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Endocast of Sambungmacan 3 (Sm 3): A New *Homo erectus* From Indonesia

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ABSTRACT

A new fossil calvaria, Sambungmacan 3 (Sm 3), described in *New Fossil Hominid Calvaria From Indonesia—Sambungmacan 3* by Márquez et al., this volume, yields one of the most advanced and complete endocasts yet recovered from Java. This communication provides a thorough interpretation of the external anatomical landmarks observable on Sm 3. Using computer tomography (CT) and traditional morphological measurements, our comparative paleoneurological analyses show that while Sm 3 has a mosaic of features that are similar to both Indonesian and Chinese *H. erectus*, it also possesses significant characters reminiscent of later hominins. These include a greater degree of asymmetry characterized by a possible left-occipital, right-frontal petalial pattern, left-right volumetric cerebral asymmetry, and marked asymmetry in Broca's cap. Moreover, the frontal lobe offers a more rounded, shortened appearance in contrast to the flat, elongated appearance of other Indonesian fossils (e.g., Sangiran 17). Another unique trait is exhibited in the transverse plane where the widest breadth of Sm 3 occurs more superiorly than in other Indonesian *H. erectus*. Thus, the endocast of Sm 3 presents a unique morphology not seen previously in the hominin fossil record. While the strong modern human characteristics in this endocast may not represent a particular ancestry, they do allow us to recognize a new dimension of the remarkable variation in Indonesian *Homo erectus*. Anat Rec 262:369–379, 2001.

Key words: brain evolution; human evolution; Broca's cap; computer tomography; petalia

Indonesia has been the site of the longest continuous occupation by any hominin species. The discovery of *Homo erectus* by Eugene Dubois in 1891 near Trinil, Java began a new chapter for human evolution outside of Africa. Since that time several fossils have been unearthed in Indonesia dating from 1.8 MYA to 53,000 years ago. Our understanding, however, of Indonesian *H. erectus* is clouded by an incomplete fossil record, and the unrelenting Indonesian geology which has yielded few stratigraphic certainties. This has led researchers to infer the behaviors of Indonesian *H. erectus* from the morphological features of the fossils and from the brain endocasts that can be derived from the more complete crania.

In describing the endocast of Trinil 2 (*H. erectus* I), Tilney (1927) positioned *H. erectus* far above gorilla but below modern humans. With one of the more detailed

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endocast descriptions of that time, he considered the frontal lobe of *H. erectus* to be well developed. In addition, Tilney regarded the morphology of the inferior frontal lobe as evidence that *H. erectus* "had learned to speak—to communicate in verbal language" (Tilney, 1927). Tilney's enthusiasm for the mental capacity of *H. erectus* in Indonesia was not echoed by others of the time. Albeit Weidenreich (1937) considered Indonesian *H. erectus* to possess more advanced features in its endocast than Chinese *H. erectus*, he stopped short of granting *H. erectus* language capabilities. Dubois (1933), *H. erectus*'s discoverer, apparently took a different view, agreeing with the description of Black (1932) that *H. erectus* from China was more advanced in its endocast features than from Java.

A more recent set of studies by Holloway (1980, 1981a) revisited the endocranial evidence for *H. erectus* from Indonesia. These revised endocranial capacities and new measurements dismissed most of the gyral and sulcal interpretation attempted in early descriptions (e.g., Kappers, 1929; Kappers and Bouman, 1939). In addition, Holloway's observations of a left-occipital, right-frontal petalial pattern, and a well-developed inferior frontal region for Indonesian *H. erectus*, indicated possible cognitive lateralization (Holloway, 1980, 1981a; LeMay, 1976). Despite the revised endocranial estimates and morphological observations of Indonesian *H. erectus*, one problem which has plagued the early Indonesian sample is a high degree of incompleteness. A new fossil calvaria, Sambungmacan 3 (Sm 3), from near the village of Poloyo, described by Márquez et al. (2001), yields one of the most complete endocasts from Indonesia. The present communication provides a thorough interpretation of the anatomical landmarks observable on Sm 3 and a comparative analysis with other Indonesian endocasts.

MATERIALS AND METHODS

The interior of the Sm 3 calvaria was cleaned of all matrix in preparation for making a silicone rubber endocast. To prevent the rubber from adhering to the interior surface, a separator was applied. Current casting methods use silicone rubbers instead of latex. Silicone compounds are preferred, because they give excellent detail reproduction with high tear strength for long lasting molds and less shrinkage, and do not require vulcanization at elevated temperatures as does latex rubber. The silicone rubber chosen for casting Sm 3 was Rhodorsil silicone rubber (RTV-585, Rhone-Poulenc), a premium grade silicone mold-making material that cures at room temperature to form a tough flexible rubber. Because the base of the skull is missing in Sm 3 the silicone rubber was applied in layers on the fossil endocranium to give the greatest amount of detail. Layers were applied to the interior of the skull with a brush in a swirling motion. Each layer was allowed to cure, and a total of four layers were applied. Two endocast molds were made using this technique. Comparative measurements between the endocast and endocranium show shrinkage of less than 1mm.

Restoration of the endocast to its most likely original volume involved reconstructing only the base of the endocast, as there was no noticeable distortion in the calvaria. Lips produced from silicone rubber extending over the surface of the broken edges of the calvaria were trimmed, and the missing portions were reconstructed using nondrying modeling clay (Klean Klay). Two of the authors (DCB and RLH) performed independent reconstructions (Fig. 1). While the neurocranium is almost complete in Sm 3, portions of the basicranium from the posterior-most aspect of the foramen magnum to the rostrum of the frontal lobes are missing. The third inferior frontal region is present and ends infero-medially. Hence, the frontal rostrum and the orbital portion of the frontal lobe were reconstructed. The sphenoid contribution to the base of the calvaria is missing, and thus the temporal poles are lacking in Sm 3. Both poles and the midline basicerebral structures, representing the hypophyseal fossa were reconstructed. Posteriorly, most of the area representing the petrous portions of the temporal bones are present, while those corresponding to the basiocciput, including the clivus, foramen magnum, and the jugular portion of the occipital bone, are missing and have been reconstructed (Fig. 1). Compared to other Indonesian endocasts (Holloway 1980, 1981a) Sm 3 is remarkably complete. In addition there is no apparent distortion to the skull.[1]

Volume Determinations

Volume measurements were made independently for the two endocasts reconstructions. Measurements were done by water displacement (Holloway, 1980). First, each endocast was submersed in water for a period of several minutes to ensure that any air trapped in the endocast was removed. A 3,500cc beaker, fitted with a specially designed overflow spout, was filled to overflow and allowed to drain. Next, the endocast was slowly lowered into the beaker. As the endocast was lowered the resultant runoff was collected in another pre-weighed beaker and subsequently weighed. This method gives an immediate volume because the specific gravity of water is 1. Five determinations were made for each of the endocasts and the average was calculated.

Measurements and Indices

While linear measurements may be of limited use in endocasts (Holloway 1981b), chord and arc measurements were taken to provide quantification of the overall shape configuration of the endocast. Chord and arc measurements for length (frontal pole to occipital pole), maximum width and depth from the vertex to the most inferior portions of the temporal lobes in the midsagittal plane, bregma-lambda, bregma-asterion, and biasterionic breadth were taken to the nearest 0.1mm on digital images using SigmaScan Pro (SPSS Scientific). Arc measurements were performed using a flexible fiberglass tape on the actual endocast. The indices and ratios derived from these measurements were compared to those calculated for other Indonesian *H. erectus* endocasts, *Pan*, *Gorilla*, *Australopithecus* (Sts 5), and modern *Homo sapiens*.

Computer Tomography Scans

CT scans of the endocasts of Sm 3, Trinil 2 (*H. erectus* I), Sangiran 2 (*H. erectus* II), Sangiran 12 (*H. erectus* VII), and Zhoukoudian Locus E (Sinanthropus III) were performed in order to obtain approximate volume estimates of each hemisphere minus the cerebellum (Fig. 2). CT scans were done at Mount Sinai Hospital/NYU Health

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[1] See Marquez et al., preceding this article, for a full description of the Sm 3 calvaria.

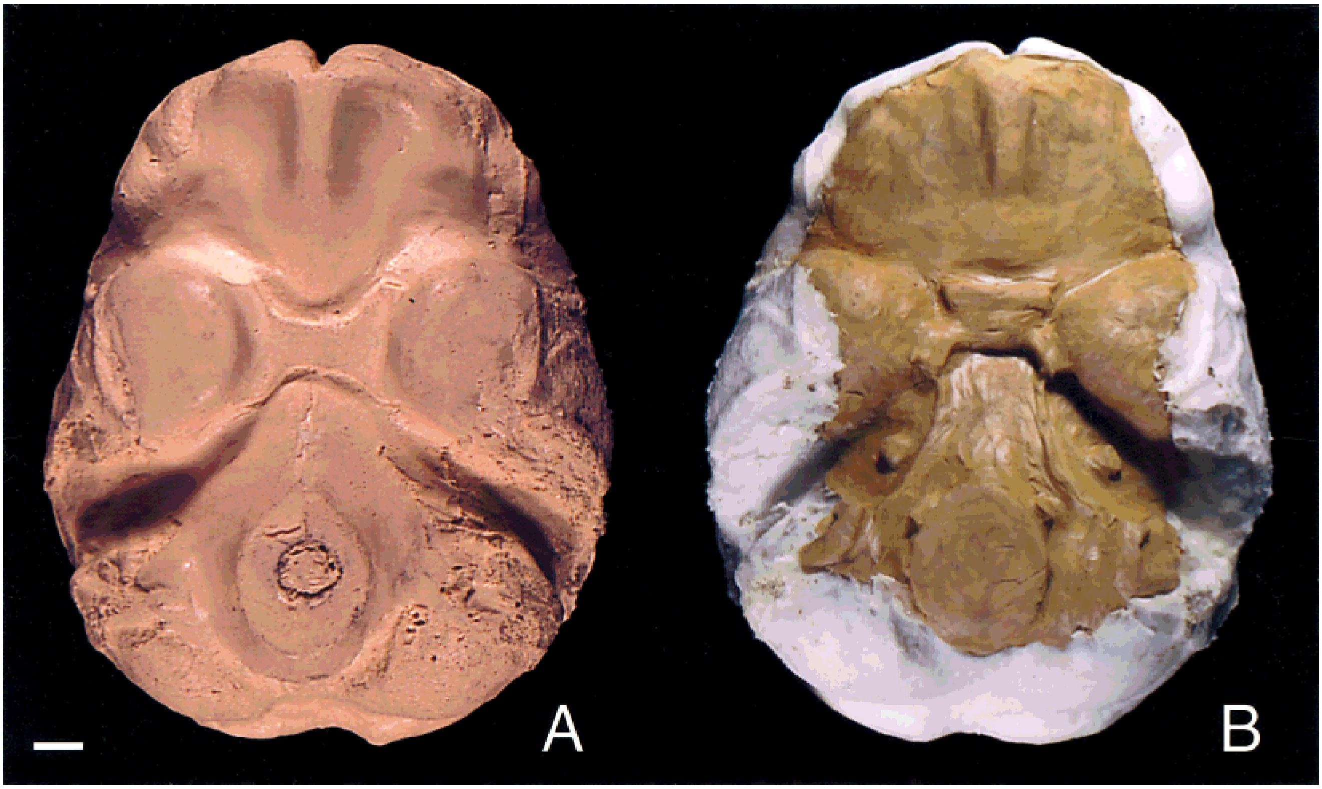

Fig. 1. Basal view of the reconstructed endocast of Sm 3. **A:** reconstruction by DCB. **B:** reconstruction by RLH. The reconstruction of the basal features is minor, and the range of volumes is between 914cc (RLH) and 921cc (DCB). Scale bar = 1cm.

Center using a Hi-Speed CT/i scanner (GE Medical Systems) with a 25cm field of view (DOV), 140kV, 160mA, and a 1:1 pitch helical scan. Single slice sagittal scans were taken at 5mm intervals through the entire endocast. The midsagittal plane was used as a point of reference, and scans to the lateral margins of the endocast were extended from this reference plane. This method was used so that a midsagittal volume could be used to accurately determine the volume of each cerebral hemisphere.

After the scans for a single endocast were complete, area measurements were performed on each slice obtained for that specimen. The sagittal areas (mm^2) calculated include frontal, temporal, and parieto-occipital lobes. Using the midsagittal landmark, it was possible to make an estimate of asymmetries in the endocasts. Because anatomical landmarks that are used in CT scans of brains are not present in an endocast, the volumetric measurements obtained here are simply estimates based on human models of gyral and sulcal configuration which are used to describe lobar boundaries.

RESULTS

Morphological Observations

The endocast of Sm 3 is globular, having a more rounded appearance than other Indonesian endocasts (Fig. 3A and 3B). While the overall shape of the endocast is easily defined, the description of the petalial pattern possessed by Sm 3 is less straightforward. Using the petalial definitions set forth by LeMay (1976) and Holloway and de Lacoste-Lareymondie (1982)[2], the Sm 3 endocast can be characterized as having a right frontal petalia with the right frontal wider from the midline to Broca's cap than the left (Fig. 3E). The petalial pattern of the occipital lobes (Fig. 3D) is less clear. There is a possible left occipital petalia. Depending on the orientation of the endocast, the right occipital lobe may extend more posteriorly than the left, yet the width of the left occipital lobe is larger. Thus, while a right frontal petalia is present in Sm 3, a classic occipital petalia is lacking, although the width of the left occipital lobe is suggestive of a left occipital petalia.

The fronto-occipital arc measurement of the right hemisphere is 223mm and that for the left is 224mm, yielding an average of 223.5mm. This is well above the 209.5mm average arc measurement obtained for early Indonesian *H. erectus* (Holloway, 1981a). This difference between measurements for Sm 3 and other Indonesian endocasts also extends to other measurements including those of overall length, which yield an average length of 151.1mm.

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[2] Petalias are small extensions of parts of the cerebral cortex that show asymmetry in growth and extend slightly more in one hemisphere than in the opposite hemisphere. Right handers, for example, show a petalial pattern in which the left occipital lobe protrudes farther back than the right occipital lobe, while the breadth of the right frontal lobe is greater than that of the left frontal lobe.

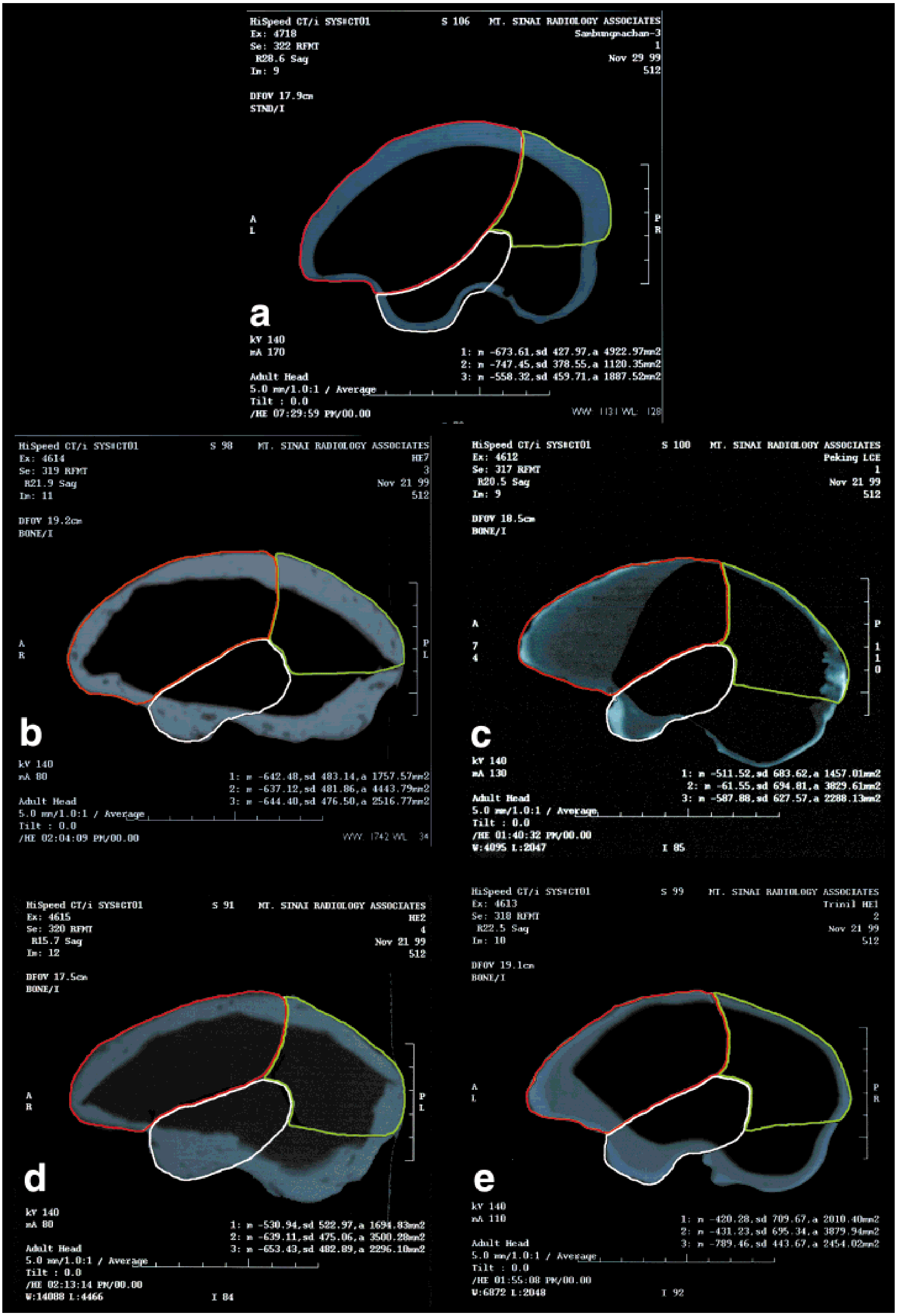

Fig. 2. Parasagittal CT scans of Sm 3 (**a**), Sangiran 12 (**b**), Zhoukoudian Locus E (**c**), Sangiran 2 (**d**), and Trinil 2 (**e**). Areas corresponding to frontal (outlined in red), temporal (outlined in white), and parieto-temporal (outlined in green) lobes were combined with the distance between CT sections to give cerebral hemispheric volumes.

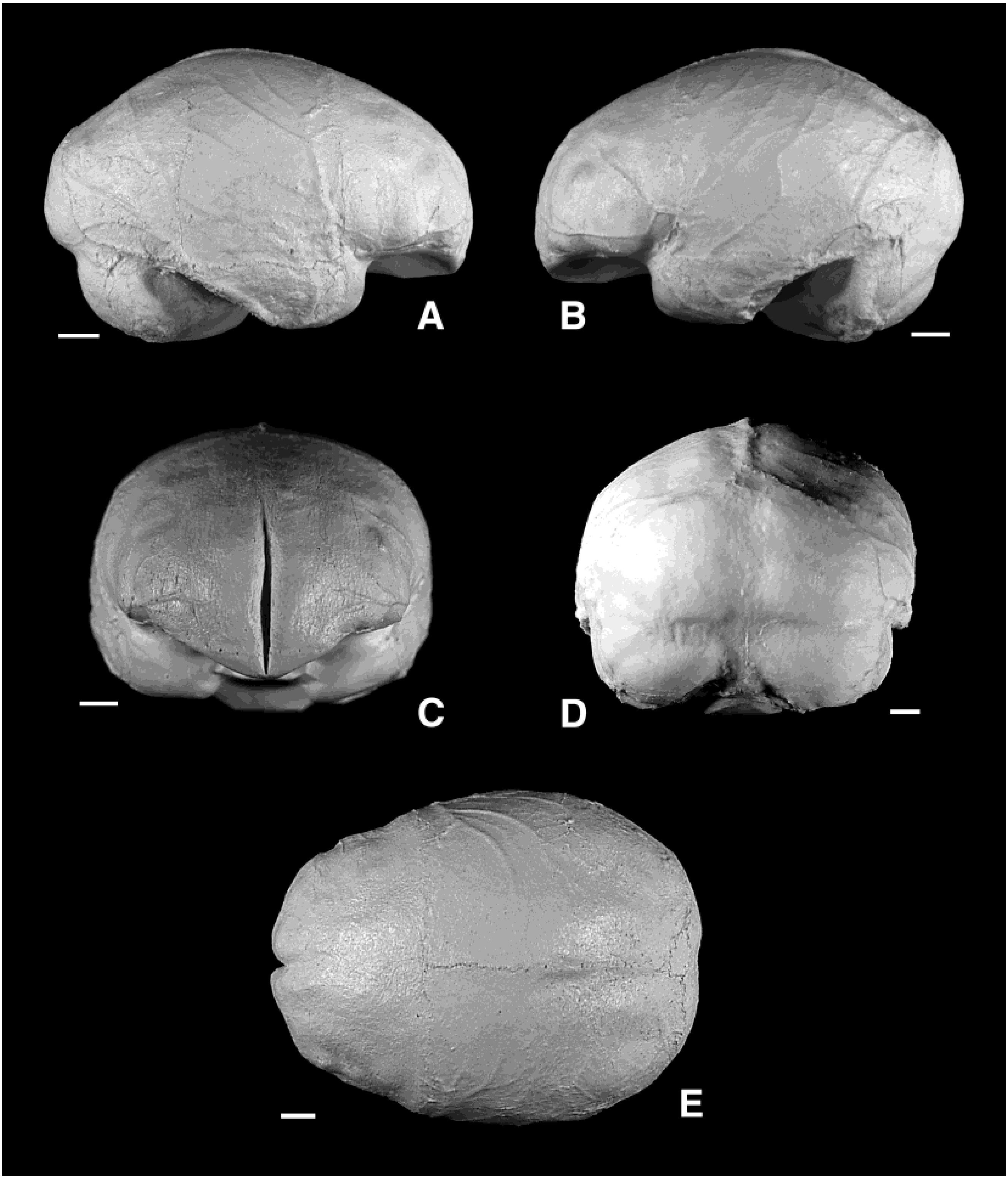

Fig. 3. **A**: Right lateral view of the reconstructed endocast of Sm 3. **B**: Left lateral view of the reconstructed endocast of Sm 3. **C**: Frontal view of reconstructed Sm 3 endocast. **D**: Occipital view of Sm 3 endocast. **E**: Dorsal view of Sm 3 endocast. Scale bars = 1cm.

TABLE 1. Endocast measurements

Measurement (mm)	Sm 3 (1977?)	*H.e.* I (1981)	*H.e.* II (1937)	*H.e.* IV (1938)	*H.e.* VI (1963)	*H.e.* VII (1965)	*H.e.* VIII (1969)	*H.e.* average N = 7
Volume (ml)	917.5	940	813	908	855	1,059	1,004	928 ± 84
1. Frontal-pole to occipital pole								
a. chord	151.1	156	148	156^{E}	158^{E}	161^{E}	161	156
b. arc	223.5	208	202	205^{E}	210^{E}	230^{E}	202	211.5
2. Maximum breadth								
a. chord	113.6	125	120	125	117	130	129	123
b. arc	192	205	192	195	185	208	212	198
3. Depth, vertex to temporal pole	101.25	98	93	95	94	99	100	97
4. Bregma-lambda								
a. chord	82.9	83	70	N.A.	82	92	90	83
b. arc	89	87	72	N.A.	87	97	93	87.5
5. Bregma-asterion								
a. chord	105.9	110	106	112^{E}	113	104	113	109
b. arc	123	132	125	135^{E}	133	130	136	131
6. Biasterionic breadth	95.6	92^{E}	92	73^{E}	85^{E}	96^{E}	95	89.8

Endocast measurements, both in arc and chord dimensions. ^{E} means "estimated," since reconstruction of the frontal portions was necessary, or where the region was otherwise missing. N.A. means "not available," meaning that lambda and bregma are not evident on *H. erectus* IV. Dates indicate date fossil discovered. Specimen designations: *H.e.* I (Trinil 2), *H.e.* II (Sangiran 2), *H.e.* IV (Sangiran 4), *H.e.* VI (Sangiran 10), *H.e.* VII (Sangiran 12), *H.e.* VIII (Sangiran 17).

In a dorsal view the endocast widens posteriorly from the frontal lobes, reaching the area of maximum width approximately midway through the parietal lobes (113.2mm) (Fig. 3E). The vertex of the endocast is approximately in the same location midway through the parietals to the inferior temporal lobes. Since the base of the skull is missing, the depth of the endocast at the vertex to the inferior temporal lobes is estimated, at 101.25mm. Other measurements are presented in Table 1.

The frontal lobes are rounded anteriorly, lacking the characteristic mid-frontal depression seen in other Indonesian endocasts that gives them a flattened profile. The inferior third of the frontal lobe is preserved. On both sides there is a well-developed Broca's, orbital, or frontal cap (Anthony, 1913; Anthony and de Santa-Maria, 1912; Keith, 1931) (Fig. 4). This cap which corresponds to Brodmann's areas 47 and 45 is slightly larger on the left side than the right. The width of the frontal lobe at the cap is 81.2mm with the left frontal lobe width being 39.7mm and the right frontal lobe width at the cap at 41.5mm (Fig. 3E). The right cap protrudes more laterally than the left, yet the left is slightly larger than the right, owing to a cap length of 17.4mm versus 14.5mm on the right (Fig. 4).

There is asymmetry in the cerebellar lobes with the right lobe being slightly wider (49.4mm) than the left lobe (46.2mm). The left lobe, however, protrudes farther posteriorly than the right, albeit its overall size is smaller. Despite this morphology a clear occipital petalial pattern does not emerge. In addition, it is impossible to assess the overall size of the occipital lobes as there are no landmarks demarcating its anterior boundary, such as the parieto-occipital fissure.

Meningeal vessels. Like most other endocast from Indonesia, the meningeal vessels of Sm 3 are well preserved (Fig. 3A and 3B). On the left side the middle meningeal artery can be seen at the postero-medial edge of the temporal lobe where the posterior and anterior trunks emerge. On the right side the middle meningeal artery can be seen at the point of the anterior-posterior bifurcation. The parietal branch of the left middle meningeal artery ascends dorsally along the postero-lateral edge of the temporal lobe in an area antero-inferior to the petrotympanic fissure. Dorsal to this it divides into a posterior branch, which runs parallel to the lambdoid suture. The parietal branch sends a gently sloping, postero-dorsally running occipital branch across the lambdoid suture approximately 1.5cm above asterion. On the right side the posterior trunk of the middle meningeal artery ascends postero-dorsally along the postero-lateral edge of the temporal pole. The parietal trunk of the middle meningeal artery does not divide into two distinct branches on the right hemisphere. Instead the posterior trunk splits into three equal branches: anterior, middle, and posterior (or occipital). The anterior branch of the posterior trunk begins approximately 1.5cm antero-dorsally from asterion, turning sharply anteriorly as it ascends along the posterior portion of the parietal lobe. The middle branch ascends dorsally toward the lambdoid suture, crossing it approximately 2.0cm above asterion. The posterior branch crosses the lambdoid suture just superior to asterion and travels posteriorly.

The anterior trunk of the left middle meningeal artery is visible at its origin. It travels anteriorly along the inferior edge of the unreconstructed temporal lobe, then ascends at its antero-lateral edge. The anterior trunk divides into an anterior and posterior branch approximately 1.3cm above the temporal lobe. The anterior branch travels horizontally approximately 1.0cm then bifurcates into an inferior branch which runs anteriorly along the inferior third of the frontal lobe, and a superior branch which ascends anteriorly across the mid-frontal region. The posterior division of the anterior trunk of the left middle meningeal artery ascends parallel to the coronal suture, giving off numerous parietal branches. The anterior trunk of the right middle meningeal artery is also visible at its origin. It ascends along the inferior border of the right temporal lobe. The anterior trunk disappears at

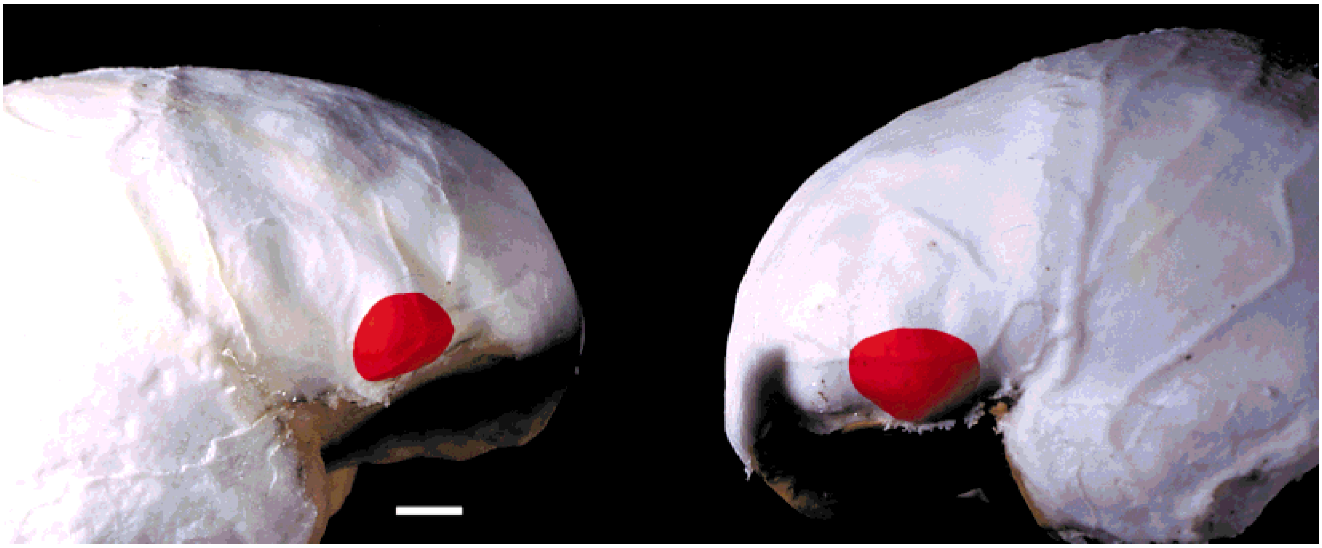

Fig. 4. Right (left side of figure) and left (right side of figure) lateral views of the reconstructed endocast of Sm 3. Red-shaded portions overlie the area occupied by Broca's cap. Scale bar = 1cm.

a break in the endocast near the antero-inferior margin of the temporal lobe. The anterior trunk is visible again along the inferior third of the frontal lobe and continues anteriorly, ending at the frontal pole. The posterior division of the frontal trunk of the right middle meningeal artery is not visible at the bifurcation of the anterior and posterior branches of the anterior trunk due to the missing section of the endocast. The posterior division is visualized beginning near the squamosal-sphenoid junction. It continues posteriorly to the coronal suture and gives off numerous posteriorly directed branches as it ascends parallel to this landmark.

The venous sinuses. A raised ridge corresponding to the sagittal sinus is visible beginning at bregma and becomes more marked near the apex of the endocast. This ridge disappears as it continues posteriorly towards lambda. While the confluence of the sinuses is not prominent at the internal occipital protuberance, it appears that the primary drainage is to the left transverse sinus, as this sinus is more marked than the right transverse sinus (Fig. 3D). This left-right asymmetry continues along the entire course of the transverse sinuses through the sigmoid sinuses. The prominent left sigmoid sinus can be followed from its origin near the anterior border of the cerebellum to its inferior border, ending at the missing area of the endocast before foramen magnum. The right transverse and sigmoid sinuses are less pronounced than the left; however, this morphology may be due to the presence of a marked marginal sinus. The often centrally located occipital sinus is not visible on the endocast; however, the right marginal sinus is visible along the medial border of the cerebellum, approximately 1.2cm below the right transverse sinus. The marginal sinus continues along the medial border inferiorly until it meets with the sigmoid sinus at the base of the right cerebellum. The continuation of the confluence of these two sinuses cannot be followed to the jugular foramen as this portion is missing. The right marginal sinus appears more prominent than the right sigmoid sinus, and therefore may have represented the primary drainage pathway on this side of the brain. While this condition is not unusual for *Homo* (Kimbel, 1984), it has not been noted before in Indonesian or other *H. erectus* crania or endocasts.

Endocranial Volume

An averaged volume of 917cc was obtained for the Sm 3 endocast based on independent measurements from DCB (avg. 921) and RLH (avg. 914). The average cranial capacity obtained by Holloway (1981a) for Indonesian *H. erectus*, not including the Solo specimens, is 929.83cc. While this places Sm 3 below the average for this group, it does, however, fit well within the normal range of variation seen in Indonesian *H. erectus* (813cc–1059cc).

Computer Tomography

CT scans of endocasts are of limited use, but they do provide an estimate of cerebral hemispheric volume unattainable through linear measurements. Volumetric estimates of the Sm 3 endocast yield a left cerebral hemispheric volume of 435.9cc and a right cerebral hemispheric volume of 414.5cc (Table 2). As a percentage of the total cerebral volume, the left hemisphere represents 51.3% of the total volume, indicating a left hemisphere dominance. This difference in the volumetric estimates of the left and right hemispheres is fairly undramatic in Sm 3. Sangiran 12 (*H. erectus* VII) demonstrates a left cerebral hemisphere that is 53.8% of the total volume. Sangiran 2 (*H. erectus* II) shows a reverse asymmetry, with the right cerebral hemisphere representing 51.2% of the total cerebral volume. Trinil 2 (*H. erectus* I) demonstrates a similar pattern, albeit less pronounced with the right cerebral hemisphere representing 50.3% of the total volume of the cerebrum. The fifth endocast examined here, from Zhoukoudian (Locus E), demonstrates the same right hemisphere dominance seen in Trinil 2 and Sangiran 2. It has a right hemisphere that is 52.3% of the total cerebral volume.

TABLE 2. Endocast cerebral hemisphere area from CT (cm^3)

	Right hemisphere	Left hemisphere
Sm 3	435.9 (51.2%)	414.5 (48.7%)
Trinil 2	424 (49.7)	428.5 (50.3)
Sangiran 2	328.6 (48.8)	345 (51.2)
Sangiran 12	452.8 (53.8)	388 (46.2)
Zhoukoudian Locus E	370 (47.7)	406.5 (52.3)

Area measurements in cubic centimeters. Hemisphere as a percentage of total cerebral volume in parentheses.

DISCUSSION

The endocast of Sm 3 possesses an endocranial volume of approximately 917cc. This places Sm 3 in the middle of the range of endocranial volumes obtained for other Indonesian endocasts (Table 1) (Holloway, 1981a). At 1,059cc Sangiran 12 possesses the largest endocast of this group, while the diminutive Sangiran 2 has the smallest at 813cc. These measures would seem to indicate that Sm 3 is not significantly different from the other endocasts known from this region. A comparison of endocranial volume in the light of other measures, however, places Sm 3 in a unique position. A long, low cranial vault characterizes Sangiran 2, Sangiran 12, and the other Indonesian endocasts known from this region, but not Sm 3. The shorter, higher vault of Sm 3 is evident in the degree of difference between the arc and chord measurements for length (frontal pole to occipital pole) and maximum breadth. In the current comparative sample of Indonesian fossils the degree of difference between the arc and chord indices of these two measures is small (approximately 0.25 for length; 0.38 for breadth). The differences between arc and chord measurements of these indices for the Sm 3 endocast, however, are greater (0.32 for length; 0.41 for breadth). The more globular shape of the Sm 3 endocast demonstrates the degree of difference shown here. Instead of a characteristic long, low vault, Sm 3 possesses a short, high vault. Further testament to the unique shape of the Sm 3 endocast compared to other Indonesian fossils is seen in the endocast indices provided in Table 3. The indices for the other Indonesian endocast underline the platycephalic characteristic of their endocasts as seen in the length:height, breadth:height, and height^3:volume ratios. These indices for Sm 3 not only fall outside the range of variation exhibited by the early Indonesian fossils (Table 3), but also fall within the average range exhibited by some pongid and hominin groups. However, measurements on the posterior aspect of the endocast (bregma-lambda; bregma-asterion) do not indicate much variation between Sm 3 and the other Indonesian endocasts.

The meningeal and venous sinus patterns in Sm 3 (Fig. 3A and 3D) are reminiscent of Asian *H. erectus* and modern human patterns (Grimaud-Hervé, 1997). While Saban (1982, 1983) predicted that the middle meningeal branch pattern becomes more complex moving from australopiths to humans, some *H. erectus* fossils appear to possess branching patterns similar to those observed in modern humans (e.g., Sangiran 8). The branching pattern observed in Sm 3 is more complex than Sangiran 8, albeit the endocast of Sm 3 is more complete. The venous sinus drainage is also more reminiscent of modern humans due to the unique feature of a marginal sinus on the right side. While this feature is common in some robust australopiths (Falk and Conroy, 1984), it is occasionally seen in modern human populations (Kimbel, 1984), and we doubt that it has any functional or taxonomic significance, contra Falk's radiator hypothesis (Falk, 1990).

CT has proven to be a useful tool for reconstructing skeletal features. Its use, however, in assessing the nature and volume of internal structures within the skull has been more problematic (Conroy, 1998, 2000). Despite the limited nature of these results, important conclusions can be proposed based on this information. Lobular volumes obtained from CT scans of Sm 3, Trinil 2, Sangiran 2, Sangiran 12, and Zhoukoudian III (Fig. 2) were estimates derived from modern human models. The assumption used to derive the area of each lobe was that *H. erectus* had already approached the modern human condition of gyrification. While it is speculative to apply the results obtained from this approach to a comparison between *H. erectus* and the living pongids or modern *Homo*, it is possible to limitedly compare the individuals examined here. Estimates indicate a left hemisphere dominance in Sangiran 12 (left 0.53 vs. right 0.46) and Sm 3 (left 0.51 vs. right 0.49). This contrasts with a right hemisphere dominance in the other specimens sampled. Since Sm 3 only exhibits a clear right frontal petalia and no obvious occipital petalia, it is difficult to infer hemispheric dominance, and therefore handedness. Morphological data combined with the CT volumetric estimates, however, do indicate a left hemispheric dominance, suggesting a pattern consistent with right-handed individuals (Galaburda et al., 1978; LeMay, 1976, 1977). Other Indonesian endocasts (Trinil 2, Sangiran 2) exhibit a left-occipital, right-frontal petalial pattern suggestive of right-handedness. The frontal area of Sangiran 12 has been reconstructed, but estimates of asymmetry based on the reconstruction by Holloway (1981a) and the CT data indicate a possible leftward asymmetry, perhaps to a greater degree than is seen in Sm 3.

Work on the frontal lobe of the Hominoidea indicates that the size of the frontal lobes relative to the size of the cerebral hemispheres has been conserved with the frontal lobes comprising approximately 35% of the total cerebral volume (Brodmann, 1912; Holloway, 1968; Semendeferi et al., 1997; von Bonin, 1948). This indicates that differences between the frontal lobes of apes and humans lie not in the total area that this lobe occupies relative to the rest of the brain, but instead to the underlying complexity of the lobe (Semendeferi et al., 1997). While others have attempted to derive features of particular gyri and sulci from the frontal lobe of *H. erectus* endocasts (Kappers, 1933; Kappers and Bouman, 1939; Tilney, 1927), assessment of precise cerebral surface features is limited (Holloway, 1978). The endocranial surface morphology of Sm 3 is reduced compared to other Indonesian fossils, but a few features are markedly pronounced.

One feature of significance first noted by Anthony (1913; see also 1912) is an area of the inferior frontal gyrus called Broca's cap (a.k.a. frontal cap, orbital cap) (see also Kap-

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[3] It should be noted that while Falzi et al., 1982 did not find statistically significant asymmetries in surface measurements of Broca's area in a sample of 12 brains, there was statistically significant asymmetry in this region when intrasulcal and extrasulcal measurements were combined.

TABLE 3. Endocast indices

	Sm 3	*H.e.* I	*H.e.* II	*H.e.* IV	*H.e.* VI	*H.e.* VII	*H.e.* VIII	*Gorilla* n = 39	*P. trog.* n = 33	*P. pan.* n = 40	*Homo* n = 4
Breadth: length	0.75	0.80	0.82	0.80	0.74	0.80	0.80	0.77	0.83	0.83	0.78
Breadth: height	1.12	1.27	1.29	1.31	1.24	1.31	1.29	1.17	1.21	1.20	1.08
Length: height	1.49	1.59	1.59	1.64	1.68	1.63	1.61	1.52	1.46	1.44	1.40
Bregma-lambda arc:chord	1.04	1.05	1.03	N.A.	1.06	1.05	1.03	1.04	1.05	1.06	1.09
Bregma-asterion arc: chord	1.16	1.20	1.18	1.20^{E}	1.18	1.25	1.20	1.15	1.17	1.20	1.23
Height^3: Volume	1.13	1.00	0.99	0.94	0.97	0.92	1.00	1.05	1.11	1.12	1.25
Breadth arc: chord	1.70	1.64	1.59	1.56	1.58	1.60	1.64	1.60	1.53	1.56	1.72

Specimen designations: *H.e.* I (Trinil 2), *H.e.* II (Sangiran 2), *H.e.* IV (Sangiran 4), *H.e.* VI (Sangiran 10), *H.e.* VII (Sangiran 12), *H.e.* VIII (Sangiran 17).

pers, 1929; Keith, 1931). On Sm 3 as with many other Indonesian endocasts (Holloway 1980, 1981a), Broca's cap is well developed (Figs. 3C, 4). In humans and apes, Broca's cap contains portions of Brodmann's areas 47 and 45 (Fig. 5) (Brodmann, 1909, 1912; Kappers, 1929). Convention in the early part of the 20th century demarcated the entire inferior third frontal convolution as the center of speech (Brodmann, 1909; Keith, 1916). Utilizing newer technologies, including fMRI, recent studies have reduced the size of this speech region (Broca's area) to the pars operculum (area 44) and pars triangularis (area 45) of the third frontal convolution (Amunts et al., 1999; Damasio, 1992; Desmond, et al., 1995; Hinke et al., 1993) (cf. Harasty et al., 1997; Neville et al., 1998; Nieuwenhuys et al., 1988; Price, 2000). While there is some argument over the degree of asymmetry in function (Hinke et al., 1993) and area (Falzi et al., 1982), the histological distinctions between these areas has been established for some time (Brodmann, 1909). Despite the continuing argument over the localization of aspects of speech in Broca's area, consensus supports a lateralization in speech function with a predominant left over right asymmetry (Desmond et al., 1995; Falzi et al., 1982; Foundas et al., 1998; Hinke et al., 1993; Peterson et al., 1988; Price, 2000). In certain cases surface area measurements of areas 44 (pars opercularis) and 45 (pars triangularis) have yielded no asymmetries (Falzi et al., 1982). In most cases, however, there exists a left over right asymmetry for these areas (Amunts et al., 1999; Foundas et al., 1998; Galaburda, 1980; see Uylings et al., 1999 for review). In a comprehensive study examining the cytoarchitectonic borders of areas 44 and 45, Amunts et al. (1999) demonstrated that area 44 shows a consistent left over right asymmetry. Area 45 was shown to be no more symmetrical than area 44, although the asymmetry is more variable. In addition, in an MRI study of 32 individuals Foundas et al. (1998) found a clear left over right asymmetry of pars triangularis and pars opercularis. These results match the frequency of left-sided dominance within modern *Homo* (Branche et al., 1964), and reflect the functional lateralization of speech (Steinmetz et al., 1991).

Current information regarding the lateralization of speech in modern humans is of limited usefulness in assessing the speech capabilities of Sm 3. It is most difficult to assign a level of speech or language capability to a fossil. For example, even with a complete skull, it is not possible to construct a cytoarchitectonic map of a fossil brain, which would be the only way to reliably compare these endocasts with living humans. Nevertheless, the features available on endocasts can provide some reasonable speculation as to the abilities of fossil individuals. The Sm 3 petalial pattern, while not distinct, suggests a torque pattern usually found in right-handed modern humans (LeMay, 1976). Such a pattern corroborates hemispheric dominance in *H. erectus*, albeit this is speculative. In addition, Sm 3 possesses a pronounced Broca's cap that is highly left over right asymmetric. Although the right frontal lobe is broader at the point of Broca's cap, the left cap is larger overall (Fig. 4). In addition, as the area corresponding to the third inferior frontal convolution travels toward the Sylvian fissure there is a noticeable bulge anterior to the frontal branch of the middle meningeal artery, continuing vertically along the coronal suture. While this feature cannot be assigned a Brodmann's map area; the presence of this feature is provocative for the inference of an enhancement of speech areas. Holloway (1983) noted the presence of Broca's cap in pongids, yet the presence of the feature is inconsistent, unlike *Homo*. Tobias (1975) suggested that the australopiths showed a variable presence of this feature. It was not until *Homo habilis* that this feature began to present itself more consistently in the fossil evidence (Holloway, 1983; Tobias, 1975). Tobias (1983) claims that this indicates that there was the possibility for speech in *H. habilis*. While this evidence is merely corroborative, it does strongly suggest that some form of speech was established in later *H. erectus*. The degree of asymmetry seen in associative speech features in Sm 3 is corroborative, albeit not causally indicative, of the idea that Sm 3 and other Indonesian *H. erectus* had developed a level of speech ability not seen in previous hominin groups.

The remarkable degree of completeness of the Sm 3 endocast provides important information to the understanding of Indonesian *H. erectus*. The unique features of this endocast such as a short, high vaulted, globular endocranium, along with left-right asymmetries, indicate that the cerebral evolution of later hominins was more complex than previously thought. In addition, the presence of a well-developed, asymmetric Broca's cap and left-right hemispheric asymmetry point to a degree of possible cognitive specialization approaching later hominins.

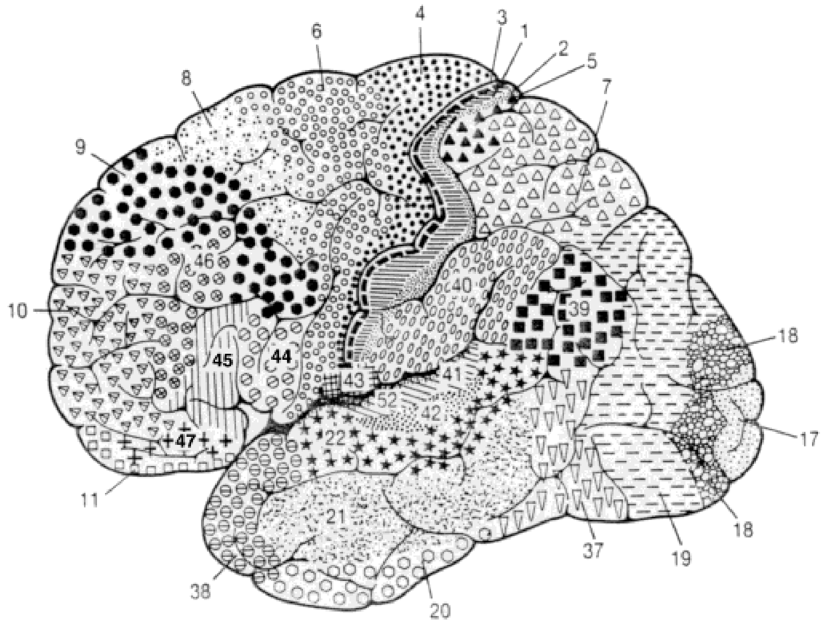

Fig. 5. Brodmann's (1909) cytoarchitectural map of the human brain. Broca's motor speech areas (44, 45) in bold along with area 47. (Adapted from Brodal, 1969)

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