

## REVIEW ARTICLES

# Endocasts—the direct evidence and recent advances in the study of human brain evolution<sup>\*</sup>

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**Abstract** Brain evolution is one of the most important aspects of human evolution, usually studied through endocasts. Analysis of fossil hominid endocasts allows inferences on functional anatomy, physiology, and phylogeny. In this paper, we describe the general features of endocast studies and review some of the major topics in paleoneurology. These are: absolute and relative brain size evolution; brain shape variation; brain asymmetry and lateralization; middle meningeal vessels and venous sinuses; application of computed tomography and virtual imaging; the history of Chinese brain endocast studies. In particular, this review emphasizes endocast studies on Chinese hominin fossils.

**Keywords:** endocast, human fossil, brain evolution, cranial capacity, human evolution.

In the process of human evolution, how has the brain changed? When did it happen? Why did it happen? These questions are some of the hottest topics in paleoanthropology today. The study of brain evolution falls under the sub discipline of paleoneurology and is based on the direct examination of the fossil record of humans and their closest hominid relatives<sup>[1]</sup>. Paleoneurology facilitates a more comprehensive understanding of human evolution, phylogeny, language, and intelligence. Endocasts (endocranial casts) supply the most direct evidence for the studies of human brain evolution. The endocast is the impression taken from the inside of a cranium that retains the surface features of the brain. The cast does not display the original brain anatomy, but does reflect the external features of brain anatomy in detail. Accordingly, endocasts become the most important material to analyze and understand human brain evolution.

Endocasts can exist in three ways. First, they may be produced naturally during fossilization. Such “fossil brains” are actually natural casts formed by sediments that filled the empty cranium of the animal after death and then become lithified. A good exam-

ple of this is the *Australopithecine* “Taung endocast” (Fig. 1(a)). The second is an artificial endocast, which may be manually produced with plaster, latex, or other materials. The Zhoukoudian endocasts are good examples (Fig. 1(b)). The third method is a virtual endocast, using high-resolution computed tomography (CT) scans to develop a three-dimensional image of the interior of the crania. A good example is the African ancient fossil “Bodo endocast” (Fig. 1(c)).

Paleoneurologists explore brain evolution through morphological and anatomical analysis of the endocranial characters and volumes. Studies of brain evolution originated in Germany in the 1920s. Tilly Edinger (1897–1967) was the founder of modern paleoneurology. Edinger published the first book about brain evolution entitled “*Fossil Brains*”, in addition to writing a series of papers about different animal endocasts<sup>[2]</sup>. In 1891, Eugène Dubois, an anatomist from Holland, studied the endocast of *Pithecanthropus erectus*. He found that the ratio of brain size to body size does not have a clear pattern. Dubois suggested that if *P. erectus* was an ape, then its brain was too large for the body size as indicated

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by the femur. Conversely, if *P. erectus* was a human, then the creature's brain was too small for its body size. Dubois suggested that *P. erectus* was a "missing link" between apes and humans<sup>[3]</sup>. In 1925, Raymond Dart found the South African Taung skull (holotype for *Australopithecus africanus*), that

still retained the natural endocast. The cranial capacity of Taung is small (ca. 500 mL), but the sulcal pattern of the endocast is in human-like position. These findings attracted other scientists to study human brain evolution in more detail<sup>[4]</sup>.

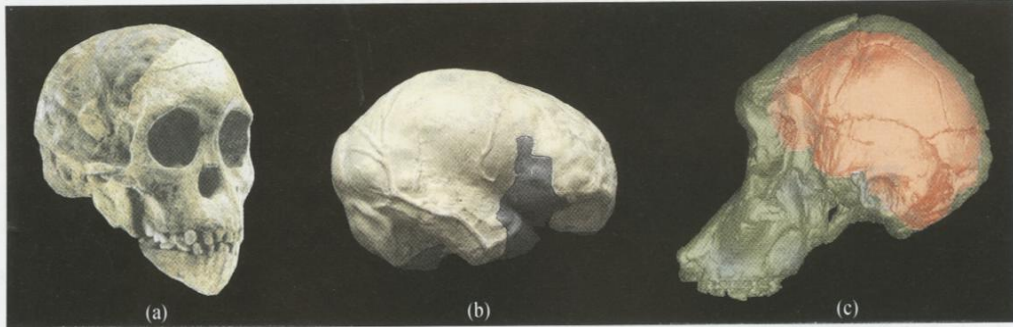


Fig. 1. The sources of fossil human endocasts. (a) Natural endocast; (b) artificial endocast; (c) virtual endocast.

## 1 Brain size evolution

Overall brain size increase is one of the most important features during human evolution. Endocasts can estimate cranial volume. The difference between endocranial capacity and actual brain size is about 5%<sup>[3]</sup>, with the former being slightly larger than the latter. Since cranial capacity is close to actual brain size, and can be measured on fossil hominids, it is generally to be used to represent the latter. Throughout this paper, we use cranial capacity and absolute brain size interchangeably. Paleoneurologists study both absolute and relative brain sizes.

### 1.1 Absolute brain size

Absolute brain size is the actual size of a brain, usually expressed by a measure of weight and volume. There is a strong increase in brain size through time<sup>[6-8]</sup>. *Sahelanthropus tchadensis*, the earliest possible hominid found in Chad (6.0–7.0 Ma), retained a cranial capacity of about 400 mL, which is close to extant chimpanzees. The brain size of *Australopithecus* (4.4–1.0 Ma) is between 400 and 500 mL. The cranial capacity of *Homo habilis* (2.5–1.6 Ma) ranges from 510 to 725 mL. *Homo erectus* (1.7–0.2 Ma) has a brain size between 600 and 1251 mL. Compared with *H. habilis*, *H. erectus* brain size increases 25%–40%. Archaic *Homo sapiens* (250–40 ka) has a cranial capacity range between 1100 and 1500 mL, close to moderns. The cranial capacity of anatomically *Homo sapiens* is between 1300 and 1750 mL, which is a slight increase

from archaic *Homo sapiens* (Fig. 2). The increase in cranial capacity does not appear to be a unidirectional trend. For instance, recent studies of some Holocene populations indicate that brain size has decreased. The cranial capacities of Europeans decrease by 95–165 mL for males and 74–106 mL for females during the Holocene<sup>[9]</sup>.

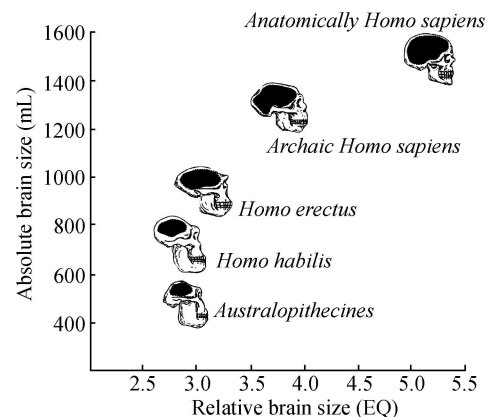


Fig. 2. The absolute and relative brain size of the fossil hominids changed through time.

Brain size increased positively during the early part of human evolution and early hominin intelligence is thought to have increased as well. However, among modern humans, there is no strong direct relationship between brain size and intelligence<sup>[10]</sup>. For instance, the Russian novelist Ivan Turgenev's brain made the all-time record in excess of 2000 mL, while Anatole France, Nobel Prize fellowship for Literature in 1921, had one of the tiniest "normal" brains of 1100 mL on record. The average brain size of

modern humans is about 1400 mL, ranging from 1000 to 1700 mL. The intelligence cannot be simply justified if the cranial capacity exceeds 1000 mL<sup>[11]</sup>. Cranial capacity is directly related to body size. For instance, the average brain size of men is 9%–10% bigger than that of women, but men usually have bigger body size as well<sup>[12]</sup>.

## 1.2 Relative brain size

Relative brain size is the relationship between size of the brain and the body in terrestrial vertebrates. A wide variety of studies are concerned with scaling specific parameters to body size. The general formula for brain size is Encephalization Quotient (EQ). The formula for primates is below<sup>[13]</sup>:  $EQ = \text{brain weight} / (1.0 \times \text{body weight}^{0.6409})$ . By scaling cranial capacity against body size, it is possible to make inter-specific comparisons. Nevertheless, fossil specimens are often incomplete. Accordingly, body weight is usually estimated from certain skeletal elements or bone sections (e.g. femoral head, vertebrae, orbital, teeth, foramen magnum). In order to

reduce the influence of the predicted body size, an adjusted EQ formula is applied<sup>[14,15]</sup>:

$$EQ = (\text{brain weight} \times 1/1.14) / (10 \cdot 76 \times \ln \text{body weight} + 1.77)$$

Among the fossil hominids, the averages and range of EQ (Fig. 2) are: *Australopithecus* 2.95 (1.61–3.08), *H. habilis* 2.93 (2.73–3.13), *H. erectus* 3.27 (3.04–4.02), archaic *H. sapiens* 3.78 (2.71–4.78), and anatomically *H. sapiens* 5.27 (4.01–6.25). From *Australopithecus*, to *H. habilis* to *H. erectus*, EQ did not increase dramatically. However, from *H. erectus* to archaic *H. sapiens*, to modern, EQ increased tremendously.

## 2 Shape variability of the brain morphology

The structure of the human brain is extremely complex and large areas of it are still poorly understood. The brain is composed of many sulci. Three major grooves (lateral sulcus, central sulcus, parieto-occipital sulcus) divide the brain into frontal, parietal, occipital and temporal lobes (Fig. 3(a)).

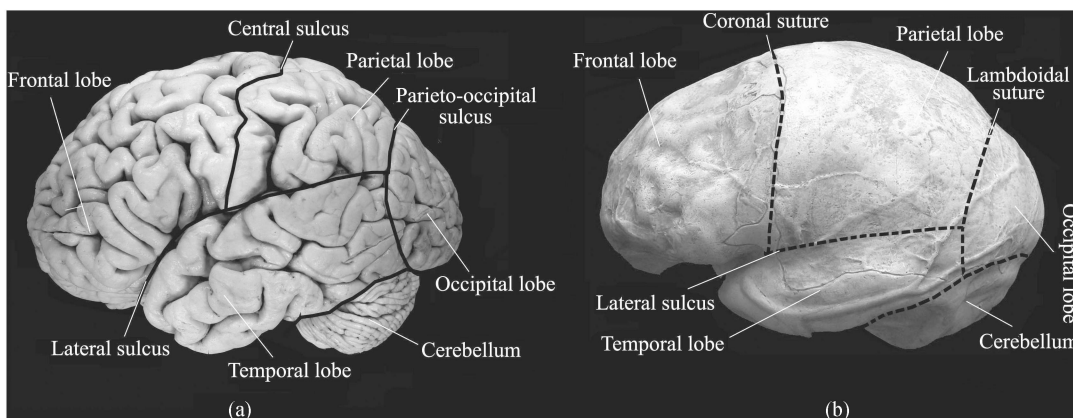


Fig. 3. Lateral view of a brain (a) and an endocast (b), demonstrating observable anatomical landmarks of both.

An endocast is the external morphology of the brain. Even though endocasts reflect the surface of the brain, the sulci are not very clear when compared with the brain itself. The landmarks that can be seen on most endocasts are (Fig. 3(b)): coronal suture, sagittal suture, lambdoidal suture and lateral sulcus. The landmarks on the endocast are not very consistent with those seen on the brain. Since we know the variation of the structural organization of the brain, we can get the general shape of the brain by measuring the endocranial cast. The organization of the brain is closely related to brain function<sup>[16]</sup>.

### 2.1 General shape of the brain

In superior view, the brain shape of chimpanzee, gorilla, orangutan, *Australopithecus*, *H. habilis*, *H. erectus*, and *H. sapiens*, is elliptic. During human evolution, human brain height changed the most, followed by length and breadth in that order respectively<sup>[5]</sup>. Bookstein et al.<sup>[17]</sup> in a study of the medial-sagittal plane of the frontal bone in Neanderthals and modern humans found that the internal and external shapes of the bone are determined by entirely independent factors. More importantly, they argued that, while the external morphology is highly

variable across taxa, the internal morphology of the frontal region (and thus the anterior brain morphology) has been remarkably conservative over the past 500 ka; the period they viewed as the time when modern human cognitive capabilities really began to form. However, not everyone supports this study. Bruner suggested that in the study of Bookstein et al., the Asian taxa were not considered, and only the shape of the anterior cranial fossa was accounted for<sup>[18]</sup>. In Bruner's study, he compared Asian, African and European endocasts. He found that the shape variation of *Homo* endocasts displayed two major patterns of variation. First, there is an archaic structural trajectory shared by nonmodern *Homo* that crosscuts the regions. This pattern is characterized by an allometric vertical development, frontal enlargement, and relative parietal shortening. Second, there is a modern pattern that also consistently appears in the different regions, characterized by parietal development leading to brain globularity<sup>[18]</sup>. Begun et al.<sup>[19]</sup> suggested that the morphology of the Zhoukoudian *H. erectus* endocasts is similar in its major features to that of KNM-WT 15000. Proposed similarities are the development of mid-sagittal keels, expanded temporal lobes, projected and broad occipital lobes, retracted cerebella hemispheres, a large anterior/middle meningeal artery, a long, narrow, and low brain shape, and small cranial capacities. In earlier studies we compared *H. erectus* endocasts from China, Indonesia, and Africa. We found that when compared with Zhoukoudian, Indonesian and African

*H. erectus* specimens, Hexian *H. erectus* from central-eastern China is morphologically more similar with the majority of the coeval Zhoukoudian specimens. This might be expected given Hexian and Zhoukoudians its temporal and geographical position<sup>[20]</sup>. These examples indicate that there is growing international interest in defining the cranial morphological variation of *Homo erectus* throughout the old world.

## 2.2 Frontal lobe

The frontal lobes are one of the most studied areas on fossil endocasts because of their presumed role in higher cognitive functions and language. The sulcus and gyrus impress well on the frontal lobe of the endocast facilitating studies of this region (Fig. 4 (a)). Compared with modern apes, the frontal area of *Australopithecus* is big, while the occipital area is small<sup>[21]</sup>. The frontal lobes of early humans are flat and narrow. During human evolution, the frontal lobes tend to be round, tall, and broad<sup>[22]</sup>. The sulcal pattern near the orbital edge of the left frontal lobe has been proposed to be very important for identifying if the *Australopithecus* or ape had language ability<sup>[23, 24]</sup>. Broca's speech area in humans is formed by part of area 45 and area 44 directly caudal to it in the left hemisphere. Ape brains have a frontal-orbital sulcus which indicates Broca's area is not enlarged, while in humans, the frontal-orbital sulcus is buried and does not appear on endocasts<sup>[23]</sup>.

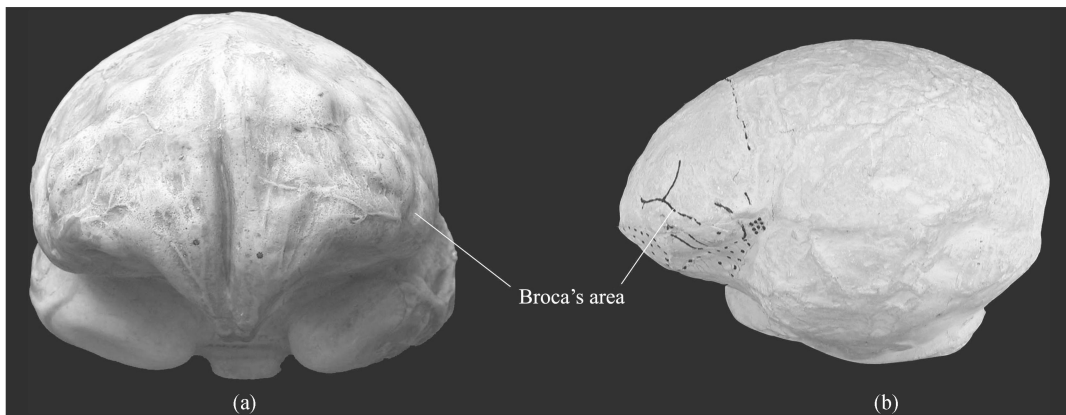


Fig. 4. The morphological features of the frontal lobe on endocasts. (a) Zhoukoudian *Homo erectus*; (b) KNM-ER 1470.

The endocast from the 2.0 Ma a KNM-ER 1470 fossil displays a sulcal pattern in the left frontal lobe (Fig. 4(b)) that is similar to living people<sup>[23]</sup>. However, this does not mean that *Homo habilis* used language as we know it. With an enlarged brain, brain

function became more complex. This likely provided the ability for human to communicate with each other with language<sup>[24]</sup>. The relationship between frontal lobe and brain breadth is of great interest to paleoneurologists. Some scientists believed that in the inner

median-sagittal profile, brain shape remained stable over a half-million years of hominin evolution<sup>[17]</sup>. However, others suggest that *H. erectus* brain shape displays marked variation across spatio-temporal facies. For instance, the brain features of Asian *H. erectus* appear to be different from that of African and European *H. erectus*<sup>[18,20]</sup>.

### 2.3 Parietal and temporal lobes

The surface of parietal lobes in fossil hominids is depressed superiorly relative to the rounded form seen in modern humans. Compared with other brain lobes, the percentage of parietal lobes is lower in fossil hominids than in modern humans. Basicranial flexion is larger in fossil hominids than moderns. Brain convolutions do not impress clearly on the parietal and temporal lobes of endocasts. The morphological features of the parietal and temporal lobes have spatial variation. For instance, the vertex of the Zhoukoudian endocasts is very prominent and located in the middle of the central-parietal lobe. From the vertex, the brain contour slopes downward in all directions. The temporal lobes of the Zhoukoudian endocasts are long and narrow<sup>[23]</sup>. However, the vertex of the Hexian endocast is flat, and the temple lobes are broad<sup>[20]</sup>. Neanderthal endocasts have a high, wide, short and flat vertex<sup>[18]</sup>. In general, the widest point or greatest breadth of most modern human crania is in the middle position. In *Homo erectus*, the widest point is usually in a low position or at the temporal lobes. During human evolution, with the brain enlargement, the parietal lobes got wider and taller, the chord from the bregma to lambda became longer, while the parietal area increased, and the brain is more globular<sup>[23]</sup>.

### 2.4 Occipital lobe

The occipital lobes display a steady reduction in volume as brain size increases through time. This process involves the rotation of the posterior complex forward and under the cerebral mass<sup>[20,23]</sup>. Compared with modern *H. sapiens*, early hominins have a bigger occipital lobe, a more posterior location (behind the parietal areas), and a very developed primary visual cortex.

One of controversial regions on the endocast is the "lunate sulcus". The lunate sulcus is posterior to the occipital lobes, and under the lambdoid suture. The position of the lunate sulcus is different between apes and humans. For anthropoids, the lunate sulcus

is a crescent-shaped sulcus that approximates the anterior boundary of the visual cortex. The lunate sulcus is located more posterior in human than in ape brains<sup>[12,26]</sup>.

In 1925, Dart found the Taung endocast in Africa. The Taung child's endocast is controversial whether it is in an ape-like or human-like position<sup>[26,27]</sup>. Holloway suggested that the lunate sulcus of the Taung endocast is located farther back and in a more human-like position; likely, representing the transition from apes to humans<sup>[26]</sup>. Falk argued that the lunate sulcus of the Taung endocast is located in an ape-like position<sup>[27]</sup>. Another important specimen is AL 162-28 (holotype for *Australopithecus afarensis*). Holloway found that the AL 162-28 brain endocast suggested a more posterior, human-like placement of the lunate sulcus<sup>[12]</sup>. However, Falk studied the endocast and suggested the lunate sulcus of the AL 162-28 brain endocast is in an ape-like position<sup>[27]</sup>. Currently, there is evidence of a posterior lunate sulcus in only one chimpanzee endocast<sup>[28]</sup>. But, how circumvolutions changed during human evolution? We currently do not know much now.

### 2.5 Cerebellum

In occipital view, the cerebella structures are located under the occipital poles in *Homo erectus*, under the parietals in more derived taxa, and almost completely under the temporal areas in modern humans<sup>[23]</sup>. In Middle Pleistocene hominins the cerebella lobes are elongated and quite separated, become tighter, more globular, and approach the midline in modern humans<sup>[29]</sup>. Bruner recently proposed a three-step model for human cerebella evolution: (1) non-allometric brain enlargement with cerebella increase (early *Homo* and *H. erectus*); (2) brain development without cerebella evolution (from African and European Middle Pleistocene to early modern *H. sapiens*); (3) a decrease in brain and body size with relative and absolute development of the cerebella structures (anatomically modern humans)<sup>[22]</sup>.

## 3 Brain asymmetries and lateralization

The two hemispheres of the human brain are asymmetric. The increase in brain complexity, as seen in advanced tool use and symbolic language, is linked to the cerebral asymmetries. An asymmetry due to the enlargement of a lobe (mainly frontal and

occipital) with respect to the hemispheric counterpart is called a petalia<sup>[22]</sup>. There is evidence that right-handedness is associated with a wider left occipital lobe and right frontal lobe, while the left-handedness has a wider right occipital lobe and left frontal lobe<sup>[23, 30]</sup>. Paleoanthropologists studying the fossil endocasts of *Australopithecus*, *H. habilis*, *H. erectus*, Neanderthals, and *H. sapiens*, found that almost all brain endocasts display distinct cerebral asymmetry. The most common and distinctive pattern is a dominance of the right frontal and left occipital lobes, namely the right frontal and left occipital petalias<sup>[5, 20, 31, 32]</sup>. It is likely that cerebral asymmetry and handedness may have evolved very early in human evolution<sup>[28]</sup>. Handedness may be reflected in flaked stone tools, possibly as early as 2.0 Ma<sup>[33]</sup>.

Asymmetries are present in the brains of birds, monkeys and apes. However, the petalial patterns are different between animals and humans. For instance, apes usually have a left occipital petalia, while most humans have left occipital and right frontal petalias<sup>[34]</sup>. Although different asymmetries are common throughout the animal kingdom, they are most distinctive in the human brain<sup>[30]</sup>.

The temporal planum appears asymmetric in humans and apes. The left temporal planum is usually larger than the right one in most humans and chimpanzees. It has been suggested that left lateralization

existed in the common ancestor of humans and chimpanzees as far back as 8.0 Ma<sup>[35]</sup>.

## 4 Vascular patterns

Due to the tight structural relationship between the brain and the inner table of the vault, the endocranial surface is a useful record of the vascular patterns. The most visible marks on the endocranial surface are the traces of the middle meningeal artery and venous sinus system (Fig. 5). The morphology of the vascular patterns reflects the increase in blood requirements for different brain components due to changing proportion and sophistication of the cerebral functions during human evolution.

### 4.1 Middle meningeal artery

Middle meningeal arteries are the main blood vessels to supplying the dura mater, skull, and diplöe (Fig. 5). The middle meningeal artery stems from the external carotid, and is generally comprised of three branches: anterior (bregmatic), middle (obelic) and posterior (lambdatic). The development of the middle meningeal arteries is probably related to the increase in cranial capacity and functional complexity of the brain<sup>[36]</sup>. During human evolution, the reorganization of the brain lobes reveals a change in the anastomotic system. Some general patterns can be used as simple and useful indications of more complex variability<sup>[23]</sup>.

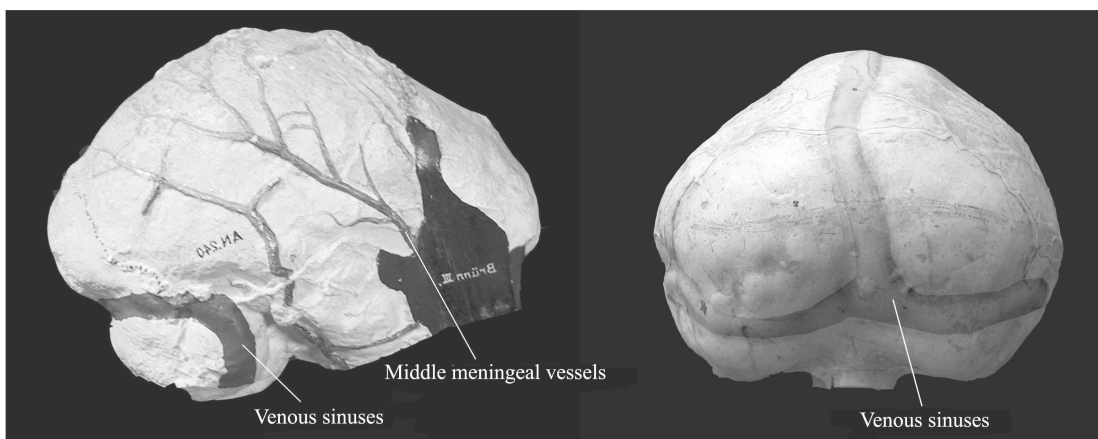


Fig. 5. The vascular patterns on the endocast.

Earlier work on meningeal artery patterns in apes and monkeys has traditionally relied on Adachi's system. The system is based on humans and focuses on the origin of the middle branch of the middle meningeal artery<sup>[37, 38]</sup>. Falk studied the middle

meningeal artery in apes and humans, and found that three genera of apes (*Pan panisus*, *Gorilla gorilla*, and *Pongo pygmaeus*) display different meningeal artery patterns. The middle braincase of great apes receives meningeal arterial blood vessels (internal

carotid arteries) that enter the middle cranial fossa through the back of the orbit. During the course of vascular evolution in *Homo*, the middle meningeal artery (that obtains its blood from the external carotid) eventually took over supplying of the entire middle braincase in the vast majority of the population<sup>[39]</sup>.

The meningeal vessels are similar on both the Hexian and Zhokoudian endocasts, where the posterior branch of the middle meningeal vessels is larger than the anterior ones. The pattern of meningeal arteries of KNM-WT 15000 and Sm 3 endocasts is different from Chinese *H. erectus*, where the anterior branch is larger than the posterior ones. The branches of the meningeal vessels are rich and slender in modern humans. From *H. erectus* to modern *H. sapiens*, the blood supplying the parietal bone became more elaborate during the subsequent course of hominid cranial expansion<sup>[39]</sup>.

#### 4.2 Venous sinuses

On the endocranial surface of the occipital lobe, the venous sinus system can be observed (Fig. 5). The venous sinus patterns are different among apes, *Australopithecines*, and humans. There are two venous sinus systems. One is called the Transverse-Sigmoid System (TSS), which receives the straight sinus from the cerebral volume and the two transverse sinuses running laterally through the occipital and parietal bones to the jugular fossae through the curved sigmoid sinuses<sup>[40]</sup>. This can be seen in modern humans and most fossil hominids. A second but less common drainage network complementary to the TSS is the Occipito-Marginal System (OMS). One or two occipital sinuses pass from the confluence downward through the lower rim of the internal occipital crest. These occipital sinuses then pass laterally to the foramen magnum as marginal sinuses to join the jugular veins at the jugular fossa. An enlarged OMS appears common in Hadar early hominids and robust australopithecines, but few are present in gracile australopithecines, *H. habilis*, *H. erectus* and *H. sapiens*. For instance, in some fossils (e.g. KNM-ER 23000, Sambungmachan 3, Salé and Vértesszöllő II), an enlarged OMS appears on one side or both sides of the foramen magnum<sup>[41-43]</sup>.

Currently, there are two hypotheses to explain the venous sinus patterns. Falk suggested that an enlarged OMS was the result of an epigenetic adaptation

of the circulatory system associated with selection for bipedalism. When an enlarged marginal sinus is present, OMS usually becomes the main route to deliver blood instead of TSS<sup>[44]</sup>. However, Kimbel noted that the utility of the enlarged OMS for hominid phylogeny reconstruction is doubtful owing to marked temporal and spatial fluctuations in the frequencies of different venous drainage patterns in the *H.* lineage<sup>[45]</sup>.

### 5 Recent advances in brain evolution of the world

Human fossils are very rare, and a well preserved cranial specimen even rarer. It is not possible to dissect the precious material for anatomical studies. Some hominin fossils, such as crania, are filled with heavily calcified matrix. For instance, the Yunxian fossil crania was distorted by post depositional processes and covered in hard calcareous breccias. The Bodo fossil crania is incomplete, and filled with a heavy calcified matrix, that forms a natural endocast. In these cases, traditional methods for the study of the internal structure of heavily fossilized bones are limited. Recently, three-dimensional (3D) visualization computer techniques can be used on matrix-filled fossil skulls to establish a virtual 3D endocast and non-invasive dissection of the fossil specimen. Computer Tomography (CT) scanning can make it possible for paleoanthropologists to extend the study of fossil specimens from the exterior to the interior<sup>[46, 47]</sup>. The first australopithecine cranium to which CT scanning was applied was specimen MLD 37/38. This fossil contains a heavily-calcified and very solid matrix. In addition, the anterior part of the braincase was missing. With high-resolution CT scans, the missing cerebrum was restored by drawing, and a virtual endocast was reconstructed by Conroy et al., with a 425 mL cranial capacity calculated<sup>[48]</sup>. Later, the virtual endocasts of australopithecines Stw 505 and Sts 71 were made by paleoanthropologists<sup>[49, 50]</sup>.

Currently, CT scans are widely used in paleoanthropology and paleoneurology<sup>[51-54]</sup>. In 2003, a new hominid species, *Homo floresiensis* (18 ka), was found on the Indonesian island of Flores. *H. floresiensis* has a brain size of 380 mL, which is similar to that of *A. afarensis* specimen AL 288-1 who lived approximately 3.5 Ma. *H. floresiensis* is a tiny hominin with an ape-sized brain. This finding caused a great debate in paleoanthropology. Falk et al.<sup>[54]</sup>

studied the brain by comparing a virtual endocast from *H. floresiensis* with endocasts from *H. erectus*, *H. sapiens*, a human pygmy, and a human microcephalic (Fig. 6). Morphometric, allometric, and shape data indicate that *H. floresiensis* type specimen, LB1, is not a microcephalic or pygmy. LB1's brain/body size ratio is similar to that of an australop-

ithecine, but its endocast shape resembles that of *H. erectus*. *H. floresiensis* has frontal, temporal lobes and a lunate sulcus in derived positions, which are consistent with higher cognitive processing<sup>[54]</sup>. Computed tomography and virtual imaging have facilitated these more recent developments in paleoneurology.

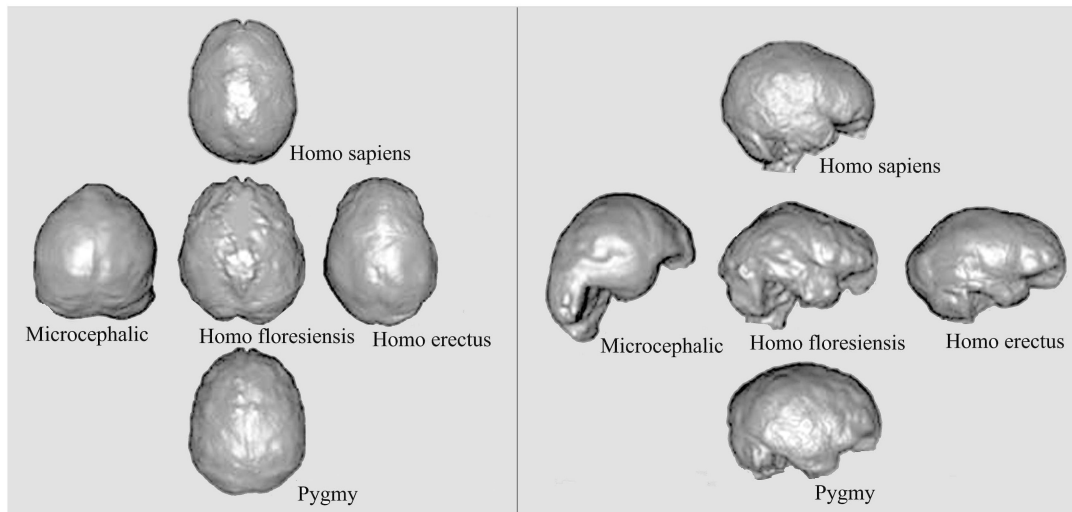


Fig. 6. Comparisons of virtual endocasts with CT scan devices (adapted from Falk et al.<sup>[54]</sup>).

## 6 The study of brain evolution in China

Davidson Black, a Canadian anatomy and anthropology professor, was the first person to study Chinese *H. erectus* endocasts. In 1932, Black reconstructed the endocast of Zhoukoudian *H. erectus* (skull III), and derived a cranial capacity of 964 mL, which is far bigger than apes and within the lower range of normal variability of modern humans. Black found that the anterior branch of the Zhoukoudian middle meningeal artery is bigger than that of modern men. He drew attention to the presence of an inferior frontal prominence representing Broca's convolution (inferior frontal gyrus, not Broca's area), on the lower margin of the frontal inferior region. The tip of the orbital cap is directed ventrally, which is a characteristic of the modern human contour. In anthropoid apes, the tip of the cap is directed forward from the point of separation from the temporal lobe. The lateral surface passes gradually over the orbital surface without a distinct line of demarcation. Black suggested that Zhoukoudian *H. erectus* might have been right handed and began to use fire based on the more complex brain morphology<sup>[55]</sup>. In 1934, at the request of Black, Shellshear and Smith gave the most detailed description of the fissural impressions of the

Zhoukoudian endocast of Skull III<sup>[56]</sup>. They found that the Zhoukoudian endocast displayed primitive characteristics that did not appear in *P. erectus*. For example, the Zhoukoudian endocast has a flat frontal lobe and a well-marked frontal keel, similar to chimpanzees.

In the mid to late 1930s, Weidenreich reconstructed the endocasts of ZKD II<sup>[5]</sup>, ZKD X, ZKD XI and ZKD XII from the original skull fossils<sup>[57]</sup>. Weidenreich suggested that there is a relationship between skull, brain and body sizes during human evolution. When the skull size increased, the brain size enlarged. When the facial size decreased, the maxilla and mandible reduced the most<sup>[58]</sup>. Since the 1950s, a few rather complete human skull fossils were found in China, but studies have primarily focused on the exterior morphology of the crania. There have been a paucity of paleoneurological studies in China, lagging far behind other countries.

In 2001, we began to study the brain evolution of Chinese fossil hominins. Using traditional methods, we reconstructed some hominin endocast specimens<sup>[20, 25, 36, 59]</sup>. In the coming years, we plan to study the endocrania of Lantian *H. erectus*, Nanjing



*H. erectus*, Dali, Maba, Liujiang and others using CT scanning. Currently, the morphological studies of these fossils are only restricted to the exterior of the specimens. Accordingly, the important information retained in the interior of the crania has not been studied. With CT scanning and 3D visualization techniques to reconstruct virtual specimens, it is now possible for Chinese hominin paleontologists to conduct paleoneurological studies of our national treasures. In the long run, these more advanced studies will not only address questions related to Chinese evolutionary history, but make the Chinese data important to paleoanthropologists throughout the world.

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