such studies, with another 137 in her survey of 1937. Edinger championed paleoneurology as an important corrective to comparative neuroanatomy that had, and still has, a tendency to regard living extant brains as evidence of evolutionary lines of descent, a tendency that has been particularly common in much of psychology and comparative neuroscience, as well as anthropology. Edinger's (1949) study of the evolution of the horse brain, a classic text that integrated data on size and organizational changes throughout the Tertiary, is still worthy of citation:

> *On the other hand, paleontology can . . . reject the continuation* of the quoted sentence, "*until in man*, we have the great development of the frontal areas . . ." The brain of *Homo sapiens* has not evolved from the brains it is compared with by comparative anatomy; it developed within the Hominidae, a late stage in the evolution of this family whose other species are all extinct.

Another valuable historical treatise on endocasts is "Paleoneurology," written by Veronica Kochetkova (1978) with important editing by Harry and Irene Jerison. This book deals almost exclusively with the paleoneurology of hominids and quantitative arc-chord measures of their endocasts, various methods used to calculate endocranial volumes from linear measurements, and also provides a valuable historical overview of primate paleoneurology. Nonhuman primate paleoneurology was best covered by the numerous writings

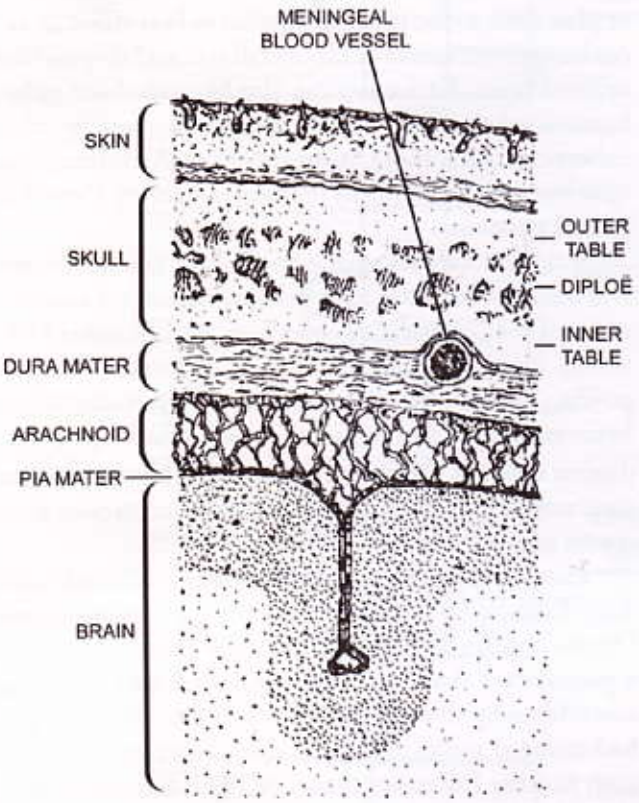

Figure 3. Tissue layers of the skull and brain.

of the late Len Radinsky (e.g., 1972, 1975, and 1979) whose premature death robbed paleoneurology, primatology, and anthropology of an extremely skilled worker and valued colleague. Additional sources that examine the history of paleoneurology can be found in Hirschler (1942), Connolly (1950), Gurche (1978), and Falk (1992).

What Data Can Brain Endocasts Provide?

Before we discuss the data available from endocasts, whether natural or human-made, it is necessary to explain exactly what is being cast. An endocast is *not* a cast of the brain; it is a cast made of the internal table of cranial bone. In life, three layers of tissue surround the brain (Fig. 3). (1) Immediately investing the brain is the **pia mater** that enfolds the brain and penetrates into the sulci of the brain. (2) Surrounding the pia mater is the **arachnoid** tissue, a fibrous layer that holds the **cerebrospinal fluid** (CSF), which acts partially as a shock-absorbing device to the surface of the brain against external insults. (3) Surrounding the arachnoid tissue is the dense, thicker and tough **dura mater**, whose outer layer adheres to the internal table of cranial bone. It is these three layers that naturally "conspire" against the living brain making a totally faithful impression of all its gyri and sulci against the internal table of cranial bone (e.g., see Symington, 1916; Clark et al., 1936; Clark, 1947; Hirschler, 1942; Tobias, 1991).

Some gyri and sulci can, and do, imprint themselves through these tissues and leave traces on the internal table of bone, but this is a highly variable, and at present, an unexplained phenomenon (e.g., see Welker, 1990; Tobias, 1991; Connolly, 1950). As we will see, the endocasts of the Pliocene gracile morphs from South Africa show rather more convolutional detail than do *Homo* endocasts. Among the African apes, *Gorilla* endocasts show almost no convolutional details in comparison to endocasts of *Pan troglodytes*. In general, primary sulci such as the Sylvian or lateral fissure are present in endocasts, but fine secondary and tertiary convolutions of the frontal, parietal, and temporal association cortex are seldom visible. The Rolandic or central sulcus, though, is never present on hominoid endocasts, most likely because the arachnoid tissue and CSF form a cistern (accumulation) in that region. However, it is inaccurate to say that *no* gyri or sulci imprint upon the internal table of cranial bone; rather, the process is variable. Indeed, as we will see throughout the following descriptions, some important sulcal details are occasionally available from endocasts.

THE DATA

Size

Endocasts provide an estimate of cranial volume. We usually refer to cranial volume as *cranial capacity*, and this in turn provides an estimate of actual *brain weight*. Brain weight and cranial capacity are not, of course, identical, but are often regarded as practically synonymous, cranial capacity being on the order of roughly 10% greater than brain weight. Cranial capacity is greater because it includes the meninges, CSF, and cranial nerves. Anne Weaver (pers. comm.) has developed an algorithm for calculating brain weights from cranial capacity, which is:

$$\text{Brain volume (in cc)} = 18.575 + 0.7689 \times \text{Cranial capacity}$$

This formula is based on a sample of 12 human brains, and provided an R^2-squared of 0.99.

The cranial capacity of a brain endocast is usually measured by the technique of water displacement. The displaced water can be either measured

volumetrically (i.e., with a graduated cylinder), or, thanks to Archimedes' principle, can be weighed directly. (This author has always found the weighing of displaced water more consistent and accurate.) On comparative endocast collections that are from complete crania, the volume of water displaced is weighed directly to the nearest gram.

The endocasts in our collection at Columbia University were made using liquid rubber latex (Admold 3820). The layers were vulcanized by heat, and this shell was removed from the inside of the cranium. The endocast was floated in water as the shell was filled with liquid plaster of paris to equalize hydrostatic pressures and provide stability to the endocast shell. The whole is allowed to harden while immersed in water (Holloway, 1970a, 1973, 1975, 1978a, b).

The accuracy of size determinations from endocasts depends on at least two key factors: (1) completeness of the endocast and added reconstructed portions, and (2) lack or presence of distortion of the endocast.

Completeness of the Endocast. The endocast of Sts 5, Mrs. (or Ms.) Ples, is a complete endocast providing an endocranial volume of 485 ml, while that of the Taung specimen lacks a portion of the prefrontal region of the endocast, which must be added, and includes matrix that must be removed prior to measuring. The Taung specimen yielded an endocranial capacity of 404 ml, which is considerably lower than the 525 ml originally reported by Dart in 1925 (Holloway, 1970b). This represents not an adult volume, but a child's value, which is calculated to be 440 ml on the basis of the dentition. When the greater the part of the endocranium is missing, the reconstruction is less reliable. The reconstruction returns the missing volumetric portions by following the shape outline of what is present by replicating the most probable missing brain portions.

In earlier papers (e.g., Holloway, 1973, 1975), it was indicated that each endocast requires its own methodology. For example, Method A refers to "direct water displacement of either a full or hemi-endocast with minimal plasticene reconstruction" (Holloway, 1973: 450), such as with Taung, STS60, STS5, and SK1585. Method B refers to "an ascertainment based on the partial endocast method as described by Tobias (1967, 1971)" such as with STS19/58, MLD 1, or OH7, where undistorted portions of an endocast are compared to the whole endocast as a proportion. Method C "uses extensive plasticene reconstruction involving close to half of the total endocast" and Method D refers to the formula

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

described by Mackinnon et al. (1956). Here f is determined from other complete endocasts of the same taxon, or closely related endocasts (Holloway, 1973: 450), L is endocast length from frontal pole to occipital pole, W is maximal width or breadth of the endocast usually taken at the superior temporal level, B is the length from bregma to basion, and H is the distance from vertex to deepest portion of the cerebellar lobes. Examples of Method C would be OH 13, OH12, and Krapina 3, while Method D would include endocasts such MLD37/38 and KNM-ER 406. Kochetkova (1978) provides several additional equations that some workers have used in the past. In addition Holloway (1973, 1975) suggests a four-point scale to use in a subjective evaluation of confidence in the accuracy of determination, depending on the overall completeness of the original, amount of distortion, and so on, with 1 being the highest in confidence. On this basis the Taung 404 ml volume would be scored a 1 and MLD37/38 a 3 or 4.

Lack or Presence of Distortion of the Endocast. A partial and deformed demi-cranial example is that of Sts 71. At the right side there was plastic deformation of the occipital region and a medially depressed collapse of the temporal lobe (Holloway, 1970a, 1972, 1999). When it was first measured, after correcting for postmortem distortion, Holloway (1972) reported a volume of 428 ml. More recently Falk (1998) and Conroy et al. (1998) suggested a drastically lower volume of 375 ml, apparently unaware of the distortion. Shortly after Conroy et al. (2000) validated the earlier Holloway (1972) determination by taking distortion into account. As we will learn in the chapter on australopithecines (e.g., AL 444, Stw 505, OH 24, and the Bodo specimen), distortion can significantly affect volume determinations.

Morphometric Data (See also Part 2: Methods and Materials of Endocast Analysis)

Endocasts not only manifest overall size; they also manifest shape, which can yield both absolute measurements (chords and arcs between landmarks) and indexes or ratios between measurements. Commonly measured are cerebral length (measured from the frontal to occipital poles), maximum breadth or width, cerebral height

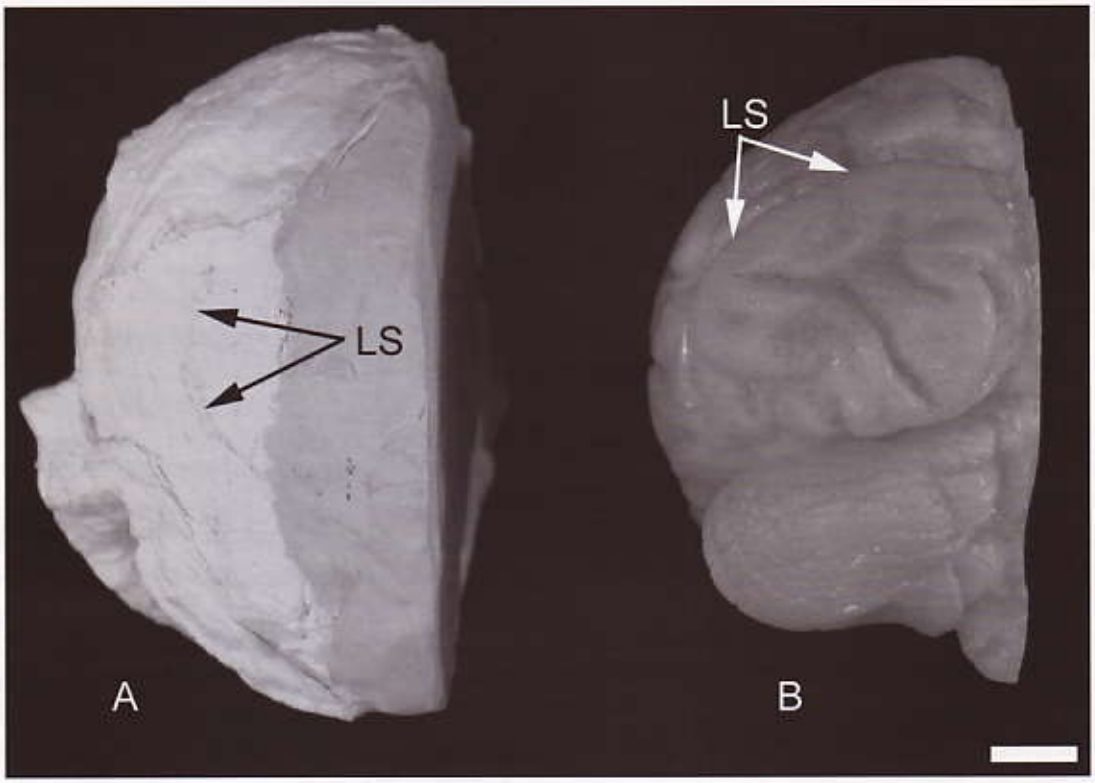

Figure 4. Demonstration of the location of the lunate sulcus (LS) in Stw 505 (A), and *Pan troglodytes* (B) (scale = 1 cm).

(vertex to the deepest portion of the temporal lobe), and width of the cerebellar lobes. Other measurements are included depending on the degree of completeness of the endocast. Sometimes it is possible to measure distances between particular sulcal landmarks and to compare these and their attending indexes with those found on actual brains, for example, as between the chimpanzee brain and the Stw 505 endocast, to ascertain the relative position of the lunate sulcus, which delimits the anterior extent of the primary visual striate cortex (PVC), or area 17 of Brodmann (Fig. 4). Connolly (1950), Kochetkova (1978), and Grimaud-Hervé (1997) offer numerous linear and arc measurements and indexes in their descriptions of endocasts and brains.

Another morphological approach has been to stereoplot radial distances from the endocast surface to a homologous central reference plane (e.g., going through the frontal and occipital poles), using a variety of multivariate statistical techniques, to compare surface shapes between taxa once size has been corrected for (e.g., Holloway, 1978b). This technique has revealed that the shape of the transitional region between Brodmann's area 17 and posterior association cortex showed the most shape change. More recently MacLeod et al. (2002) have used computer-imaging techniques to do the same thing (i.e., depict shape changes on brain endocast surfaces of particular fossil hominids from an average configuration). The degree of differences can then be color-coded, showing "hot" and "cold" spots or regions. Unfortunately, this method misses important neurological reorganizational changes that are not always reflected as shape changes, such as the reduction of Brodmann's area 17, PVC.

In addition observations on the shape of particular regions can be made as, for example, regarding the roundedness or lack thereof of the prefrontal lobes, or whether the third inferior frontal convolution, which includes Broca's area, has a more human or pongid-like appearance. Do the cerebral hemispheres overhang the cerebellar lobes? These characteristics, and many other considerations, require an appreciation of what brain endocast shapes provide, and can lead to useful hypotheses, based on actual measurements. In general, the divisions between the various cerebral lobes (frontal, parietal, temporal, occipital) are not actually visible on brain endocasts, given the distribution of CSF and meninges, so quantitative estimates of cerebral surface areas are at best only approximations.

Asymmetry Observations and Measurements

As is well known, the cerebral hemispheres are rarely perfectly symmetrical, and depending on the degree of preservation of cerebral portions from the left and right sides and the lack of distortion, one can observe whether or not there are petalial patterns, which suggest the possibility of hemispheric specializations such as handedness and language capabilities (LeMay et al., 1976). Petalias are simply extensions of the cerebral cortex into the internal table of cranial bone. For example, the human brain shows a torque growth in which, for right-handers, there is a left occipital petalia combined with a right frontal petalia. If one looks dorsally at a human brain of a right-handed person, one will often see that the left occipital extends further back than the right, while the right frontal width appears somewhat wider than the left. The opposite condition holds for most left-handers. *It is important to realize that these relationships are correlational only, and not obligatory* (see Holloway and de Lacoste-Lareymondie, 1982).

While pongid brains certainly show asymmetries (with *Gorilla gorilla* having the most asymmetrical cerebral petalias; see Groves and Humphrey, 1973), they almost never show the typical human pattern of combined occipital and frontal petalias described above. The fossil hominids, to the extent that both sides of the cranial bone are available and without significant distortion, can provide speculative suggestions regarding a limited degree of their cognitive capacities. Most of the work done on these asymmetries has been only crudely quantitative, as exact measures of the asymmetries are difficult to obtain without sophisticated specialized equipment. We believe CT-scanning and 3-D reconstructions will be extremely valuable techniques for providing more reliable metric observations on these potentially very significant asymmetries.

In addition we are studying the possibility of asymmetries in the Broca's cap regions of the fossil hominid endocasts. Our data thus far suggest that where the left Broca's cap region in modern *Homo* appears, the asymmetries are larger than on the right, at least for most right-handed individuals (Broadfield et al., 2001; Broadfield and Holloway, 2002). Broca's cap (a.k.a. frontal cap, orbital cap), introduced by Raoul Anthony (1913) when describing the La Quina brain endocast, refers to the third inferior frontal convolution, which includes primarily Brodmann's areas 47 and 45 and a portion of area 44. We are intrigued that such asymmetries have been clearly shown for modern *Homo sapiens* by Amunts et al. (1999, 2003) and Foundas et al. (1996, 1998). They appear also on the small sample of brain casts that we made for modern *Homo sapiens* (Broadfield and Holloway, 2002), and appear on a number of Indonesian endocasts of the morph currently designated as *Homo erectus* (Broadfield et al., 2001). Needless to say, since these regions in modern *Homo* have a clear involvement in parts of language processing, we are intrigued that similar asymmetries are seen in specimens perhaps as old as 2.0 million years (MY), as in KNM-ER 1470, for example. This idea has recently been challenged by Cantalupo and Hopkins (2001), who claim, on the basis of MRI images, that chimpanzees show such asymmetries as well. However, as Sherwood et al. (2003) demonstrate using cytoarchitectonic methods, the sulcal patterns in apes do not match the cytoarchitectonic differences found between Brodmann's areas 44 and 45. This leads us to conclude that MR images of sulcal patterns do not describe important functional differences, although it is important to start with gross morphological patterns of the cerebral cortex. We believe that it will be necessary to quantify the cytoarchitectonic differences between Broca's areas 44 and 45, and possibly 47, and between left and right sides in both apes and modern humans before this issue can be settled. The recent paper by Amunts et al. (2003) demonstrates clear asymmetry in cytoarchitectonic areas 44 and 45 of Brodmann as early as age 1 in infants, increasing significantly in area 45 with age and thus perhaps demonstrating both neurogenetic and microstructural plasticity related to language functions.

Meningeal Patterns and Blood Supply (Arterial and Venous)

The dura mater is supplied with blood vessels, known as meningeal vessels, and these frequently leave imprints on the internal table of bone. The patterns of these vessels have some importance as taxonomic markers (e.g., see Saban, 1984; Grimaud-Hervé, 1997), although this remains controversial. These vessels, as far as we know, have nothing to do with cerebral structure and function. However, the major venous vessels such as the longitudinal, transverse, and sigmoid sinuses provide important taxonomic information, and here too there is considerable speculation regarding their functional significance. As we will show later when we discuss the occipital/marginal (OM) sinus, which as been used as a claim to "robust" australopithecine membership (White and Falk, 1999; Falk et al., 2000; Holloway et al., 2002), the meningeal vessel structure appears in all primate taxa, including modern humans. As the true arterial blood supply to the brain arrives via the carotid arteries, the actual blood supply to the brain is almost

totally internal to the surface and thus not detectable on an endocast. We are delighted that Dr. Grimaud-Hervé has shared her knowledge of meningeal variations with us in this volume, and that her husband has provided such fine illustrations of these patterns.

BIOBEHAVIORAL SIGNIFICANCE OF BRAIN ENDOCASTS

Absolute Brain Size

As mentioned above, brain endocasts are not rich sources of information about the structure or functioning of the brain. Aside from size and coarse lobar configurations, such as the presence and placement of the lunate sulcus, or the region of the third inferior frontal convolution usually designated as Broca's area, or degrees of hemispheric cerebral asymmetries, brain endocasts remain mute testimony to what their once-living cerebral and subcortical contents could do.

The human species seems to be particularly attuned to matters of size, whether of the brain or other anatomical parts, and this for a variety of reasons. First, size is something that can be measured, and measurements can either be replicated or not. Intuitively we all assume that the size of something has some relationship to its effectiveness and power (as well as its cost, metabolically), and that we can in essence find the importance of the entity displayed in the property of size variation. Our brains are three to four times larger than those of our closest relative, the chimpanzee, whose brain in turn is roughly three times as large as those of the Old World monkeys, such as macaques and baboons. For brain size in these species, we regard the correlation, however crude, with behavior to be self-evident. We also tend to believe that organs that vary in size and that have some relationship to behavior follow a Darwinian evolutionary model. Indeed, this is basically how we tend to view our own braininess, that our brains became larger, and our larger brain sizes were selected for as we evolved because we were capable of more complex and intelligent behavior. We even recognize that there had to be constraints on this paradigm, at least in terms of two factors, namely metabolic costs and parturition, with the latter having to do with the size of the infant's head and the pelvic inlet and outlet and the efficiency of bipedal locomotion. The evidence points to our early ancestors of 3 to 4 MYA having brain sizes around 400 ml and our cranial capacities being around 1400 ml; the intermediate values for early and later *Homo* are, in this view, thought to reflect some natural selective forces operating on brain size and intelligent behavior correlated with it. On the other hand, the more micro-evolutionary events in our brain's evolution are not transparent. There may well have been times when natural selection favored larger body sizes, and the brain, due to its allometric relationship with body-size, increased *without* selection necessarily acting on behavior. Also, selection for increased body size might have resulted in increased brain size, as the two variates are related.

There are problems inherent in simply accepting past brain size as an indicator of increasing behavioral sophistication in the fossil record. If natural selection worked in the past to increase our brain size, isn't brain size today also being selected for (or against)? And therein lays the rub, so to speak. The variation in modern human brain size, which ranges in weight from 900 to 2000 grams, is roughly the same as the total evolutionary change in brain size from *Australopithecus* to us, which is about 1000 ml. One of the cardinal lessons human biology has evinced is that variation in modern brain size has no significance for modern human behavior. To believe otherwise is, simply put, discriminating and racist. The conundrum we end up with is how can we explain the evolutionary past if there is no significant behavioral correlation between intelligence (however defined) and our brain size? Assuming that 3 MY separates ourselves from *Australopithecus*, 1000 ml divided by 3 MY gives a very rough estimate of 0.000333 ml per year, or about 0.00666 ml per generation, if a generation is calculated as 20 years long. It simply eludes our imaginative abilities to believe that even changes of 1 to 10 ml could have any effect on behavior. We cannot even measure what 0.00666 ml of brain tissue might mean in any computational sense. If we go in the reverse direction, and try to argue that 1000 ml has made an enormous difference in our intellect over the past 3 MY, should we expect through uniformitarianism principles that today's individuals at the low end of brain size (i.e., around 1000 ml), should be considerably less intelligent than those with brain sizes around 2000 ml? Well, in fact, some writers do argue that the difference between a mean brain weight of 1350 grams and 1300 grams is indicative of a difference in intelligent behavior (e.g., see Rushton, 2000, 2002, who has perhaps gone the farthest with this idea).

It has been almost uniformly accepted by the anthropological community that the correlation between brain size and intelligence is negligible, and surely insignificant, yielding at most an R coefficient of about 0.25 (e.g., see Van Valen, 1974, who argued that small differences could be important over many generations).

More recent research, using noninvasive MRI techniques has published correlation coefficients (R) varying between 0.4 to 0.6 with statistical significance in college students (for a review, e.g., see Willerman et al., 1991; Andreasen et al., 1993; Tramo et al., 1998; Anderson, 2003). To this, we can bring forth many objections with the basic concepts of brain size, "intelligence," statistical comparisons, and the like, and include the fact that men and women differ significantly in brain size (men being on average about 9–10% larger in brain size) but not in terms of intelligence. Of course, a full discussion of this point would take us far beyond the scope of this book; we raise it to show the problems inherent in blithely accepting past brain size as an indicator of increasing behavioral sophistication in the fossil record. This relationship is almost impossible to scientifically demonstrate without comparing our own species' variability in this regard (or other species), something most scientists are loathe to do.

Nevertheless, none of the considerations above will ever deter us from measuring how large/small our fossil ancestors' brains were. Nor will they prevent us from measuring brain size against time within and between taxonomic levels to attempt to ascertain changes in selection pressures (e.g., see Holloway, 1975, 1981 for specific illustrations of brain size/time models possible).

Relative Brain Size

As mentioned at the beginning of this chapter, as primates, we have the largest absolute brain size, but not the largest relatively speaking. Could it be that our relative brain size was really more important in our evolutionary development than our absolute brain size? And, isn't there a relationship between the size of our brains and our bodies within the primate order? The latter question is clearly answered in the affirmative, as the study of the relationships between sizes of organs and the body—the study of *allometry*—attests.

We know, for example, that when we plot the logs (base 10) of brain and body weights together for all the primates, there is a clear-cut allometric relationship with an exponent of about 0.75 (Martin, 1983), suggesting a metabolic relationship. Relatively speaking, we have about three to four times the brain size expected for a primate of our body size, our brain size being around 2% of our body size. Indeed, knowing our brain and body size allows us to compute a coefficient known as the encephalization coefficient (EQ), by which we can measure ourselves against other animals. Such coefficients are themselves relative, since they depend on the database used to derive the basic brain/body allometric equations (see Holloway and Post, 1982, for discussion of the relativity of relative brain measures). One thing is certain, however: whichever databases we use, whether for all primates, all mammals, or just the great apes, we (modern humans) always end up with comforting finding that we have the highest value.

It must be underlined that EQs are relative, depending on the data set chosen. For example, some of the most cited EQs are those resulting from Jerison's (1973) equation,

$$EQ = \frac{\text{Brain weight (of any species)}}{0.12 \times \text{Body weight}^{0.66}}$$

Humans have an EQ of 6.91, the chimpanzee 4.02, and the gorilla 1.8, using Jerison's equation and the values for body and brain weights in Holloway and Post (1982: 63). It should be remembered here that Jerison purposefully fitted a slope of $^2/_3$ (0.66) to his polygon, including the "higher vertebrates" and that that slope was not empirically determined, in contrast to Martin's (1981, 1983; see also 1990) equation. But, if we use the allometric equation based on 88 species of primates (Bauchot and Stephan, 1969), the constant is different (0.0991) and the exponent is 0.76. In this case the human EQ is 5.46, the chimpanzee 2.25, and the gorilla 0.939.

Since the human animal remains the most encephalized primate known, we offer an EQ equation that provides an immediate percentage of the modern human value for each species of primate:

$$EQ = \frac{\text{Brain weight}}{1.0 \times \text{Body weight}^{0.6409}}$$

In this example, the human EQ is 100, or unity, based on an average brain weight of 1330 grams for modern *Homo sapiens* and an average body weight of 65,000 grams (Tobias, 1971). We further assume that if there is no body weight, there is no brain weight, and the regression line falls through the origin. By this equation, the chimpanzee EQ is 39.5%, and the gorilla EQ is 19.1%. To obtain these EQs, we used a chimpanzee brain weight of 420 grams, and a body weight of 46,000 grams. For gorilla, we used an average brain weight of 465 grams, and a body weight of 165,000 grams (these are the values given by Stephan et al., 1981). The value of brain weight for chimpanzee is on the high side, the value for gorilla on the low side (see Holloway and Post, 1982, for further discussion).

Of course, when the EQs calculated by a particular equation are divided by the human EQ value (whether Jerison's, Martin's, Holloway and Post's, etc.), the results can be expressed as a percentage of human value. Rank order correlation of these results provides a correlation of at least 0.9, indicating a close but not perfect agreement. Thus the rank of EQs for some animals changes depending on the database used. We prefer the **homocentric** equation simply because it gives in percent an immediate EQ of the average modern human value. However, we wish to make the point here that EQs do not evolve. EQ values may increase or decrease for an animal line depending on the equations used, but what is changing are brain/body weight variables, which may or may not be under selection pressures at any given time.

The application of these equations to particular fossil hominids requires an accurate estimation of body weights, and in a given living population these vary considerably. For example, based on a data set of 48 chimpanzee brain and body weights, the EQs (using Holloway and Post's *Homo*centric equation) varied between 29% and 57% of the modern human value of 100%, while for 23 gorillas, the EQs varied between 17% and 37%. Using the Danish brain weight sample discussed in Holloway (1980), and culling out extreme body weights, adult human EQs varied between 70% and 145%, the average and modal value being 100%. Consequently we should expect some of our early hominids to overlap with chimpanzee EQ values.

In our quest to better understand the changes in our own "encephalization" through time, we require not only accurate determinations of brain sizes but also of body sizes. The fact is, however, that none of our fossil finds, aside from whole skeletons, ever provide us with enough material to obtain highly accurate body weights. Much fine work has been done (Jungers, 1988; McHenry, 1988, 1992; Ruff, 1990, 2000, 2003) in trying to estimate body weights from partial skeletal materials, such as limb bone lengths, using comparative and human skeletal materials where body weights are known, but these still only provide estimators that are less accurate than brain sizes. Nevertheless, a study of these relationships is useful as it has already shown that mid-Pliocene hominids were more encephalized than their more recent pongid-like ancestors. This result alone suggests natural selection to have worked on relative brain size early in our evolutionary history, since these hominids had roughly the same brain sizes as our largest chimpanzees, which is around 400 to 450+ ml. To the degree that data are available, we will discuss the relative brain sizes and possible advances in encephalization in a later chapter on specific hominid taxa.

The Reduction of Primary Visual Cortex and the Lunate Sulcus

One of the few measurable differences between the gross neuroanatomy of human and pongid brains, aside from overall size, is that the primary visual striate cortex (PVC)—Brodmann's area 17—is relatively reduced in volume in the human brain. Figure 5 shows a typical

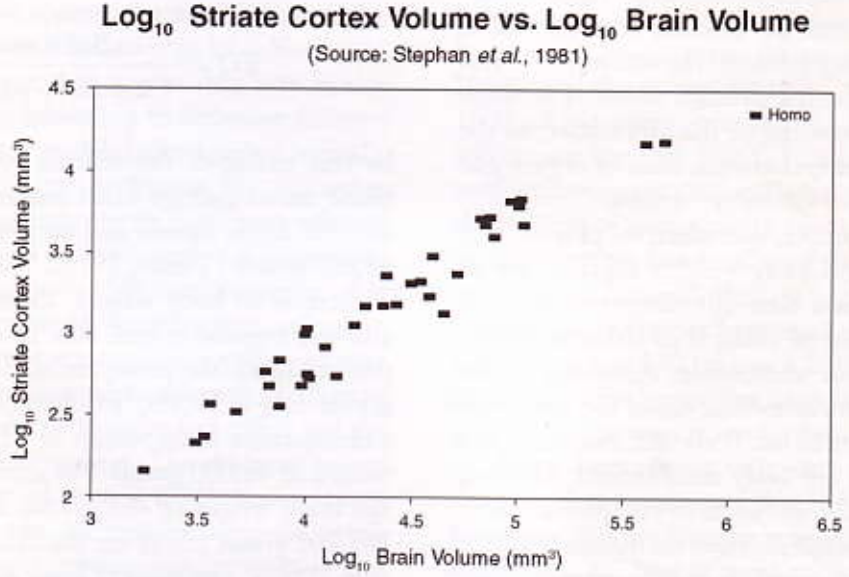

Figure 5. Log-log plot of volume of the primary visual striate cortex against brain volume.

log-log plot of the volume of the PVC against the volume of the brain for a collection of different primate species ranging from strepsirhines to modern humans. The correlation is about 0.98, and as is obvious, the log-log transformation provides a satisfying straight line, with the human point departing significantly from the regression line. The departure is 121% for the human value: that is, the human value is 121% less than would be predicted for another primate with the human brain volume. (Incidentally, for such a high correlation coefficient, the least-mean-squares method of regression is preferable over the reduced major axis method.) The prediction for the volume of the lateral geniculate nucleus, from which the optic radiations to the occipital lobe emerge, is 144% greater than actually occurs in the human brain: that is, as with the PVC, the lateral geniculate nucleus is 144% less than expected in the human brain. Since the human animal is not deficient or defective in its vision, this apparent reduction could be a sign that the posterior parietal association cortex (and/or other cortical regions) has relatively enlarged, but we are not aware of any quantitative studies that have explored this notion.

In great apes, and in the Haplorhini in general, the PVC is anteriorly bounded by a primary sulcus known as the lunate sulcus (LS). The LS is both always present and very prominently visible in pongid brains but seldom visible in human brains. (See Smith 1904, 1907, who defined the lunate sulcus, and also Connolly, 1950; Levin, 1936; Ono et al., 1990, measured its variability in modern *Homo sapiens*.) It occasionally (but very rarely) is demonstrable on the brain endocasts of apes and modern or fossil hominids. Therein lies the difficulty: *When, in the course of human evolution, did the PVC become reduced (or the posterior parietal association cortex increased) in volume from a pongid to human condition, and can the change be demonstrated in the fossil hominid record?* Can we use the lunate sulcus as a guide to the relative decrease of PVC and thus a relative increase in posterior parietal association cortex? As we demonstrate in this book, the mid-Pliocene hominids show evidence of this important cortical reorganization. In particular, the new Stw 505 specimen from Sterkfontein, South Africa, shows an indisputable LS in a more posterior position than found on any pongid brain or pongid brain endocast that we have examined. This means, of course, that while both absolute and/or relative brain weights for early hominids may or may not exceed common chimpanzee brain weight values, the cortex had become reorganized prior to any significant enlargement, such as found in the genus *Homo* (see Table 2 for a summary of hominid brain reorganizational changes, and also Holloway et al., 2003, for discussion and examples of this variability in chimpanzee brains).

The Frontal and Prefrontal Lobes

Given the apparent steepness of the modern human forehead, the lack of such steepness in chimpanzees and other apes, and the large brow ridges of most hominids, including those currently aligned with the Neanderthal calvarium, it would seem intuitively correct that the frontal lobes of the cerebral cortex, and in particular, their prefrontal portions, would be relatively enlarged in modern *Homo sapiens*, and that most

TABLE 2 **Reorganizational changes in the evolution of the human brain**

Brain Changes *(Reorganization)*	Taxa	Time (MYA)	Evidence
(1) Reduction of primary visual striate cortex, area 17, and relative increase in posterior parietal cortex	*A. afarensis* *A. africanus*	3.5 to 3.0 3.0 to 2.0	AL 162-28 endocast Taung child, Stw 505 endocast SK 1585 endocast
(2) Reorganization of frontal lobe (third inferior frontal convolution, Broca's area, widening prefrontal)	*Homo rudolfensis* *Homo habilis* *Homo erectus*	2.0 to 1.8	KNM-ER 1470 endocast Indonesian endocasts
(3) Cerebral asymmetries, left occipital, right-frontal petalias	*Homo rudolfensis* *H. habilis, H. erectus*	2.0 to 1.8	KNM-ER 1470 endocast Indonesian endocasts
(4) Refinements in cortical organization to a modern *Homo* pattern	*? Homo erectus to present?*	1.5 to 0.10	*Homo* endocasts *(erectus, neanderthalensis, sapiens)*

of brain evolution has involved the enlargement of the frontal lobe. Countless chapters in neuroanatomy and neurology texts do provide evidence for the frontal lobes' involvement in complex cognitive tasks, and, indeed, in our veritable humanness. When one looks at the brain endocasts of a series of hominids from the mid-Pliocene to modern humans, it *does* look like the frontal lobe becomes rounder, higher, and broader—in effect, less pointed.

When RLH wrote his dissertation in 1964, he was quite surprised to find from the literature that actual measurements of the frontal lobe by von Bonin (1948) showed that when frontal lobe size was plotted against total brain size for different primates, the resulting slope was a straight 45% degree line, and that the human value did not digress from it (see also Holloway, 1968). Semendeferi and her colleagues later confirmed this observation in several articles (Semendeferi et al., 1997, 2001, 2002) based on MRI image analysis and quantification, and their analyses also extended to portions of the prefrontal cortex, Brodmann's areas 9, 10, and 13. A similar set of findings, this time using cytoarchitectonic criteria, was published by Uylings et al. (1992) on the orangutan, also a large-brained ape. Slopes for regressions between frontal lobe size and prefrontal size were all very close to 1.0, or almost complete isometry, with the human points falling almost perfectly on the regression line. Nevertheless, one finds estimates such as Deacon's (1997) that the human prefrontal lobe is 202% larger than an ape's, a finding based on calculations made from Brodmann's earlier 1909 observation on cytoarchitectonic homologues between macaque, chimpanzee, and humans. No one has confirmed independently any of those earlier findings, and we believe the recent findings of Semendeferi and colleagues should lay this issue to rest once and for all. However, Schoenemann (1999) believes the surface area of the prefrontal lobes is twice as large in humans than in non-human primates. Indeed, specimens such as the Neanderthal calvarium and La Ferrassie cannot be shown to have had smaller frontal lobes than modern *Homo sapiens*, as Holloway (1985) initially tried to show. Later, Bookstein et al. (1999) showed, using complex morphometric analyses, that the forehead roundness of Neanderthals and modern *Homo sapiens* does not differ in any significant way.

Of course, with a three to four fold expansion of brain size from mid-Pliocene hominids to *Homo sapiens* (Table 3) it can be argued that the human frontal lobe and its prefrontal portions must have increased in size absolutely. If one believes in Rubicon models, then perhaps once the absolute volume surpassed some critical level, the behavioral hallmarks of humanness suddenly emerged, namely language, forethought, planning, inhibition of impulsive behavior, symbolic behavior, and much else. This is similar to the "spandrels" view promulgated by Gould and Lewontin (1979). This position views such behavioral developments as mere epiphenomena without any basis in past selection pressures. Such a view has numerous ontological problems as it ignores many aspects of both the fossil hominid and comparative neuroanatomical evidence that proves that

TABLE 3 **Summary of size changes in human brain evolution**

Brain Changes (Brain Size Related)	Taxa	Time (MYA)	Evidence
(1) Small increase, allometric[a]	*A. afarensis to A. africanus*	3.0 to 2.5	Brain size increases 400–450 ml, 500+ ml
(2) Major increase, rapid, both allometric and nonallometric	*A. africanus to Homo habilis*	2.5 to 1.8	KNM-1470, 752 ml (ca. 300 ml)
(3) Small allometric increase in brain size to 800–1000 ml (assumes *H. habilis* was KNM 1470-like)	*Homo habilis to Homo erectus*	1.8 to 0.5	*Homo erectus* brain endocasts and postcranial bones (e.g., KNM-WT 15000)
(4) Gradual and modest size increase to archaic *Homo sapiens*, mostly nonallometric	*Homo erectus to Homo sapiens Neanderthalensis*	0.5 to 0.10	Archaic *Homo* and Neanderthal endocasts 1200 – 1700+ ml
(5) Small allometric reduction in brain size among modern *Homo sapiens*	*Homo s. sapiens*	0.015 to present	Modern endocranial capacities

[a] Allometric means related to body size increase or decrease, while nonallometric refers to brain size increase without a concomitant body size increase.

reorganization occurred during human evolution. We reject this view in favor of a view that sees selective forces acting upon different regions of the brain and its underlying hardwiring, with ontogenetic development occurring at different times in the course of human evolution (see Holloway, 1979). This is in essence what we mean by mosaic brain evolution.

As we will show, Broca's regions do appear to have undergone an evolutionary development in *Homo*, with the modern *Homo* condition of asymmetries in that region appearing in many of the specimens currently assigned to *Homo erectus* (e.g., Sm 3) brain endocasts, and possibly even earlier (e.g., KNM-ER 1470).

The Temporal Lobe

Recently Rilling and Seligman (2002) have shown that the human temporal lobe is about 20% to 30% larger than would be expected for a primate with its brain weight. This study is based on several specimens for each species, whereas the original Stephan et al. (1981) data set was based on 45 species, including *Homo*, but with one data point for each species. Rilling and Seligman were also able to show, using paired *t*-tests, that the differences between predicted and observed temporal lobe volumes were statistically significantly larger in modern humans. This represents yet another example of reorganization of the cerebral cortex. In time we expect these workers to indicate whether the parietal lobes have also undergone an increase in relative size in *Homo sapiens*.

In sum, we believe that the judicious use of brain endocasts can enlarge our understanding of the course of hominid brain evolution as they reveal that changes in size, both absolute and relative, and reorganization, including asymmetries, were important evolutionary developments at different times during human mosaic brain evolution. That evolution appears to have involved far more than simple brain size enlargement, and such reorganizational events should not be ignored.

Endocranial Morphology and Terminology

Here we outline the general morphologies exhibited on endocasts based on features visible in extant chimpanzees and modern humans (Figs. 6–10). While the morphologies presented in the following images may be visible on the exhibited endocasts and brains, the reader is reminded that there are large variations in the features exhibited on any endocasts. Moreover the different specimens discussed in this volume are often incomplete, so we lack the range of features often seen in a detailed, complete endocast. As with the first two volumes of this series, we have followed the general outline of Schwartz and Tattersall (2002, 2003, in press) by using morphs (a group of biological organisms that differs in some morphological respect from other groups) to avoid systematic implications in describing the different endocasts, except when referring the reader to earlier arguments concerning the taxonomy of a fossil within the Significance section of an entry. This is because, despite our own opinions on systematics, the descriptions of the individual endocasts should be devoid of opinion that may lead the reader to view one feature as absolutely more important than another. In other words, it is up to the reader to determine the meaning of the features discussed here. Of course, while we do lend our opinion regarding systematics and taxonomic designations at the end of this volume, endocranial features on their own rarely, if ever, lend themselves to promoting one taxonomy over another.

The terms below are features present on endocasts (for the definition of endocast, see above). These terms are not, in general, unique to endocasts but are derived from anatomical structures, and in many cases specific neuroanatomical structures, of the brain or endocranium. Since the soft tissue structure does not preserve on an endocast the reader should be aware that the identified structures are hard representations of underlying structures and not the anatomical feature present in a living organism. Thus the definitions below describe the feature as it occurs on an endocast:

Bec. The inferior terminus of the frontal region that would correspond to that portion overlaying the cribriform plate of the ethmoid bone.

Encephalization Quotient. Measure of the amount of brain tissue that an animal possesses beyond that expected for its body weight, based on some taxonomic series.

Endocast. Cast, either natural or human-made, of the endocranium.

Gyrus. A convolution of the brain. A raised ridge between grooves, sulci, and fissures of the brain.

Lunate Sulcus. Sulcus that usually defines the anterior limit of the primary visual striate cortex in nonhuman primates. This structure is usually fragmented in humans.

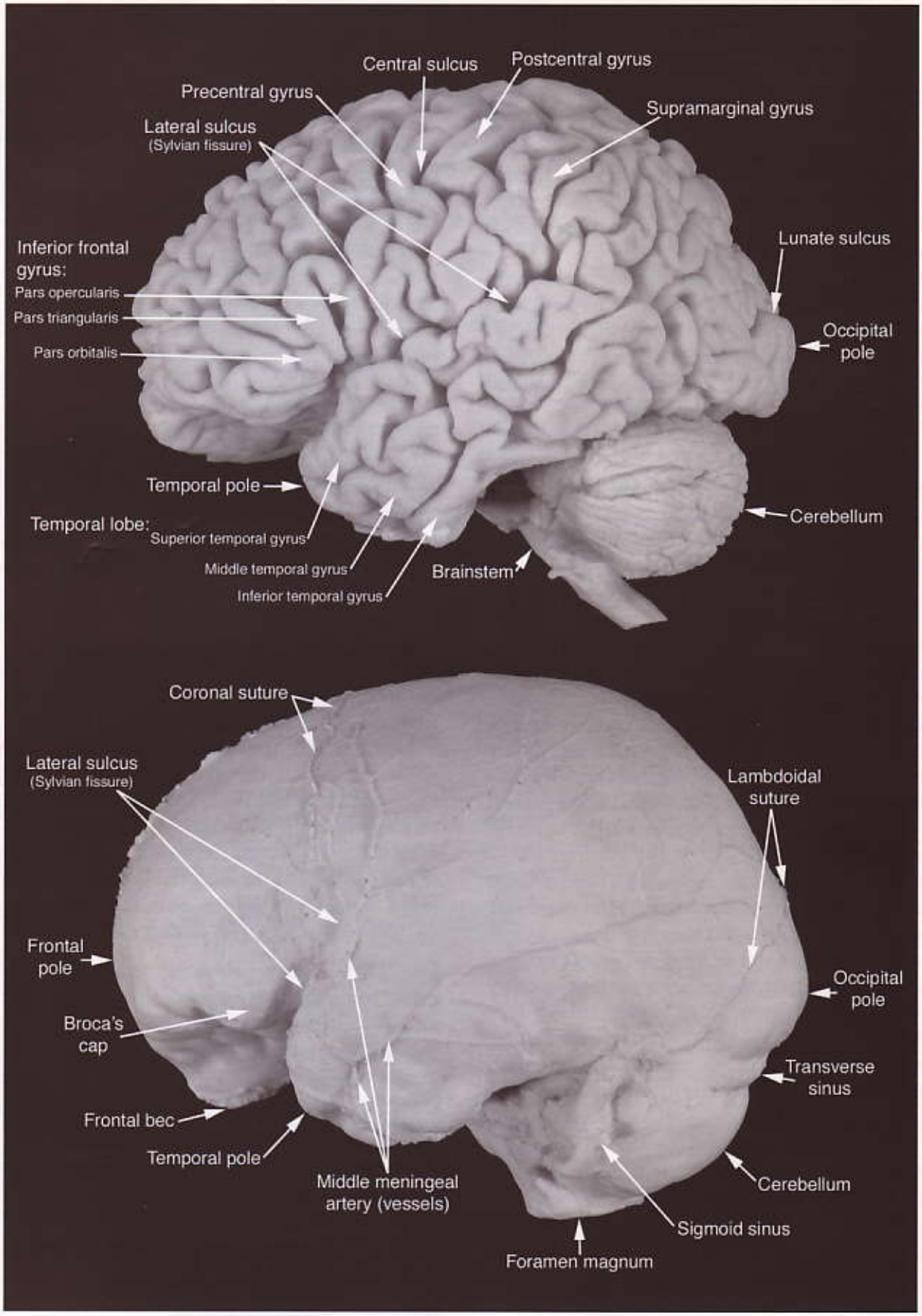

Figure 6. Lateral view of a modern human brain (*top*) and a modern human endocast (*bottom*), demonstrating the observable anatomical landmarks of both (casts' source, Kronen Osteo).

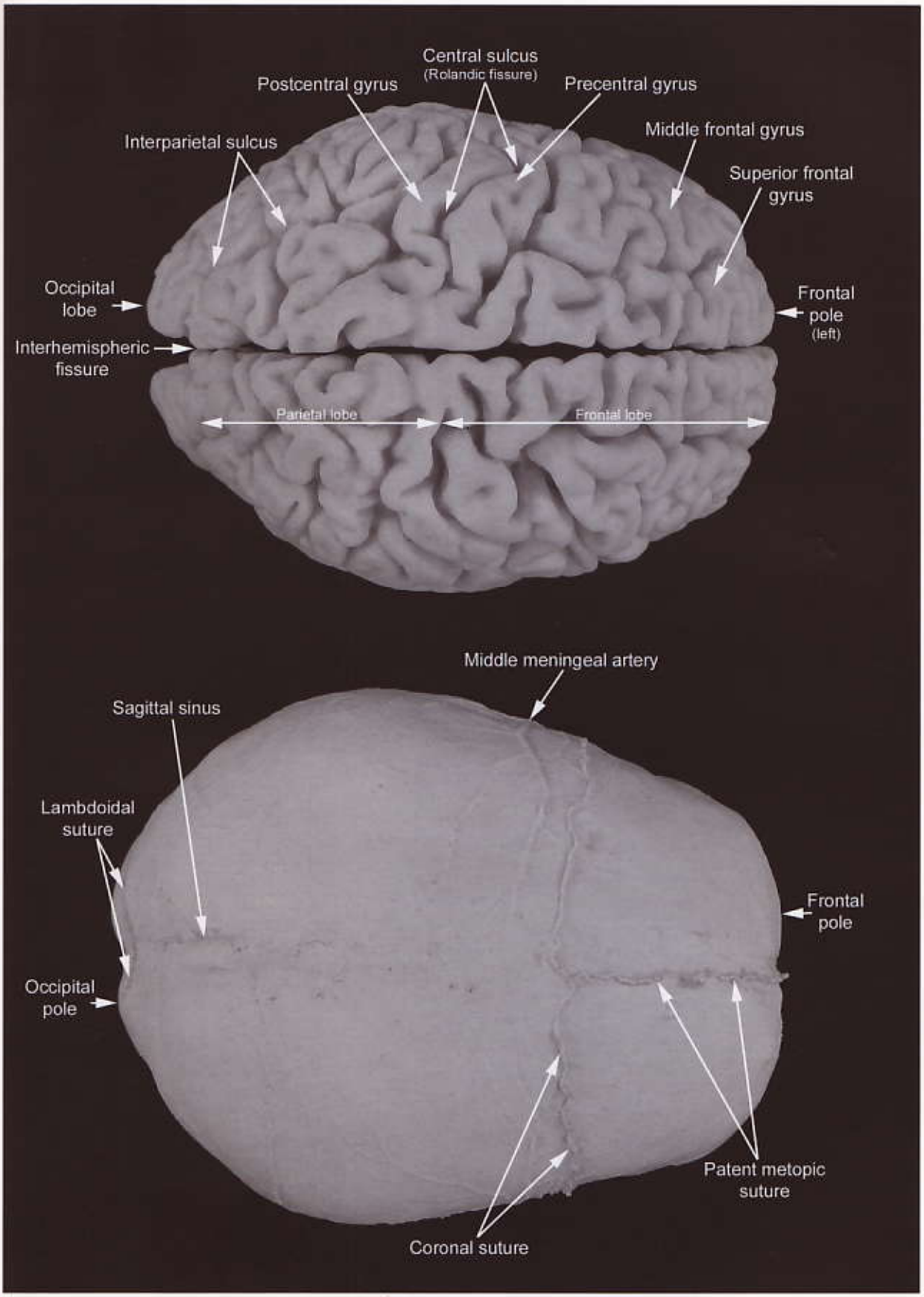

Figure 7. Dorsal view of a modern human brain (*top*) and a modern human endocast (*bottom*), demonstrating the observable anatomical landmarks of both (casts' source, Kronen Osteo).

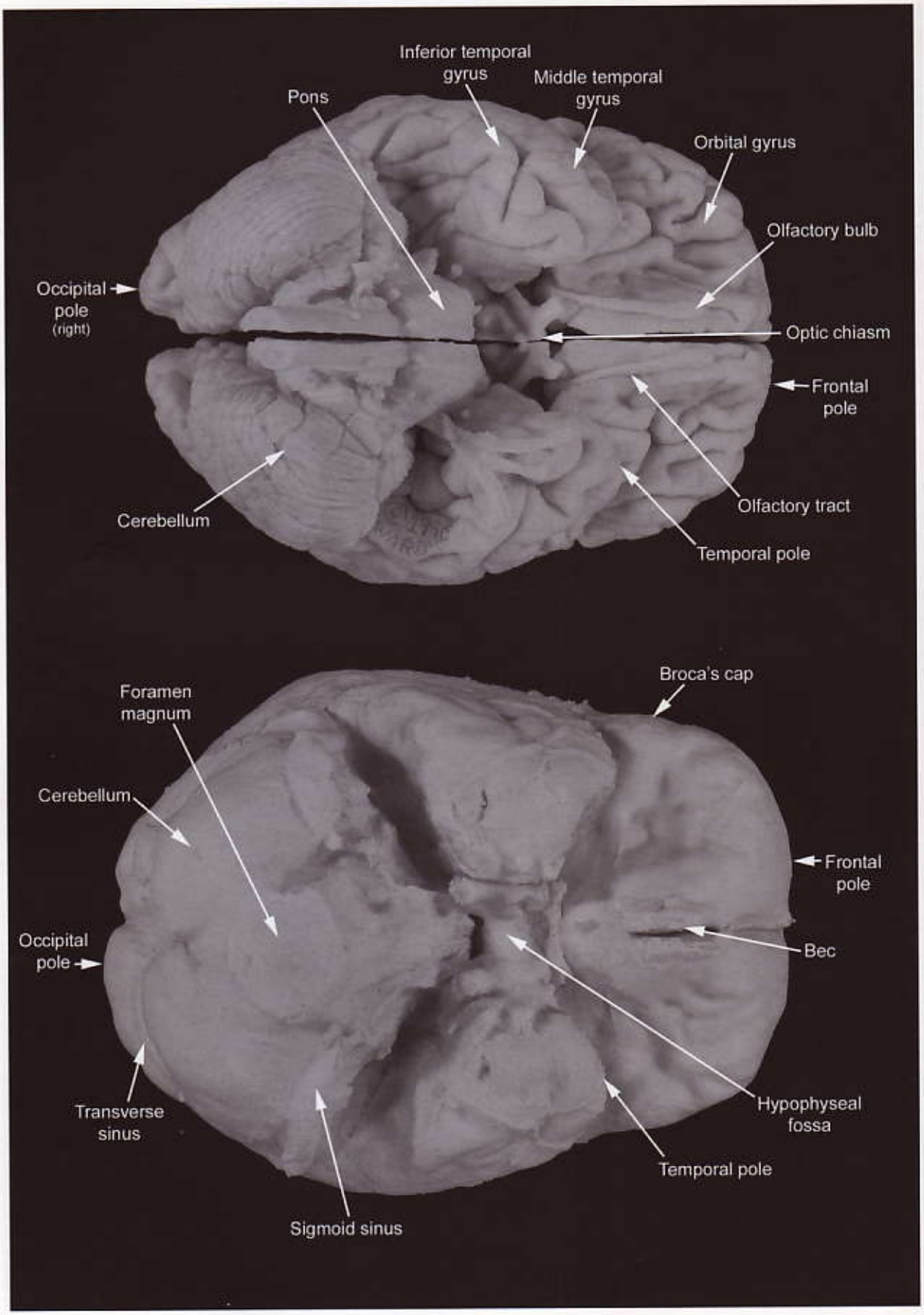

Figure 8. Basal view of a modern human brain (*top*) and a modern human endocast (*bottom*), demonstrating the observable anatomical landmarks of both (casts' source, Kronen Osteo).

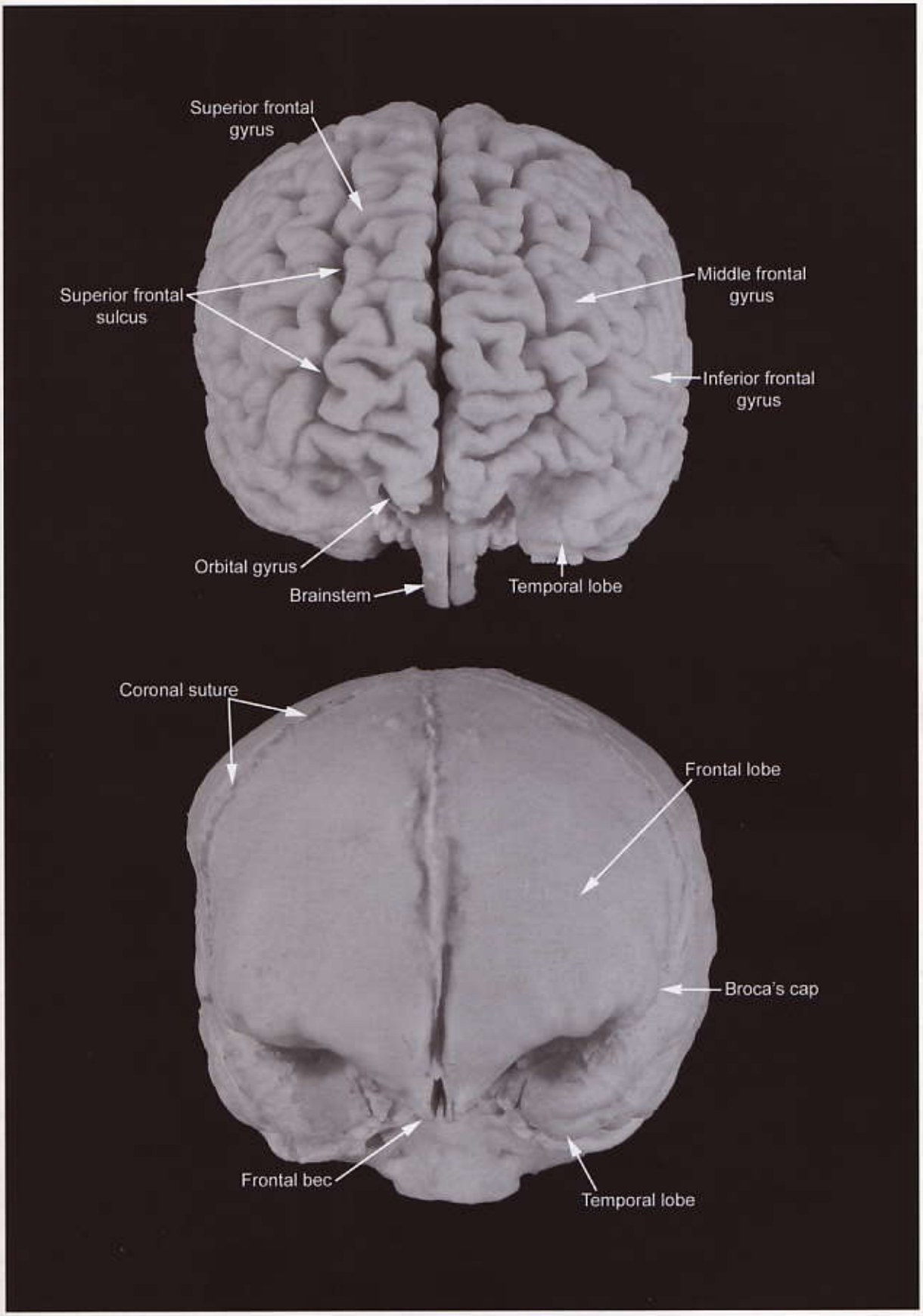

Figure 9. Frontal view of a modern human brain (*top*) and a modern human endocast (*bottom*), demonstrating the observable anatomical landmarks of both (casts' source, Kronen Osteo).

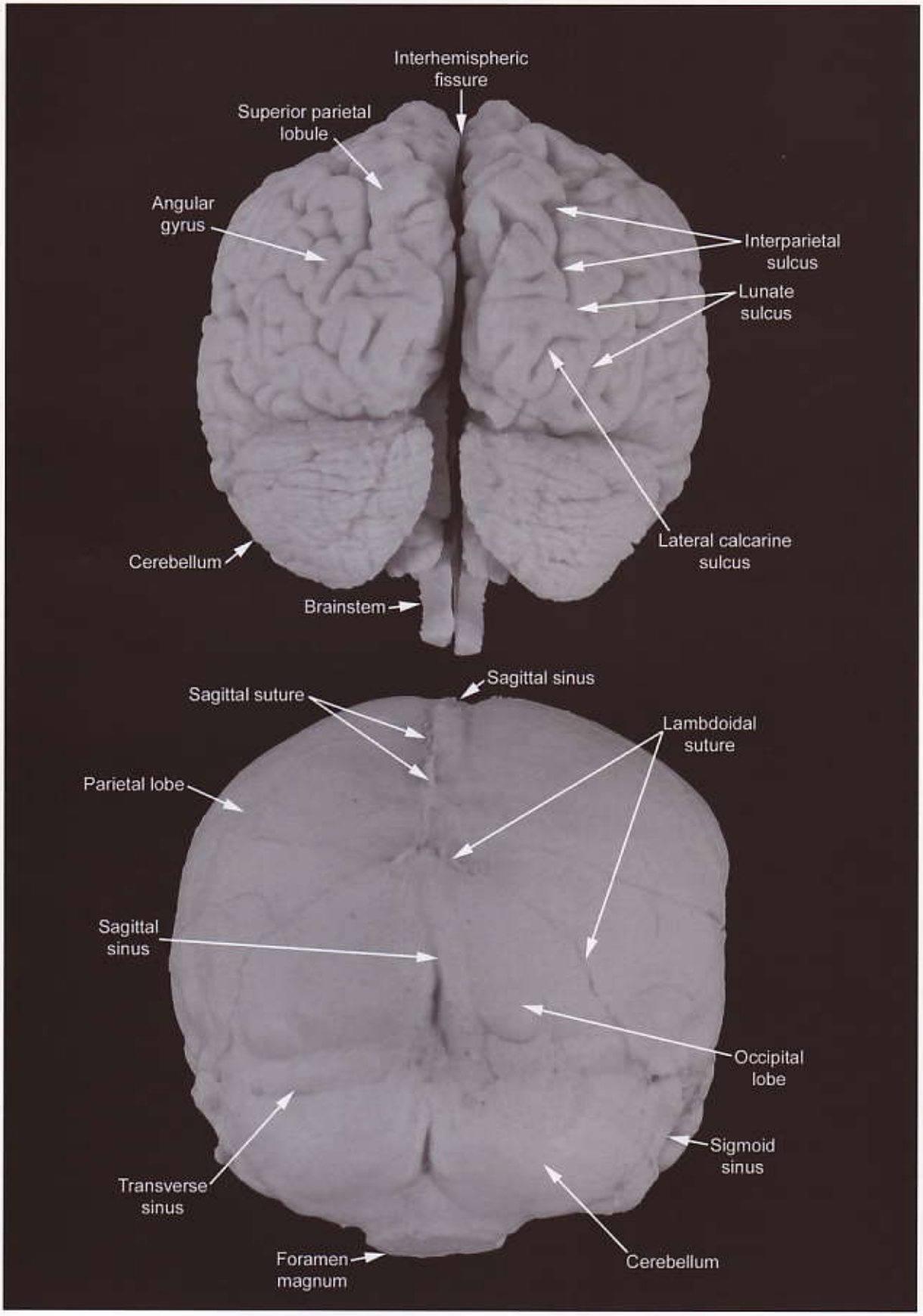

Figure 10. Occipital view of a modern human brain (*top*) and a modern human endocast (*bottom*), demonstrating the observable anatomical landmarks of both (casts' source, Kronen Osteo).

Meningeal Vessel. An uneven, often branching, ridge that is the result of the meningeal vessels. The principal meningeal vessel in the endocranium is the middle meningeal artery, which arises from foramen spinosum. For further discussion of this feature, see Part 5.

Petalia. An indication of differential development of one cerebral hemisphere over the contralateral as measured by the projection of the lobe over the contralateral lobe or by differential width. For example, a right frontal petalia indicates that the right frontal lobe projects anteriorly beyond the left frontal lobe, and/or is wider than the left lobe. In an occipital petalia one occipital lobe would project posteriorly beyond the contralateral.

Pole. The end or point of greatest projection of a cerebral lobe. The frontal pole is that part of the frontal region that projects most anteriorly. The occipital pole is that region of the occipital lobe that projects most posteriorly. The temporal pole represents the terminal or antero-inferior end of the temporal lobe. These are for the most part highly homologous structures.

Sinus. In endocasts, a raised region that corresponds to the sagittal, transverse, sigmoid, occipital or marginal venous sinuses. The sinuses represent reasonable reference marks. For example, the sagittal sinus lies between the cerebral hemispheres, aiding in the location of the endocast midline. The transverse and sigmoid sinuses represent the superior, anterior, and lateral-most margins of the cerebellum.

Sulcus. A groove or furrow between two convolutions or gyri of the brain.

Suture Line. A ridge that corresponds and is the result of an overlying suture such as the coronal, sagittal, or lambdoidal sutures of the skull.

Descriptive and Figure Format

Each entry is presented following the below format:

Gross Description. An overview of the morphology of the endocast, including condition.

Volume and Method. Known volumes and the methodology, if available, as to how the volume was ascertained. Reliability of the volume estimate.

Endocast Details. Specific morphology observable on the endocast.

Morphometric Data. Linear and chord measurements.

Significance. Importance of the endocast for the interpretation of human brain evolution

Views of each endocast are presented in a single figure in the following format:

Top row from left to right: left lateral view, right lateral view.

Middle row from left to right: dorsal view, basal view.

Bottom row from left to right: frontal view, occipital view.

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