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human brain pp. 124 & 165

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ABSTRACT 

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ABSTRACT ▾



## Supplementary Materials for **The primitive brain of early *Homo***

Marcia S. Ponce de León\*, Thibault Bienvenu, Assaf Marom, Silvano Engel, Paul Tafforeau, José Luis Alatorre Warren, David Lordkipanidze, Iwan Kurniawan, Delta Bayu Murti, Rusyad Adi Suriyanto, Toetik Koesbardiati, Christoph P. E. Zollikofer\*

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Published 9 April 2021, *Science* **372**, 165 (2021)  
DOI: 10.1126/science.aaz0032

### **This PDF file includes:**

Materials and Methods  
Supplementary Text  
Figs. S1 to S5  
References

## Materials and Methods

### M1. Sample

The extant sample comprises crania of  $N_h=110$  modern humans (*Homo sapiens*),  $N_c=81$  chimpanzees (*Pan troglodytes* spp.),  $N_b=27$  bonobos (*Pan paniscus*),  $N_g=43$  gorillas (*Gorilla gorilla* spp.), and  $N_o=32$  orangutans (*Pongo pygmaeus*). Specimens were grouped according to their maxillary dental eruption stage (immature: one or more permanent molars fully erupted; adult: all permanent molars fully erupted). Specimens are from the Collections of the Department of Anthropology and Anthropological Museum of the University of Zurich, the Royal Museum for Central Africa (Tervuren), the Bavarian State Collection for Anthropology and Paleoanatomy (Munich), the Peabody Museum of Archaeology and Ethnology at Harvard University, the Natural History Museum London, and the Duckworth Collection at Cambridge University. The fossil sample consists of the specimens listed in Table 1 (see main text).

### M2. Computed Tomography and data segmentation

Computed Tomography (CT) of all specimens was performed with medical CT devices, using beam collimations between 0.5 and 1.0 mm, and performing cross-sectional image reconstructions with voxel sizes between  $0.2^3$  and  $0.5^3$  mm<sup>3</sup>. The Dmanisi cranium D4500 was further analyzed with synchrotron tomography on beamline ID17 at the European Synchrotron Radiation Facility (ESRF). The cranium was placed in a semolina-filled PVC cylinder to guarantee fixation and to prevent direct irradiation of the detector. Scanning parameters were as follows: 45 $\mu$ m taper optic with cerium-doped taper protection (required retrodistortion map application before further processing); energy: 96keV; propagation distance 5000mm; monochromator: Si 111 curved double Laue; sensor: FReLoN 2K14; camera mode: frame transfer mode, no shutter; scintillator: Gadox 60; insertion device: W150; ID Gap: 25mm; machine filling mode: 200mA; projection number: 5000; scan geometry: 360° in half-acquisition mode, step-by-step scanning; exposure time: 0.15s; time per scan: 37min; number of scans: 116; image reconstruction: single-distance retrieval using Paganin algorithm, ring artifact correction.

For each cranium, the endocranial surface was digitally extracted from the CT data volume following procedures described in ref. (87), and using the software packages Avizo and Geomagic Studio. Endocranial volumes (ECV) were evaluated from the surface data using the software Avizo.

### M3. Cranio-cerebral topographic criteria for the identification of frontal lobe structures on fossil endocasts

Broca's Cap (BC) is a conspicuous feature in the fronto-orbital region of both great ape and human endocasts, but the underlying brain areas are not homologous across groups (7, 8). In great apes, BC largely comprises Brodmann area 44, and its inferior delimitation is formed by the fronto-orbital sulcus (Fig. 1A, *fo*). In humans, BC largely comprises Brodmann areas 45 and 47, and its inferior delimitation tends to coincide with the lateral orbital sulcus (9) (Fig. 1B, *lo*). While the BC regions of great ape and human endocasts comprise different brain regions, they often assume similar morphologies:

- Both great apes and humans exhibit wide interindividual variation in the depth of the endocranial imprints that delimit BC inferiorly. Based on imprint depth alone, it is not possible to clearly discriminate between the presence of *fo* versus *lo* in fossil endocasts.
- Furthermore, sulcal ramification patterns in the brain regions underlying BC are variable in both groups (13, 88), such that the association of individual endocranial imprints with specific cerebral sulci often remains ambiguous.
- Also, cerebral structures underlying the BC region are not consistently reproduced as endocranial imprints, and tend to interfere with non-brain imprints. For example, the human ascending ramus *R* (see main Fig. 1B) largely coincides with the inferiormost portion of the coronal suture and/or the base of the anterior ramus of the middle meningeal artery.

As a consequence, in fossil endocasts, frontal lobe organization cannot be reliably inferred from the morphology and structure of the BC region alone. However, the topographical relationships of neurocranial and brain structures in the frontal lobe region as a whole are clearly distinct between great apes and humans (Fig. 1) (34, 35): In all great apes, the precentral sulcus (*pc*) crosses the coronal suture (CO) such that its superior part (*pcs*) is posterior to CO, and its inferior part (*pci*) is situated anterior to it (Fig. 1A). In contrast, in humans, both *pcs* and *pci* are situated on the posterior side of CO (Fig. 1B). Cranio-cerebral topography (17, 89-91) can thus be used as a reliable indicator of frontal lobe organization.

We define the following criteria to discriminate between primitive (ape-like) and derived (human-like) craniocerebral topographies in the frontal lobe region of fossil endocasts:

- *Criterion 1: Imprints of pc and CO are represented on the endocast.*
  - a) Imprints of *pc* cross CO, such that *pci* is on the anterior side of CO: this situation implies an ape-like morphology, thus primitive organization, of the fronto-orbital region. See Fig. 4, inset graph, orange symbol.



b) Imprints of *pc* do *not* cross CO, such that *pci* is on the posterior side of CO: this situation implies a human-like morphology, thus derived organization, of the fronto-orbital region. See Fig. 4, inset graph, turquoise symbol.

- *Criterion 2: Imprints of pc are not represented on the endocast, but CO is represented.*

5 In this situation, topographical relationships between the precentral sulcus, the frontal sulci, and the coronal suture that are consistent across taxa must be considered. In both human and great ape brains, the frontal sulci exhibit substantial variation in ramification patterns. As an effect, individual sulci at mid-height of the frontal cortex are variably identified as representing a middle frontal sulcus (*fm*) proper, or forming part of the inferior (*fi*) versus superior (*fs*) frontal sulci (13). Frontal sulci typically reach the precentral sulcus, but they never cross this structure. As an effect, the posterior delimitation of the frontal sulci defines the anteriormost location of the precentral sulcus. Based on these observations, it is possible to characterize the following topographies:

15 a) Imprints of *fi* and *fm* touch or cross CO: this situation implies that *pci* (even if not visible as an imprint) is located on the posterior side of CO, and that the fronto-orbital region exhibits a human-like morphology, thus derived organization, of the fronto-orbital region. See Fig. 4, inset graph, turquoise symbol.

20 b) Imprints of *fi* and *fm* fade before reaching CO, while imprints of *pci* are not visible: this situation implies that *pci* likely coincides with the location of CO, which represents an intermediate morphology of the fronto-orbital region. Because intermediate morphologies are clearly different from ape-like morphologies, they represent a derived organization of the fronto-orbital region. See Fig. 4, inset graph, grey symbol.

25 - *Criterion 3: Discrimination between endocranial imprints of the inferior precentral sulcus (pci) and imprints of bony elevations along the coronal suture.*

30 On human and great ape endocasts, the fronto-orbital region between Broca's Cap (BC) and the coronal suture (CO) often exhibits a combination of sulcal imprints, and imprints caused by raised bone margins (lipping) along CO. In fossil hominin endocasts, CO lipping can thus potentially be confounded with the imprints of a *pci* situated anterior to the coronal suture. These ambiguities can be resolved as follows:

a) Primitive condition: on great ape endocasts, imprints of *pci* course toward BC and often bisect its superior region but do not reach its inferior border (Fig. 1A).

- b) Derived condition: on human endocasts, imprints caused by lipping along the borders of CO are located posterior to BC, and typically extend downward to the level of the inferior border of BC (see e.g. fig. S3).

5

#### M4. Geometric morphometric analysis of endocranial shape

Endocranial shape was quantified with  $K=921$  three-dimensional anatomical landmarks (LMs), which are distributed equally over the entire surface of the endocast, and represent fixed point  
10 LMs ( $K_p=27$ ), curve semilandmarks (SLMs) ( $K_c=110$ ), and surface SLMs ( $K_s=784$ ). Fixed LMs and curve SLMs were acquired with Avizo. A template of regularly-spaced surface SLMs was defined for one specimen, then warped to every other specimen, using the fixed LMs and curve  
15 SLMs as nodes of a thin-plate spline (TPS) interpolation function, and projecting the warped surface SLMs onto the target specimens along endocranial surface normals. To optimize the position of SLMs and establish geometric correspondence across all specimens of the sample, the curve SLMs were allowed to slide along tangents to the curves, and the surface SLMs along  
20 tangents to the surface. Sliding was iterated until convergence to the minimum bending energy criterion (92). Since natural patterns of left-right asymmetry are not considered here, all specimens were symmetrized via relabeled reflection of landmarks. Finally, Generalized Procrustes Analysis (GPA) was applied to minimize differences in scale, position and orientation  
between the specimens' landmark configurations. Principal Components Analysis (PCA) of shape was then applied to the Procrustes-aligned specimens to explore and visualize major patterns of shape variation in the sample (Fig. 3). All procedures were performed with the R  
package Morpho (93).

25

#### M5. Computing and visualizing endocranial shape change associated with the transition from primitive to derived frontal lobe organization

30 Endocranial shape change in early *Homo* associated with the transition from primitive to derived organization of the frontal lobe (see Fig. 4) was evaluated by computing the mean endocranial shapes of the two respective samples (specimens representing the primitive organization: KNM-ER 1805, KNM-ER 1813, KNM-ER 3733, KNM-WT 15000, D2280, D2700, D3444, and D4500; specimens representing the derived organization: KNM-ER 3883, Sangiran 17,  
35 Sambungmacan 3,4, Bukuran, Solo 1,5,6,9,10,11, and ZKD XII). A Procrustes ANOVA test for between-group differences in endocranial shape yielded a  $p$ -value of 0.019 [R package Geomorph v3.1.2 (94)]. Shape change from primitive to derived mean endocranial morphology

was visualized (see Fig. 4B) as above-average expansion (positive size allometry) of local endocranial surface regions, both in terms of local outward movement of the surface (bulging), and of local surface area increase, using the methods described in ref. (95).

5

## Supplementary Text

### S1. Morphology of the Dmanisi endocasts

10 The CT-based descriptions of the endocranial morphology of the five Dmanisi crania focus on the following aspects: 1) state of preservation; 2) overall shape and petalial asymmetry; 3) cerebellar fossa morphology and position; 4) imprints of cortical sulci and gyri (from anterior to posterior) and cranio-cerebral topography; 5) imprints of venous sinus structures.

15 The endocast of the adult individual **D2280** (fig. S1A) is generally well preserved, but lacks parts of the basicranial region. It has a rounded overall shape, with a comparatively wide anterior cranial fossa (indicating wide frontal lobes) and right occipital/left frontal petalia. The cerebellar fossa is large and bulges inferiorly. Imprints of the frontal sulci on both left and right sides course toward the precentral sulcus. The precentral sulcus courses from a location near the apex of the endocast in antero-inferior direction towards Broca's Cap (BC). During its course it  
20 crosses the coronal suture at mid-height, such that its inferior portion lies anterior to the coronal suture.

On the left side, a sulcal imprint anterior to the inferior portion of the lambdoid suture is labeled (*L*) in fig. S1A. Assuming a primitive organization of the parieto-occipital cortex of the Dmanisi hominins (see Results and Fig. 4), this imprint could represent a remnant of a great ape-like lunate sulcus (*L*).  
25

The apical parietal region of the endocast exhibits marked bilateral keeling, indicating a wide superior sagittal venous sinus. The venous draining system is further characterized by a dominant left transverse sinus, a curved left sigmoid sinus located at the anterior border of the cerebellar fossa, and weakly expressed occipital marginal sinuses on both sides of the foramen magnum.  
30

The cranium of the adult individual **D2282** (fig. S1B) is fragmentary and exhibits substantial taphonomic distortion, which required digital retrodeformation and reconstruction. Several key endocranial structures are nevertheless visible. Similar to D2280, the endocranium is rounded and exhibits wide frontal lobes. The cerebellar fossae are only moderately bulging. Petalial  
35

asymmetry cannot be ascertained. On the better-preserved left side, the precentral sulcus crosses the coronal suture at mid-height and courses toward the center of BC. On the left side, a sulcal imprint at the antero-inferior border of the lambdoid suture could represent a remnant of *L* (assuming a primitive organization of the parieto-occipital cortex). Bilateral sagittal keeling indicates a wide superior sagittal sinus. The transverse sinus on the right side likely represents the dominant one.

The neurocranium of the adolescent individual **D2700** (fig. S1C) is well preserved externally but less so internally. Parts of the neurocranium were missing *in situ*, while endocranial features representing the frontal cortex were partly damaged during an early attempt at physical casting. Furthermore, structural detail in the parietal and occipital region of the endocast is blurred by a thin but dense calcite layer, which tightly adheres to the bone surface.

In lateral and posterior views, the endocast appears rounded; in superior view, it presents a marked pre-coronal constriction, a feature that is often seen on endocasts of Asian *H. erectus*. The endocast exhibits left frontal petalia. The occipital poles are moderately projecting. The cerebellar fossae are only moderately bulging. Endocranial imprints of the frontal sulci are weak compared to the other Dmanisi specimens. On both sides, the imprint of the medial frontal sulcus courses toward the coronal suture, where it approaches the precentral sulcus. The inferior portion of the precentral sulcus lies in front of the coronal suture and courses toward BC. Preservation of the endocranial base region permits estimation of cranial base angulation. The cranial base angle between landmarks basion, sella, and foramen caecum is 135° [CBA1 (36)]. The angle between the clivus plane and the midplane of the anterior cranial fossa (planum sphenoidale) is 124° [CBA4 (36)]. These values are at the upper end or above the range of variation of modern humans of similar dental age [CBA1: 132-137°; CBA4: 106-118° (37)].

The superior sagittal sinus is represented by a marked, narrow imprint with drainage into both left and right transverse sinuses, with the right side being the dominant one. The sigmoid sinus is comparatively straight (rather than recurved). Occipital marginal sinuses are expressed on both sides.

The endocranial cavity of the edentulous cranium **D3444** (fig. S1D) was only partially filled with matrix *in situ* (31), indicating rapid sedimentation. The endocranial surface suffered some taphonomic damage, such as dislocation of the left temporal pyramid, and loss of parts of the anterior cranial base and of the internal table on the left fronto-parietal region. The endocast has a globular shape that is similar to that of some modern human endocasts (see main Fig. 3).

However, it exhibits pre-coronal constriction similar to D2700. The endocast exhibits slight right frontal petalia. The frontal sulci are represented by marked endocranial imprints, which course

toward the imprint of the precentral sulcus. The inferior part of the precentral sulcus lies anterior to the coronal suture, and courses toward the center of BC. The superior sagittal sinus drains into the dominant right transverse sinus. The sigmoid sinus curves around the anterior region of the cerebellar fossa. On the right side, it drains into the occipital marginal sinus.

5

Cranium **D4500** and mandible D2600 represent the most complete skull of early *Homo* found to date. The endocast is fully preserved, except a minimal area of the internal table in the occipital region (fig. S1E). Like in D2700 and D3444, the endocranial cavity of D4500 was only partly filled with sediment *in situ*. Sediment adhering to the middle and anterior cranial fossae was removed using synchrotron imaging and semi-automated image segmentation procedures. In superior view, the D4500 endocast exhibits right-occipital petalia and associated Yakovlevian torque, as expressed by the lower position of the right compared to the left cerebellar fossa. Pre-coronal constriction is marked, but the frontal lobes remain relatively wide. Complete preservation of the internal cranial base permits direct measurement of cranial base angles CBA1=156° and CBA4=144°.

10

15

The frontal sulci are represented by marked imprints; they course toward the precentral sulcus, which is clearly represented on both sides of the endocast. The inferior precentral sulcus is located just anterior to the coronal suture and courses inferiorly toward BC. In posterior and superior views, sulcal imprints anterior to the lambdoid suture and running approximately parallel to it are visible on left and right sides of the endocast. Assuming a primitive organization of the parieto-occipital cortex, these imprints potentially represent remnants of *L* that communicated with the posterior ends of the intraparietal sulci.

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The superior sagittal sinus is represented by a marked midsagittal imprint, and bilateral keeling indicates the attachment sites of the cerebral falx. Also, the parieto-occipital region exhibits several Pacchionian depressions. Imprints of the transverse sinuses are inconspicuous. The sigmoid sinus follows a straight course along the anterior portion of the cerebellar fossa. On the right side, a marked occipital marginal sinus is present.

#### *Petalial patterns in the Dmanisi sample*

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Petalial asymmetry was scored in the four well-preserved Dmanisi specimens D2280, D2700, D3444, and D4500 (see Table 1). While the standard petalial pattern of great apes and humans is left-occipital/right-frontal (96, 97), three of the four scored Dmanisi specimens exhibit reversed frontal and/or occipital petalia (D2280: right-occipital/left-frontal; D2700: left-frontal; D4500: right-occipital), and we may ask whether their prevalence is unusually high. Using the petalial frequencies published in ref. (96) we can estimate the probability *p* of finding by chance at least 2 right-occipital and at least 2 left-frontal petalia in a sample of *N*=4 specimens: *p*=16%. In

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statistical terms, this is reasonably large to conclude that the number of petalial reversals seen in the Dmanisi sample is likely an effect of random sampling.

5 S2. Endocranial morphology of early *Homo* from Africa

Unless otherwise stated, all descriptions are based on CT scans of the original fossil specimens.

*KNM-ER 1805*

10 The endocranial morphology of this specimen has been described as exhibiting “a pongid-like fronto-orbital sulcus” (21). Examination of the frontoparietal endocranial region shows imprints representing the right and left precentral sulci, which cross the coronal suture at mid-height (fig. S2A). This supports Falk’s original interpretation (21), and provides additional evidence for a primitive organization of the frontal lobe in this specimen.

15

*KNM-ER 1813*

The left and right frontoparietal endocranial regions of this specimen exhibit sulcal imprints that can be associated with the inferior frontal and precentral sulci, respectively (fig. S2B). The latter structures extend from postero-superior to antero-inferior, crossing the coronal suture at mid-  
20 height, and coursing toward Broca’s Cap. This topography implies that Broca’s Cap is delimited inferiorly by the fronto-orbital sulcus, thus indicating a primitive organization of the inferior frontal lobe.

*KNM-ER 1470*

25 According to Falk (21) this specimen provides key evidence for a derived organization of the frontal lobe (fig. S2C): endocranial structures on the left anterior surface have been interpreted as imprints of the inferior frontal sulcus and parts of the anterior (=horizontal, *R*) and ascending (=vertical, *R'*) rami of the lateral (Sylvian) sulcus, respectively. The latter two structures (*R'* and *R* in fig. S2C) would indicate that the Broca Cap region of KNM-ER 1470 comprised pars  
30 orbitalis and pars triangularis, and therefore exhibited a modern human-like organization. CT-based re-examination of the endocranial morphology reveals that structure *R* likely is a taphonomic defect (in humans, the ascending ramus largely coincides with the lowermost part of the coronal suture; see main Fig. 1B).

35 Since imprints of the precentral sulci are not present on this specimen, structure *R'* (and its superior extension: stippled line in fig. S2C) remains ambiguous: it could represent a human-like anterior horizontal ramus of the lateral sulcus (21), or an ape-like subcentral anterior sulcus (13).

Overall, the frontoparietal region of the KNM-ER1470 endocast exhibits little structural detail, such that inferences on the location and course of the precentral sulcus cannot be drawn with certainty.

5 *KNM-ER3733*

This cranium exhibits extensive fragmentation as well as local taphonomic distortion. Also, parts of the anterior cranial fossa are still filled with matrix. CT-based examination indicates that various endocranial imprints are spatially associated with fractures. As an effect, imprints cannot definitely be assigned to brain structures versus taphonomic damage. On both sides, endocranial imprints situated anterior to the coronal suture and coursing in supero-inferior direction likely represent the inferior precentral sulcus, as it is located immediately superior (rather than posterior) to BC (see criterion 3a) (fig. S2D). These topographical relationships would indicate that Broca's Cap is delimited inferiorly by a fronto-orbital sulcus, reflecting a primitive organization of the fronto-orbital cortex.

15

*KNM-ER 3883*

The neurocranium of this specimen exhibits taphonomic damage, such that endocranial imprints only partly represent brain sulci, while others result from fragment displacement and indentation, especially on the left side (fig. S2E). On the right side, an imprint in the parietal area likely represents a portion of the central sulcus. A shallow imprint immediately anterior to the inferior portion of the coronal suture, but posterior to BC likely reflects marked lipping of the frontal squama along the coronal suture (see fig. S2E, hatched area). Imprints of the middle and inferior frontal sulci (*fm*, *fi*) reach the anterior side of the imprint of the coronal suture, indicating that *pci* was located beneath or posterior to the suture. Considering the location of the central sulcus on this endocast confirms that the precentral sulcus must have been located in close vicinity to the coronal suture. Together, the frontal region of this endocast is thus best interpreted as exhibiting a morphology that is intermediate between great ape-like and human-like cranio-cerebral topographies.

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*KNM-WT 15000*

The cranium of this specimen has been reconstructed from several fragments (60). Partial mismatch between fragments is likely due to local taphonomic distortion. The left side of the endocast is better preserved and exhibits more structural detail than the right side (fig. S2F). A faint imprint anterior to the coronal suture likely represents the inferior precentral sulcus, as it is coursing toward the center of BC. This indicates a primitive organization of the inferior frontal lobe.

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*KNM-ER 42700 (Ileret)*

CT-based visualizations of the reconstructed endocast provided in ref. (62) have a low spatial resolution, thus revealing relatively little structural detail. On the left inferior frontal region, an imprint representing the inferior frontal sulcus (*fi*) courses in postero-superior direction to reach the coronal suture. This configuration implies that *pci* must have been located posterior to this suture, indicating a derived organization of the frontal lobe.

*BOU-VP-2/66 (Daka, Bouri)*

The microCT-based visualizations of the endocast of this specimen provided in ref. (63) show various diagnostic features. The imprints of the middle/inferior frontal sulci course in antero-posterior direction to reach the coronal suture. Accordingly, the precentral sulcus must have been located posterior to the coronal suture. Together, these topographical relationships indicate a derived organization of the frontal lobe. Small sulci in the occipital pole region are possibly associated with *L*.

*UA-31 (Buia)*

MicroCT-based visualizations (64) show a smooth endocranial surface with only few imprints representing cerebral sulci. On the left side, imprints of the middle and inferior frontal sulci extend posteriorly to the coronal suture, indicating that the inferior precentral sulcus was located posterior to the suture. As in Daka and Ileret, these topographical relationships indicate a derived organization of the frontal lobe.

S3. Endocranial morphology of early *Homo* from East Asia

The endocranial morphology of early *Homo* from East Asia has been investigated since the early 20<sup>th</sup> Century (98-100), and new evidence and comparative context has been provided in refs. (101, 102). Here we focus on those aspects of endocranial morphology that are relevant for addressing questions of cranio-cerebral topography and frontal lobe organization. Unless otherwise stated, all observations and descriptions reported here are based on new CT scans of the original fossil specimens.

*Mojokerto*

CT-based segmentation of this specimen reveals few endocranial imprints in the frontal region (fig. S3A). The left endocranial surface shows an imprint of the inferior frontal sulcus that



originates above and anterior to Broca's Cap and courses in supero-posterior direction to reach the coronal suture. This implies a post-coronal location of the inferior precentral sulcus (criterion 2a), thus a derived organization of the inferior frontal lobe.

5 *Sangiran 9*

MicroCT-based visualizations of this specimen [see Fig. 2F in ref. (74)] show marked imprints representing the left middle/inferior frontal sulci. On the left side, one imprint corresponding to the middle frontal sulcus crosses the coronal suture. This indicates that the precentral sulcus was situated posterior to the coronal suture.

10

*Sangiran 17*

The well-preserved left side of this specimen shows several endocranial imprints in the frontal region representing the superior, middle and inferior frontal sulci (fig. S3B). These imprints course in approximately horizontal direction toward the coronal suture but tend to fade toward the suture such that it is not possible to ascertain whether they reached or crossed the suture. A faint imprint of the superior precentral sulcus is preserved on the left side. Overall, the most parsimonious interpretation of this pattern is that the inferior precentral sulcus (which did not leave imprints) was located in the close vicinity of the coronal suture.

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*Bukuran*

The Bukuran specimen (77) exhibits marked frontal endocranial imprints (fig. S3C). On the better-preserved left side, imprints representing the inferior, middle and superior frontal sulci reach the coronal suture, indicating that the precentral sulcus was just beneath, or posterior to the coronal suture.

25

*Trinil 2 (Pithecanthropus I) and Sangiran 2 (Pithecanthropus II)*

In Trinil 2, the endocranial imprint representing the right inferior frontal sulcus touches the marked imprint of the coronal suture [see visualizations in refs. (68, 70)]. In Sangiran 2, all imprints representing frontal sulci reach the coronal suture (68). The endocranial topography of both specimens thus indicates that the precentral sulcus was situated posterior to the coronal suture.

30

*Solo (Ngandong) specimens*

We use here the specimen names/numbers of Weidenreich (103), as presented in a synopsis of different naming/numbering systems by Huffman et al. (104). Endocranial surfaces of the Solo specimens are generally smooth, revealing comparatively little structural detail in terms of

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identifiable sulcal imprints. All specimens exhibit marked thickening (lipping) of the frontal squama in the vicinity of the coronal suture (see fig. S3, hatched areas), resulting in an endocranial depression in the region anterior to the suture. In the endocasts of Solo I and Solo IX the infero-posterior frontal region is only partially preserved, and the few endocranial imprints that can be identified are not diagnostic with regard to frontal lobe organization. Solo II represents an isolated frontal squama; endocranial imprints representing the inferior frontal sulcus touch CO. In Solo V (fig. S3D), the better-preserved left side of the endocast exhibits an imprint of the *fi* that ends at CO. Similar topographic relationships are preserved on the left side of the Solo VI endocast. Solo X reveals various small sulcal imprints on its frontal endocranial surface. Assignment to specific frontal sulci is not attempted here, but it is diagnostically relevant that these imprints are delimited posteriorly by CO. Solo XI preserves an almost complete endocranial surface, which, however, exhibits little structural detail. Traces of the inferior and middle frontal sulci can be identified on both sides; these structures end at the coronal suture.

#### *Sambungmacan 3 and 4*

Endocasts of both Sm3 (fig. S3E) and Sm4 exhibit marked imprints of the frontal sulci, with the inferior frontal sulci extending to CO. Both specimens also exhibit marked endocranial imprints just anterior to CO, but posterior to BC. These imprints are due to bony lipping along the inferior portion of the coronal suture, and do not represent the inferior precentral sulcus (see criterion 3b). Overall, the endocranial topographies of Sm3 and Sm4 indicate a derived organization of the inferior frontal lobe.

#### *Ngawi*

The endocranial cavity of this specimen (82) is well preserved but its morphology is partially obscured by a thin layer of X-ray-dense matrix adhering to the endocranial surface. The left fronto-occipital region exhibits a clear imprint representing the inferior frontal sulcus, which courses in anteroposterior direction to almost reach the coronal suture, likely indicating a frontal lobe morphology where the inferior precentral sulcus coincides with the location of the coronal suture.

#### *Zhoukoudian XII*

CT scans of high-quality casts of this specimen were used to generate a virtual reconstruction (fig. S3F). The endocranial surface of the frontal squama shows marked sulcal imprints. The imprints representing the left and right inferior frontal sulci extend to the coronal suture, indicating that the inferior precentral sulcus was situated posterior to the suture.

## *Hexian*

Photographs and drawings of the endocast of this specimen [see Figs. 3 and 6 in ref. (69)], show imprints representing the right inferior frontal sulcus touching the coronal suture.

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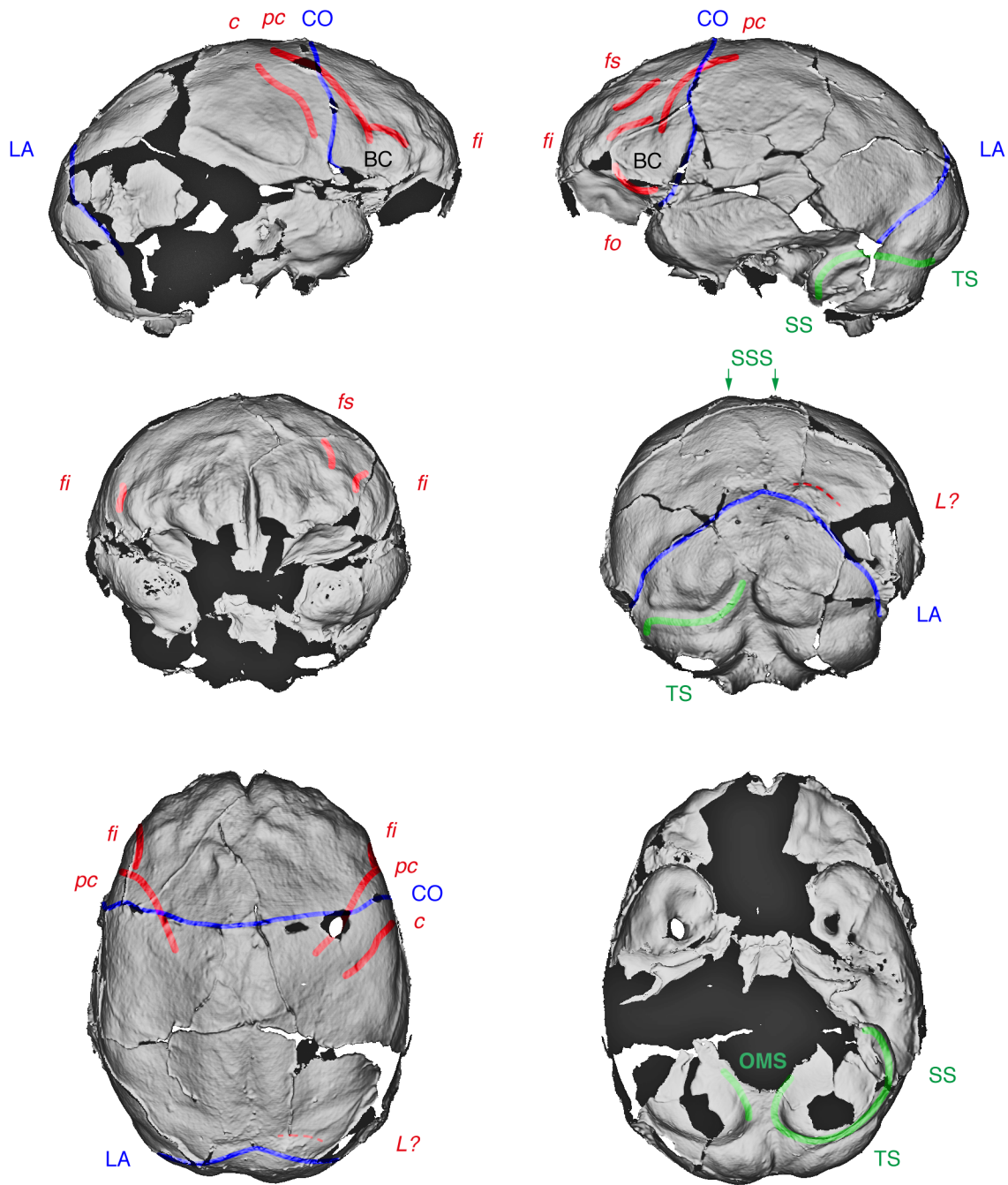
## S4. Endocranial morphology of Malapa MH1, Dinaledi DH3, and Liang Bua LB1

The endocranial topographies of the small-brained *Australopithecus sediba* (MH1) and *Homo naledi* (DH3) specimens have been reported to bear evidence of incipient fronto-orbital cerebral reorganization. In *Au. sediba* MH1 [ECV 420ccm (10); dated to  $1.977 \pm 0.002$  ma (105), and in *H. naledi* DH3 [ECV 460ccm (9); dated to 0.335-0.236 ma (106)], *pc* crosses CO, thus representing the primitive condition characteristic of *Australopithecus* (7) and early *Homo* (as studied here). Endocranial imprints in the BC region of DH3 have been reported to indicate a derived, human-like configuration of the fronto-orbital region (9). Given its comparatively young geological age, *H. naledi* might thus represent an intermediate frontal lobe organization (9), probably representing a small-bodied/small-brained population derived from a larger-bodied ancestor. However, several observations challenge this interpretation. The inferior precentral sulcus (*pci*) is located anterior to CO, thus indicating a primitive organization of the fronto-orbital region. Also, endocranial imprints in the BC region of DH3 fall within the wide range of variation of sulcal patterning in the corresponding region of chimpanzee brains (13). *H. naledi* might thus represent a group conserving the primitive brain organization characteristic of early *Homo*.

The *H. floresiensis* specimen LB1 [ECV 460ccm (107), dated to 190-50ka (86)] has been described as exhibiting “derived frontal and temporal lobes” [ref. (107), p. 242] indicative of a phylogenetic connection with Southeast Asian *H. erectus*. Although the endocast of LB1 is relatively complete, postmortem fractures, taphonomic distortion and fragment displacement hamper identification of sulcal imprints, especially in the diagnostically relevant inferior frontal region. On the left side, a marked imprint superior to Broca’s Cap is visible on both low-resolution and high-resolution CT-based renderings of the endocast [see visualizations in refs. (85, 107)], possibly representing the left inferior frontal sulcus. The imprint reaches the coronal suture, which would indicate a derived organization of the inferior frontal lobe and provide support for the hypothesis that this taxon represents a late insular form of Southeast Asian *H. erectus* (45). However, the structure coincides with a postmortem fracture at the border of an indented fragment, such that its anatomical identity remains unclear, and inferences on frontal lobe reorganization cannot be based on the criteria defined above.

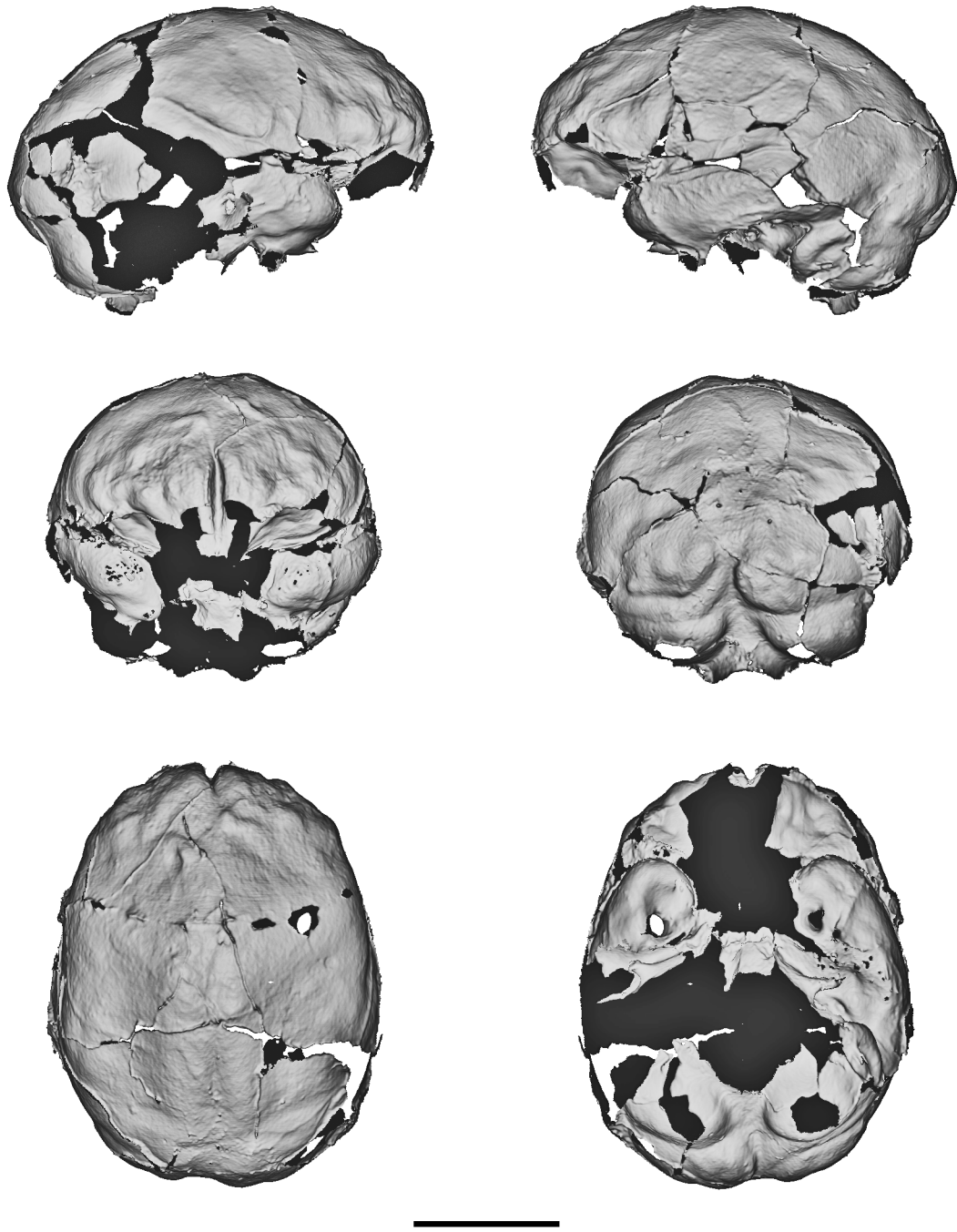
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**Fig. S1** (see following pages). Endocranial structures of the Dmanisi crania. **(A)** D2280; **(B)** D2282; **(C)** D2700; **(D)** D3444; **(E)** D4500. Each subfigure is presented in labeled and unlabeled versions. Right/left lateral, anterior/posterior and superior/inferior views. Identified endocranial imprints: red: cerebral sulci; blue: sutures; green: venous sinuses; yellow: meningeal arteries. Abbreviations: CO: coronal suture; LA: lambdoid suture; SA: sagittal suture. Cerebral sulci: *c*: central; *fi*: inferior frontal; *fm*: medial frontal; *fs*: superior frontal; *fo*: fronto-orbital; *ip*: intraparietal; *pc* (*pci*): precentral (inferior); *pt*: postcentral; *ts*: superior temporal; *s*: Sylvian (lateral); (*L*): possible remnants of great ape-like lunate sulcus. Vascular structures: SS: sigmoid sinus; TS: transverse sinus; SSS: superior sagittal sinus; OMS: occipital marginal sinus.

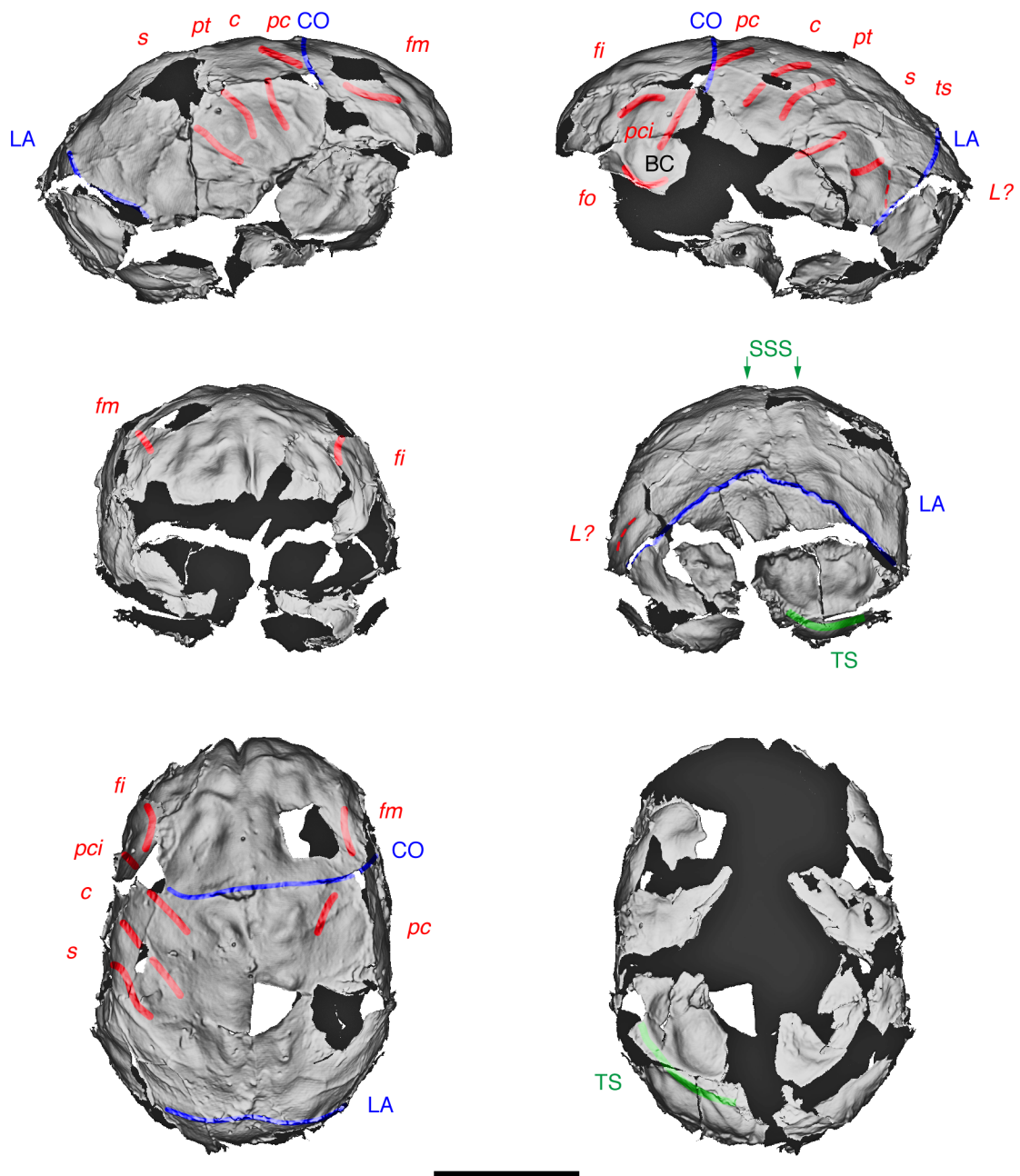


**Fig. S1 A.** Endocranial structures of Dmanisi cranium D2280. Note that the precentral sulcus (*pc*) crosses the coronal suture (*CO*) at mid-height, and courses toward Broca's Cap (*BC*), which is delimited inferiorly by the fronto-orbital sulcus (*fo*). Scale bar is 5 cm. Colors and labels see legend to fig. S1.

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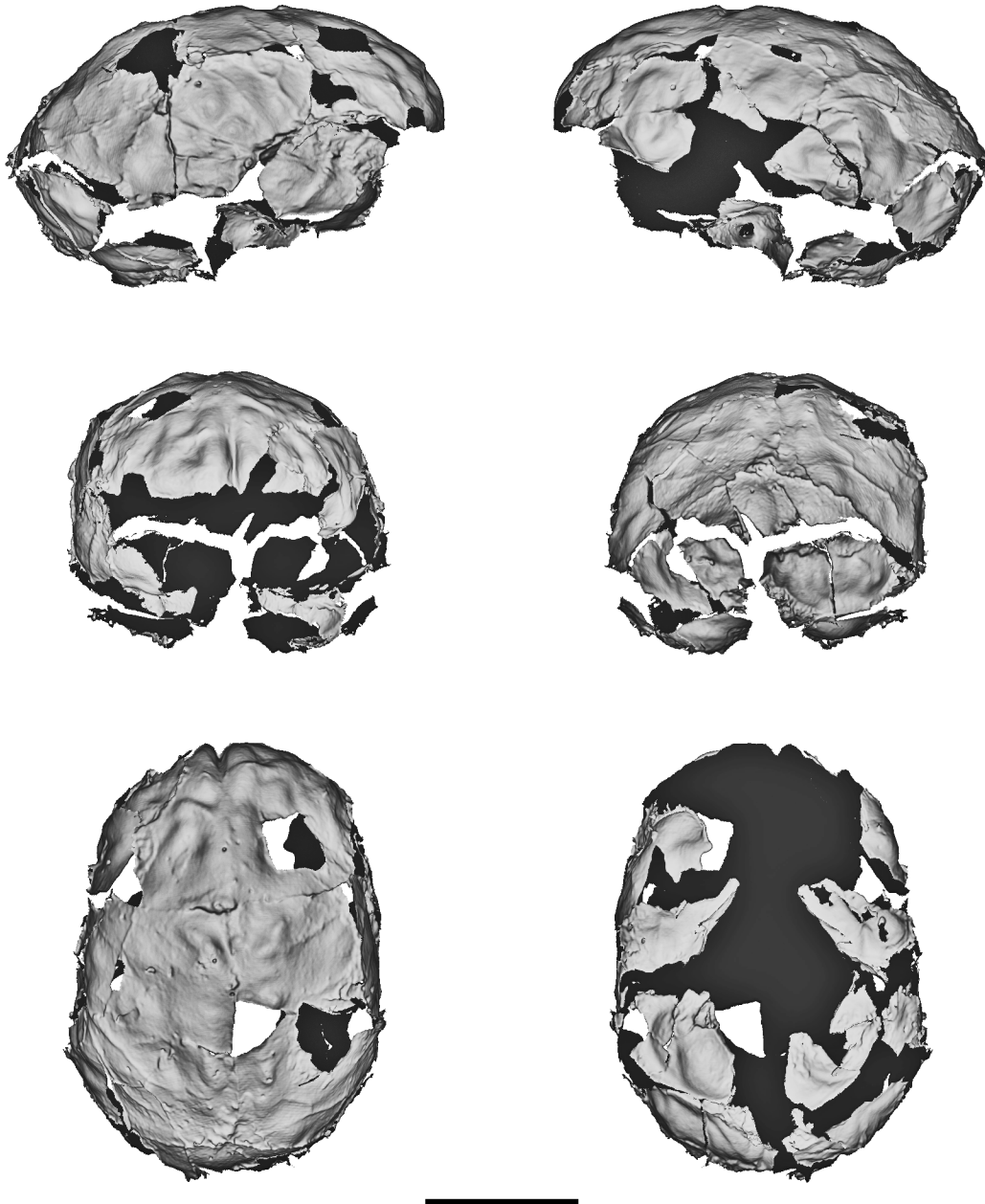


**Fig. S1 A.** Endocranial structures of Dmanisi cranium D2280. Unlabeled 3D reconstruction. Scale bar is 5cm.



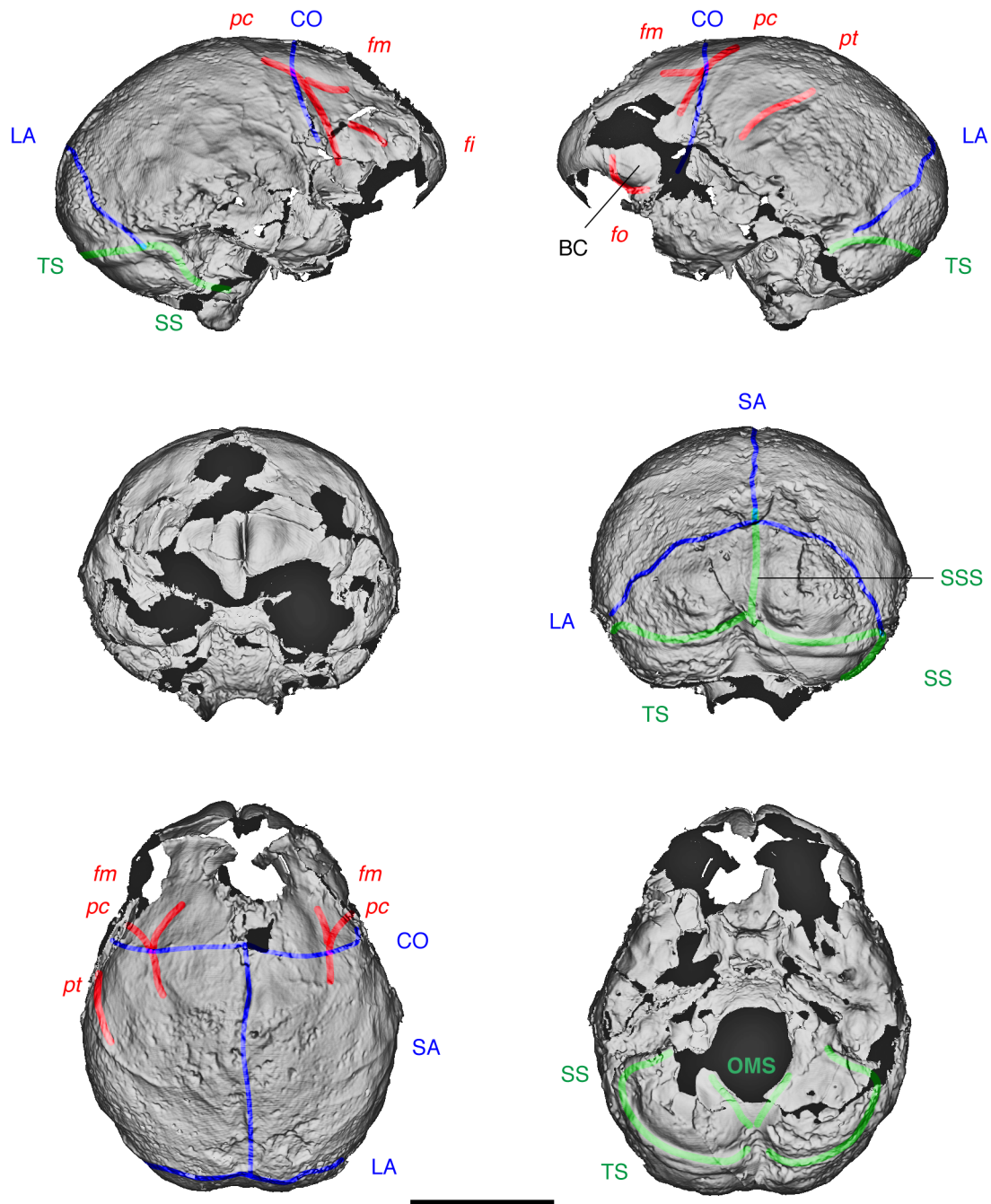
**Fig. S1 B.** Endocranial structures of Dmanisi cranium D2282. Note that the inferior portion of the precentral sulcus (*pci*) is located anterior to the coronal suture (*CO*) and bisects Broca's Cap (*BC*), which is delimited inferiorly by the fronto-orbital sulcus (*fo*). Scale bar is 5 cm. Colors and labels see legend to fig. S1.

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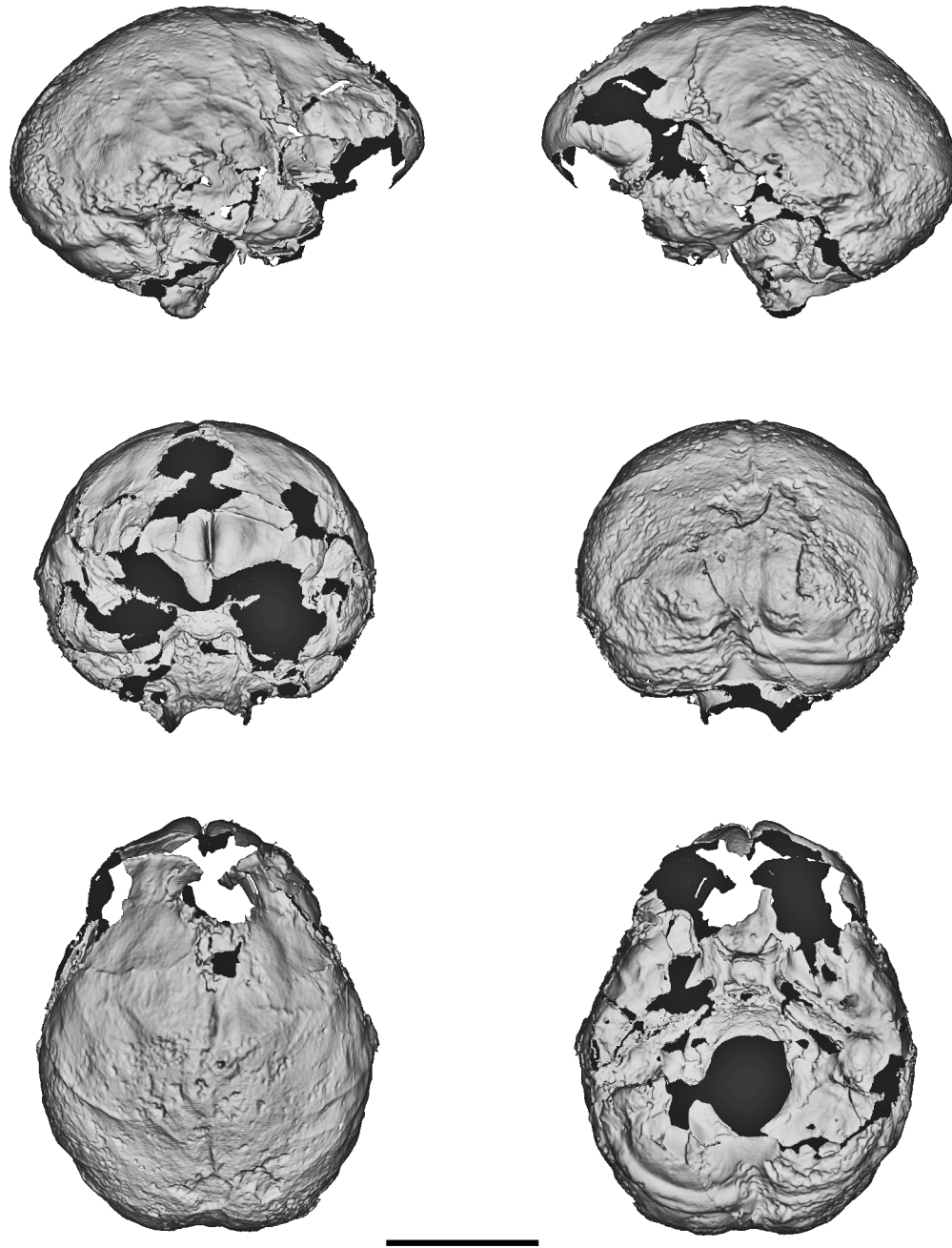
**Fig. S1 B.** Endocranial structures of Dmanisi cranium D2282. Unlabeled 3D reconstruction. Scale bar is 5cm.



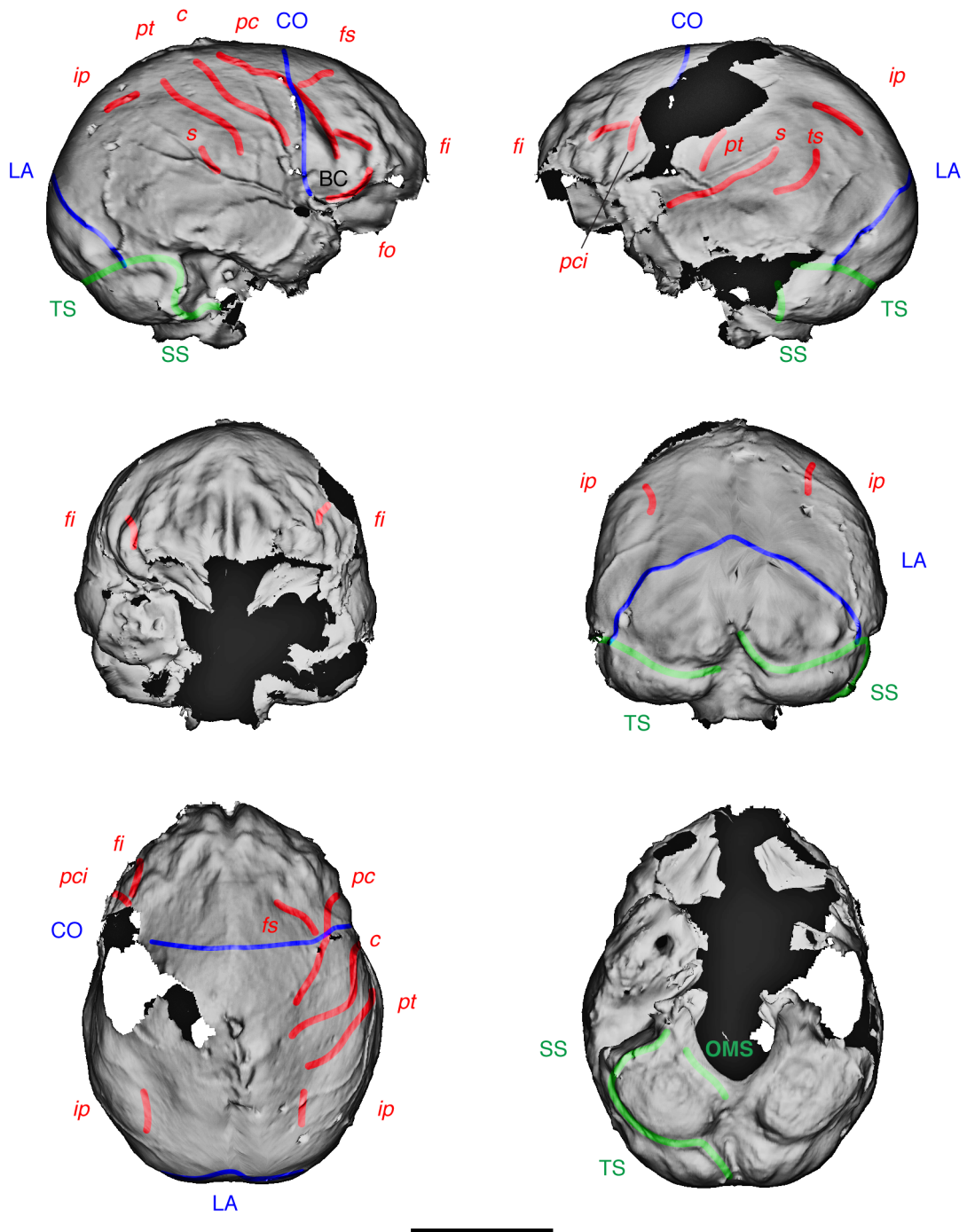


**Fig. S1 C.** Endocranial structures of Dmanisi cranium D2700. Note that the precentral sulcus (*pc*) crosses the coronal suture (CO) at mid-height, and courses toward Broca's Cap (BC), which is delimited inferiorly by the fronto-orbital sulcus (*fo*). Scale bar is 5 cm. Colors and labels see legend to fig. S1.

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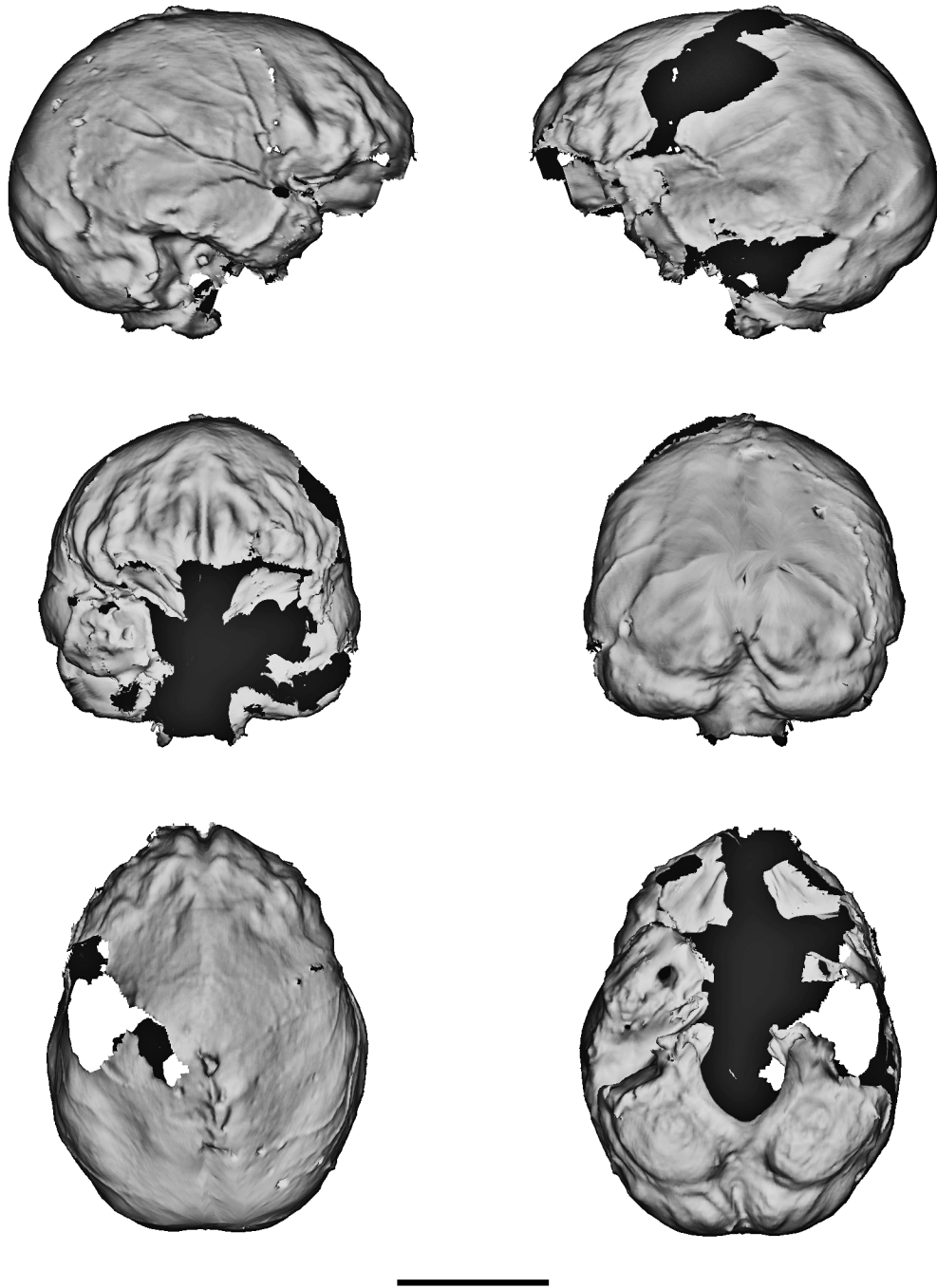


**Fig. S1 C.** Endocranial structures of Dmanisi cranium D2700. Unlabeled 3D reconstruction. Scale bar is 5cm.

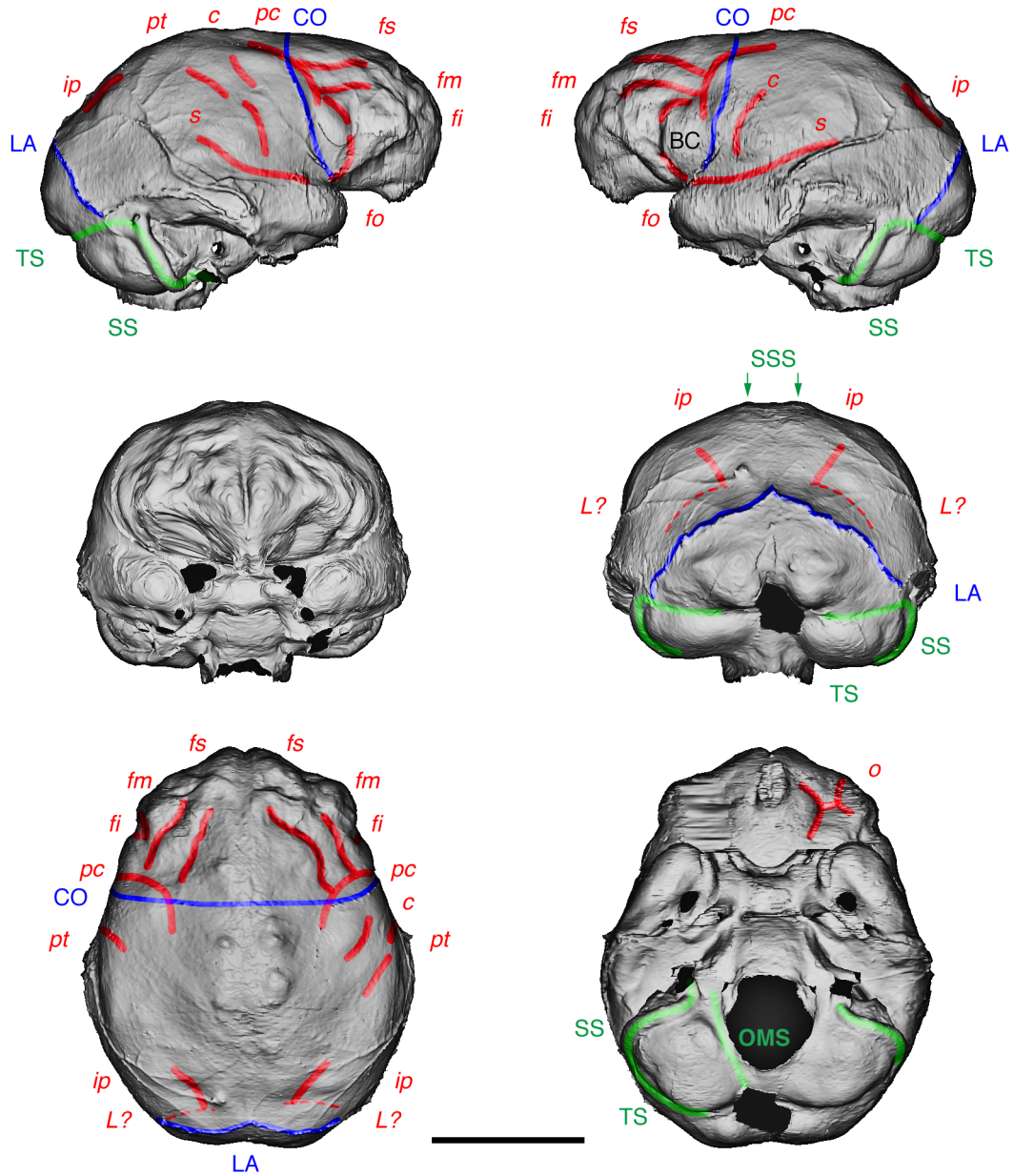


**Fig. S1 D.** Endocranial structures of Dmanisi cranium D3444. Note that the precentral sulcus (*pc*) crosses the coronal suture (CO) at mid-height, and courses toward Broca's Cap (BC), which is delimited inferiorly by the fronto-orbital sulcus (*fo*). Scale bar is 5 cm. Colors and labels see legend to fig. S1.

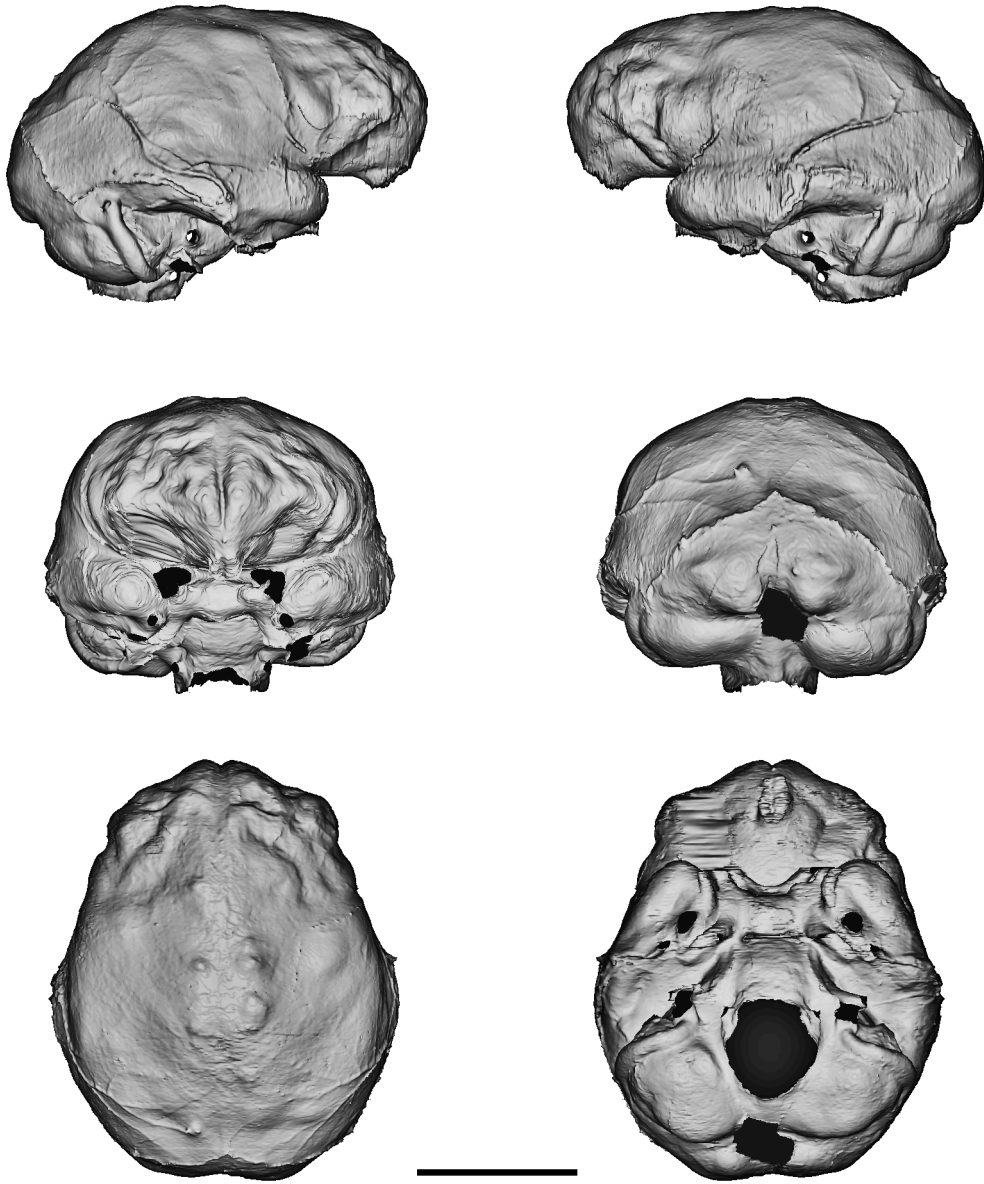
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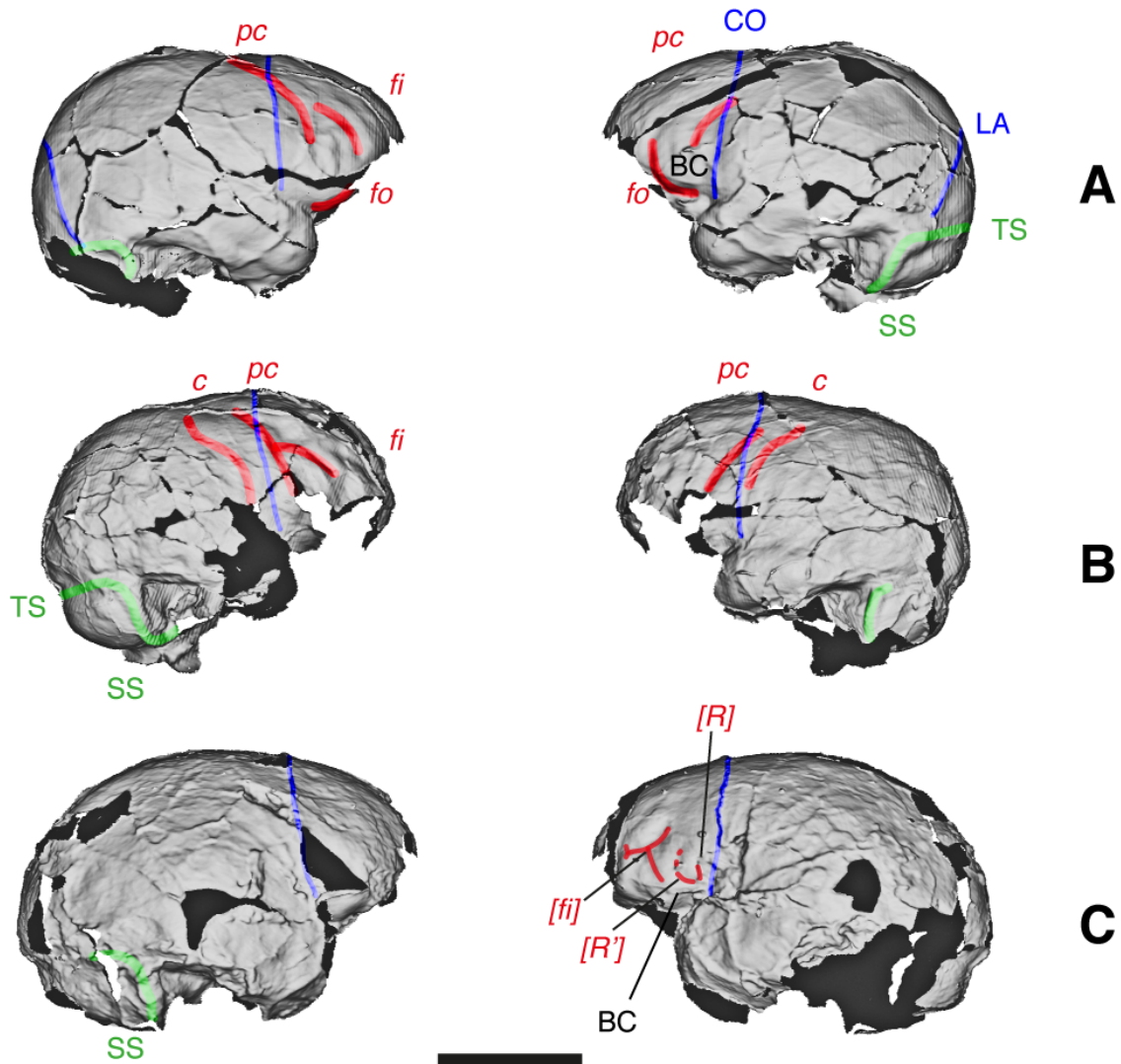
**Fig. S1 D.** Endocranial structures of Dmanisi cranium D3444. Unlabeled 3D reconstruction. Scale bar is 5cm.



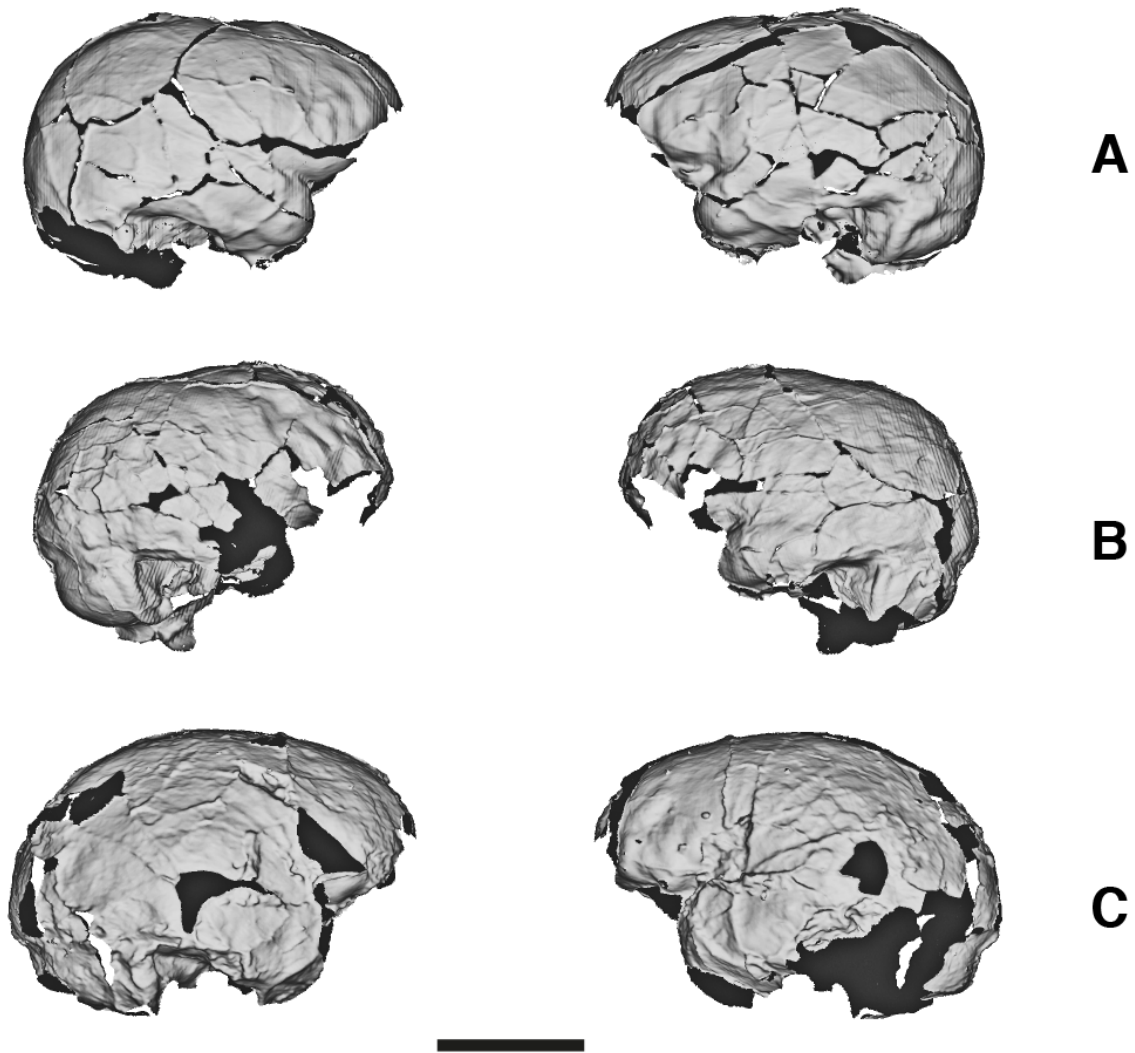
5 **Fig. S1 E.** Endocranial structures of Dmanisi cranium D4500. Note that the precentral sulcus (*pc*) crosses the coronal suture (*CO*) at mid-height, and courses toward the postero-superior portion of Broca's Cap (*BC*), which is delimited inferiorly by the fronto-orbital sulcus (*fo*). Scale bar is 5 cm. Colors and labels see legend to fig. S1.



**Fig. S1E.** Endocranial structures of Dmanisi cranium D4500. Unlabeled 3D reconstruction. Scale bar is 5cm.

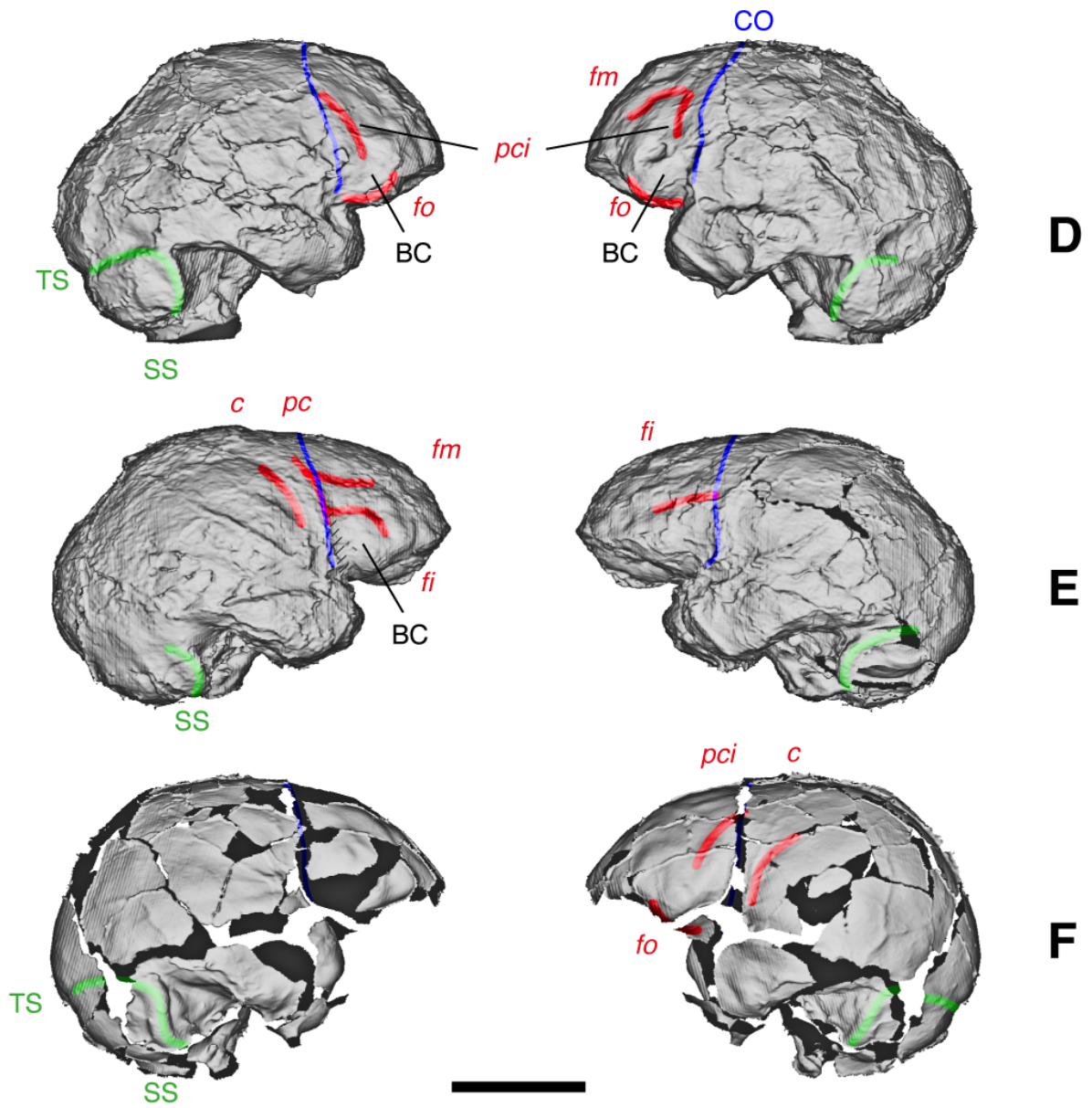


5 **Fig. S2 A-C.** Endocranial structures of African early *Homo* fossils. (A) KNM-ER 1805; (B)  
 10 KNM-ER 1813; (C) KNM-ER 1470. Colors and labels as in fig. S1. Scale bar is 5 cm. In KNM-  
 ER 1805 (A) the inferior precentral sulcus (*pci*) is situated anterior to the coronal suture (CO)  
 and bisects Broca's Cap (BC). In KNM-ER 1813 (B), the precentral sulcus (*pc*) crosses (CO).  
 The endocast of KNM-ER 1470 (C) is highly fragmented; features labeled in square brackets are  
 represented as in ref. (21).



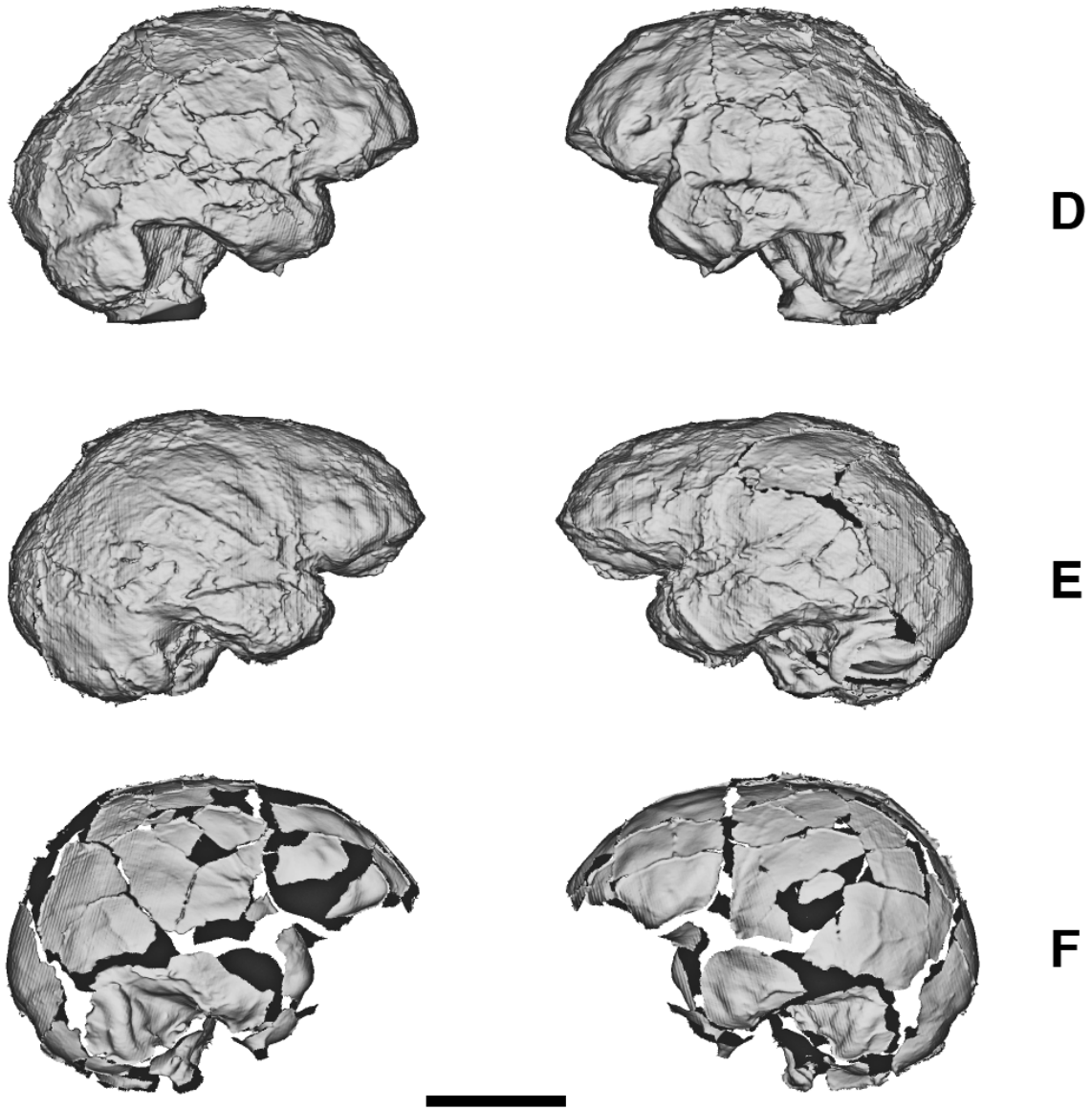
**Fig. S2 A-C.** Endocranial structures of African early *Homo* fossils. (A) KNM-ER 1805; (B) KNM-ER 1813; (C) KNM-ER 1470. Unlabeled 3D reconstructions. Scale bar is 5cm.





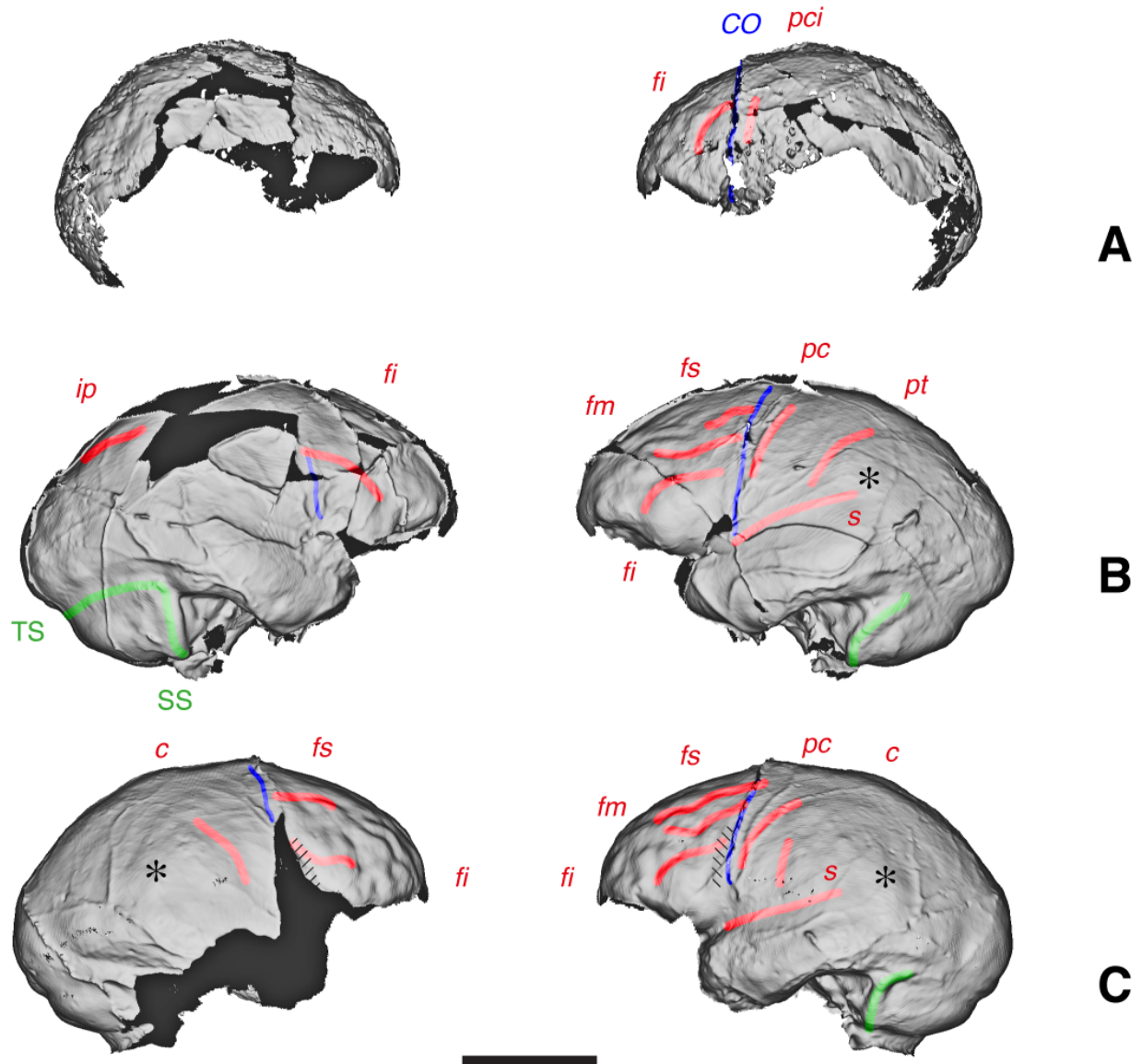
**Fig. S2 D-F.** Endocranial structures of African early *Homo* fossils. **(D)** KNM-ER 3733; **(E)** KNM-ER 3883; **(F)** KNM-WT 15000. Colors and labels as in fig. S1. Hatched area in **(E)**: imprints representing raised margin (lipping) of frontal bone. Scale bar is 5 cm. In KNM-ER 3733 **(D)**, possible imprints of *pci* are situated anterior to CO. In KNM-ER 3883 **(E)**, an imprint attributed to *pc* crosses CO, such that *pci* coincides with, or is slightly anterior to CO. The highly fragmented endocast of KNM-WT 15000 **(F)** shows an imprint of *pci* anterior to CO, and ending superior to BC.

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**Fig. S2 D-F.** Endocranial structures of African early *Homo* fossils. **(D)** KNM-ER 3733; **(E)** KNM-ER 3883; **(F)** KNM-WT 15000. Unlabeled 3D reconstructions. Scale bar is 5cm.

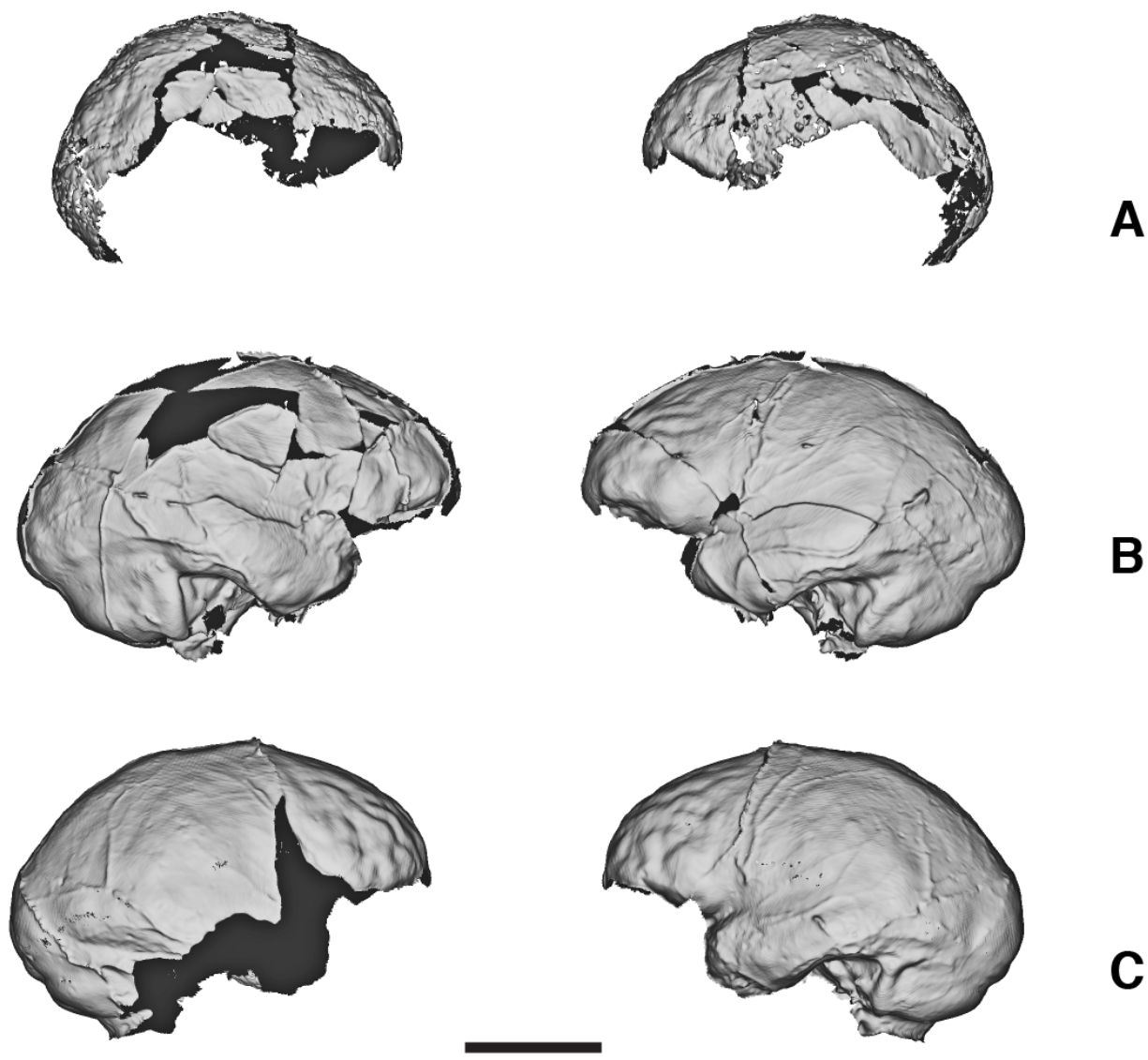
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**Fig. S3 A-C.** Endocranial structures of East Asian *Homo erectus* fossils. (A) Mojokerto; (B) Sangiran 17; (C) Bukuran. Colors and labels as in fig. S1. Hatched areas: imprints representing raised bone margins (lipping) of frontal bone; \* symbol: endocranial bulge corresponding to supramarginal gyrus. Scale bar is 5 cm. In all specimens, imprints of the inferior and/or middle frontal sulci (*fi/fm*) terminate at or close to the coronal suture (CO). If visible, imprints of the precentral sulcus (*pc*) are located posterior to CO.

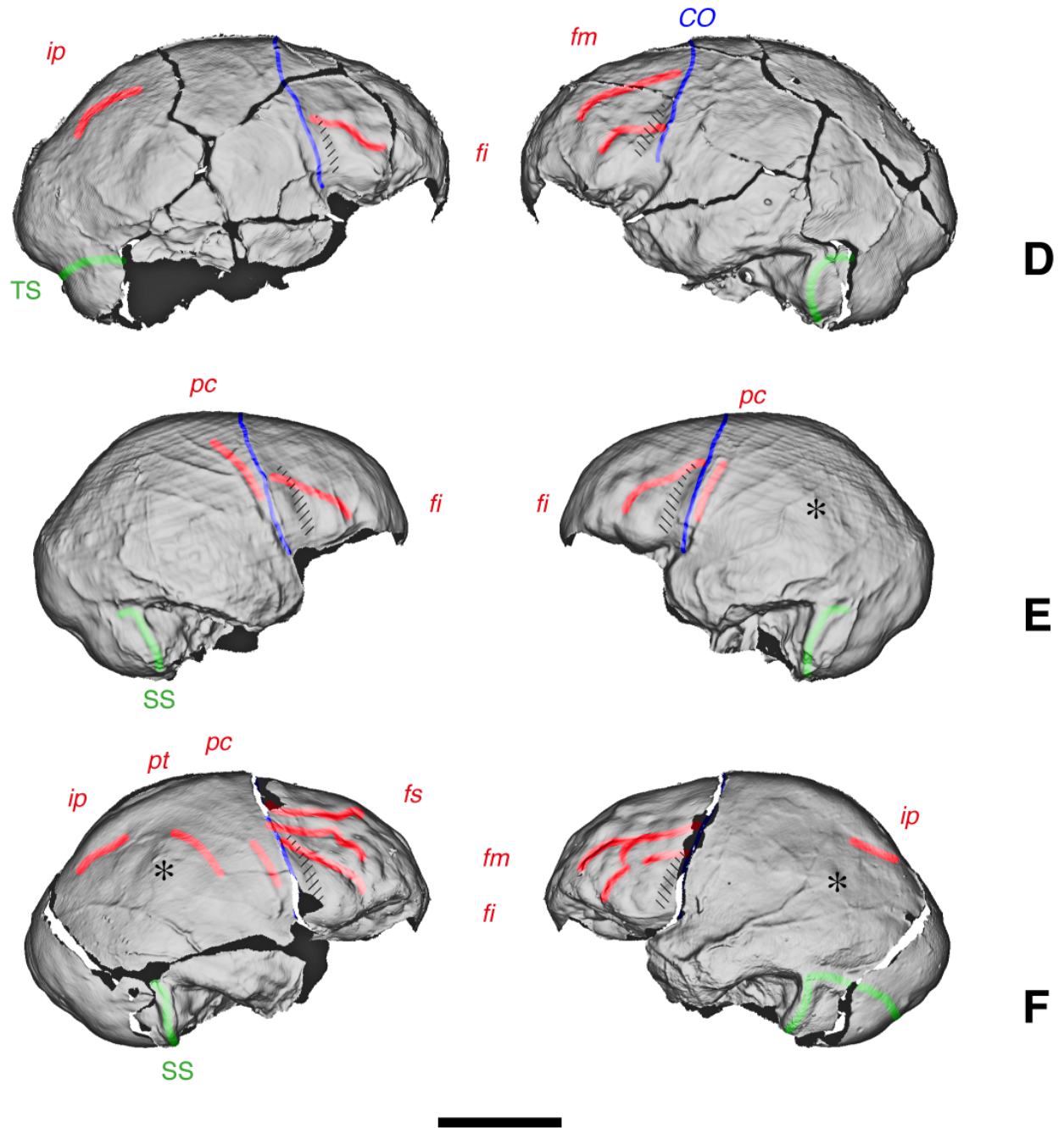
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**Fig. S3 A-C.** Endocranial structures of East Asian *Homo erectus* fossils. (A) Mojokerto; (B) Sangiran 17; (C) Bukuran. Unlabeled 3D reconstructions. Scale bar is 5cm.

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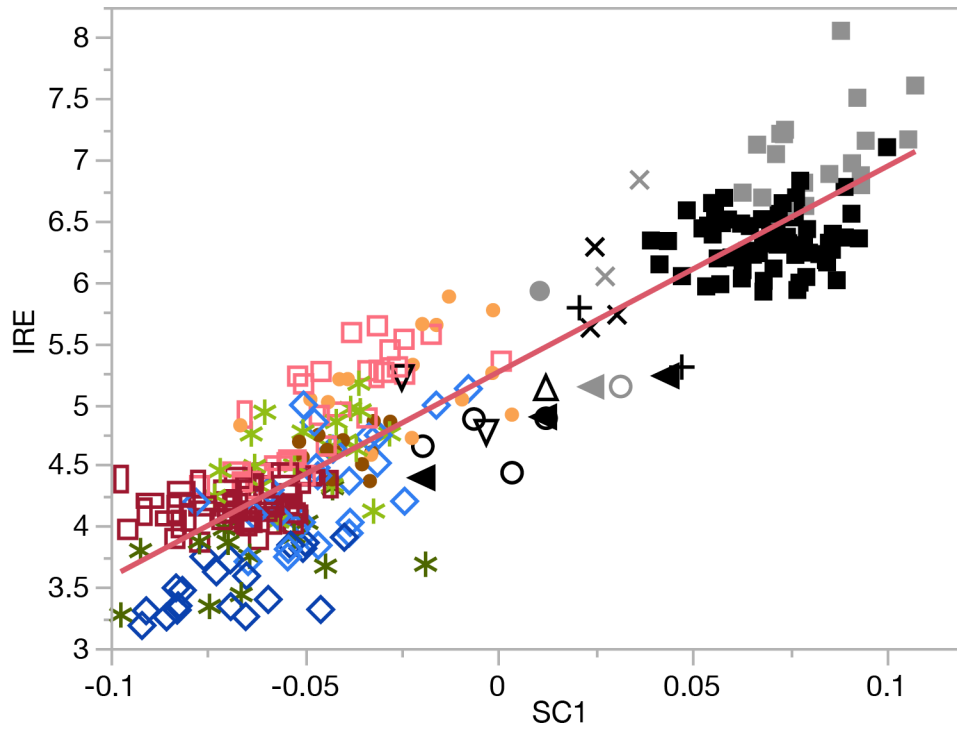


**Fig. S3 D-F.** Endocranial structures of East Asian *Homo erectus* fossils. **(D)** Solo V; **(E)** Sambungmacan 3; **(F)** Zhoukoudian XII. Colors and labels as in fig. S1. Hatched areas: imprints representing raised bone margins (lipping) of frontal bone; \* symbol: endocranial bulge corresponding to supramarginal gyrus. Scale bar is 5 cm. In all specimens, imprints of the inferior and/or middle frontal sulci (*fi/fm*) terminate at or close to the coronal suture (CO). If visible, imprints of the precentral sulcus (*pc*) are located posterior to CO.

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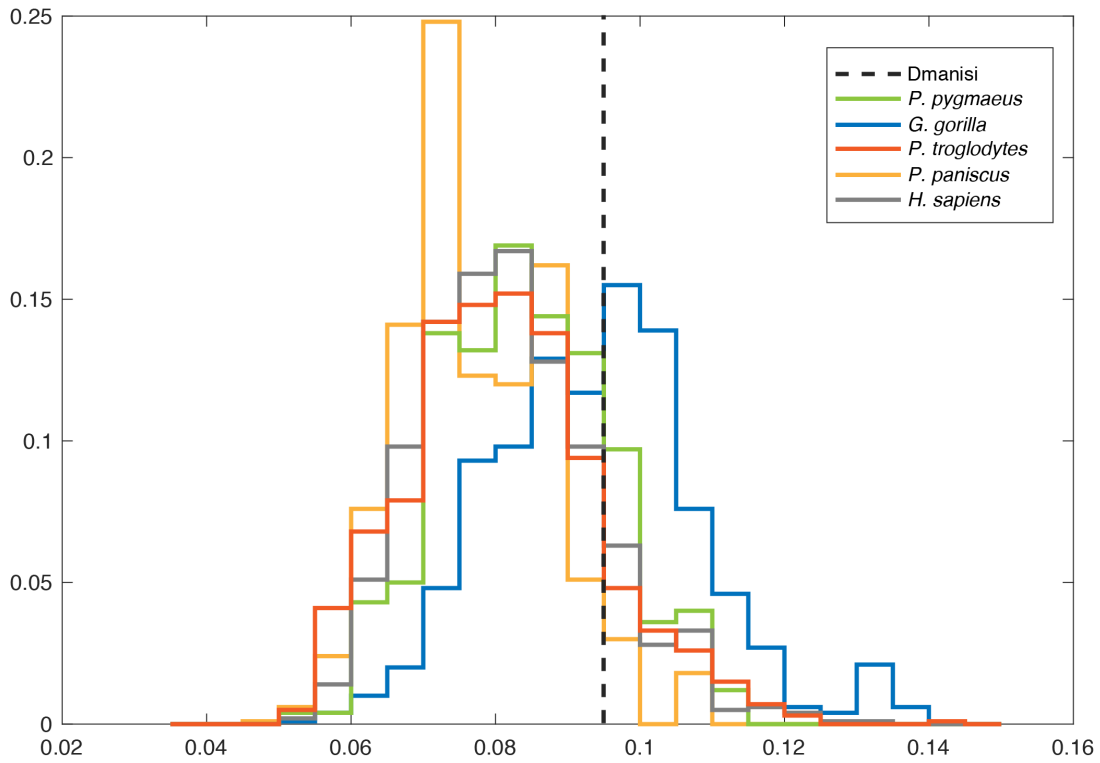
5 **Fig. S3 D-F.** Endocranial structures of East Asian *Homo erectus* fossils. **(D)** Solo V; **(E)** Sambungmacan 3; **(F)** Zhoukoudian XII. Unlabeled 3D reconstructions. Scale bar is 5cm.



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**Fig. S4.** Regression of IRE [index of relative encephalization, ratio between endocranial size and the size of the face and cranial base; see ref. (38)] against shape component SC1;  $IRE = 5.26 + 16.81 * SC1$ ;  $R^2 = 0.86$ . Symbols see main Fig. 3.

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5 **Fig. S5.** Ranges of endocranial shape variation in *P. troglodytes*, *P. paniscus*, *G. gorilla*, *P.*  
 10 *pygmaeus*, modern humans (global sample) and in the Dmanisi sample. Dashed line indicates  
 maximum endocranial shape distance between any two specimens in the Dmanisi sample  
 (D2280, D2700, D3444, and D4500); the maximum distance is that between D3444 and D4500.  
 The histograms show species-specific frequency distributions of the maximum endocranial shape  
 distance between any two specimens in random subsamples of  $N=4$  specimens ( $K=1000$   
 resamplings). Note that the maximum shape distance for Dmanisi is well within the species-  
 specific maximum-distance frequency distributions.



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