

## The Brain of LB1, *Homo floresiensis*

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**The brain of *Homo floresiensis* is assessed by comparing a virtual endocast from the type specimen (LB1) with endocasts from great apes, *Homo erectus*, *Homo sapiens*, a human pygmy, a human microcephalic, Sts 5 (*Australopithecus africanus*) and WT 17000 (*Paranthropus aethiopicus*). Morphometric, allometric and shape data indicate that LB1 is not a microcephalic or pygmy. LB1's brain size versus body size scales like an australopithecine, but its endocast shape resembles that of *Homo erectus*. LB1 has derived frontal and temporal lobes and a lunate sulcus in a derived position, which are consistent with capabilities for higher cognitive processing.**

The type specimen of *Homo floresiensis* (LB1, female) (1) has a brain size of ~400 cm<sup>3</sup> similar to that of *Australopithecus afarensis* AL 288-1 (Lucy) (2) that lived approximately 3.0 Ma. Yet its species was associated with big-game stone technology, remains of *Stegodon*, and charred animal bones that hint at the use of fire and cooking. Its ancestors also had to cross the sea to reach Flores (3). Could a tiny hominin with an ape-sized brain really have engaged in such advanced behaviors? Some workers reject the notion that LB1 represents a new species that was closely tied to *Homo erectus* (1) and suggest, instead, that it was a pathological human microcephalic (4). To help address this debate, three-dimensional computed tomographic (3DCT) reconstructions of the internal braincase (virtual endocasts) that reproduce details of external brain morphology including sulci, vessels, sinuses, cranial capacity and shape (5–8) are compared from LB1, an adult female chimpanzee, an adult female *Homo erectus* (ZKD XI), a contemporary woman, and a European microcephalic. To broaden taxonomic comparisons and supplement limited sample size, our analysis also includes endocasts of Sts 5 (*Australopithecus africanus*), KNM-WT 17000 (*Paranthropus aethiopicus*), 10 humans, 10 gorillas, 18 chimpanzees (9), an adult female pygmy, and five *Homo erectus* skulls.

Our virtual cranial capacity estimate for LB1 is 417 cm<sup>3</sup> (10). Virtual endocasts of the microcephalic, modern woman, *Homo erectus*, and chimpanzee were scaled to 417 cm<sup>3</sup> to facilitate shape comparisons (Fig. 1 and fig. S2). LB1's shape most resembles that of ZKD XI, which is typical for classic *Homo erectus* from China and Java (Trinil) (fig. S3). Both endocasts are noticeably wider caudally than rostrally (Fig. 1A), wider ventrally than dorsally (fig. S2), and relatively long and low in lateral profile (Fig. 1B). However, LB1 lacks the derived occipital expansion over the cerebellum of *Homo erectus* (Fig. 1B) and its endocast is relatively wider (more brachycephalic) (Fig. 1A and fig. S3). LB1's endocast least resembles the microcephalic's (Fig. 1 and fig. S2), which has a pointed frontal lobe, compressed occipital lobe, and flattened posterior end with the caudal-most poles on the cerebellum. Although our sample includes only one microcephalic endocast, its shape conforms to features of its corresponding skull that typify primary microcephaly (*Microcephalia vera*): small cranial vault relative to face, sloping forehead, and pointed vertex (11, 12). The only criterion for secondary microcephaly is an occipitofrontal circumference below -2 standard deviations for age and sex (11), but these data are unavailable for LB1's population. Unless a *Homo erectus*-like endocast shape is characteristic of an unrecognized form of secondary microcephaly, we reject the hypothesis that LB1 was a pathological microcephalic (4).

Length, breadth, height, and frontal breadth measurements were collected from endocasts (Table 1 and table S1) and used to generate six ratios (Table 1). In a principal component analysis LB1 groups with *Homo erectus* and is separate from the *Homo sapiens*, Sts 5 (fig. S4), and the pygmy, based on the first principal component (weighted heavily on relative height and the disparity between maximum breadth and frontal breadth), and is separate from *Homo erectus* and the microcephalic in the second principal component (weighted heavily on breadth relative to length) (Fig. 2A). LB1 bears

little resemblance to the pygmy (fig. S5). Typically, pygmy skulls are over 1000 cm<sup>3</sup> (ours measures 1249 cm<sup>3</sup>) and resemble those of neighboring humans in shape (13). Unlike LB1 whose brain/body ratio scales like an australopithecine, however, the ratio for pygmies is slightly larger than found in their non-pygmy neighbors, giving their heads a relatively large appearance (14). This is expected because pygmies scale allometrically along ontogenetic curves (15) leading to relatively enlarged heads and brains, as is the case for human youngsters relative to adults (16) (fig. S1). The laws governing allometric scaling of brain/body ratios are powerful and hold within other species of primates (17, 18). For this reason, and because the morphology of our endocast samples differ greatly, we do not believe that LB1 represents a human pygmy (19).

A second principal components analysis was performed on measurements from the base of LB1's endocast and compared to similar measurements from 10 gorillas, 18 chimpanzees, 10 *Homo sapiens*, KNM-WT 17000 (*Paranthropus aethiopicus*), and Sts 5 (9) (Fig. 2, B and C, and tables S2 and S3). The *Homo erectus* endocasts were excluded because their bases were missing. The first and second principal components group LB1 exclusively with *Homo sapiens* (Fig. 2B). The first principal component is most heavily weighted on 4/6 and 5/6 (Fig. 2C), which represent the relative projection of prefrontal cortex rostral to both the anterior and posterior margins of the olfactory bulb. The second principal component is most heavily weighted on 3/6 and (6-3)/6, which represent the relative length of the frontal lobes rostral to the temporal poles and the relative length of the brain caudal to the temporal poles. As in humans, the most anterior sectors of LB1's orbital surfaces are lengthened.

The lambdoid suture is located more rostrally on the left than right side of the endocast (Fig. 3). Both the skull and the endocast show a left frontal and right occipital petalia (Fig. 1A) that, in humans, are statistically correlated to some degree with left-handedness (20). After entering the middle cranial fossa, small anterior branches of the middle meningeal vessels course rostrally across the ventral surface of the right temporal lobe, and across the ventrolateral surface on the left. On the right, a branch from another meningeal vessel enters the middle braincase from the orbital region and courses caudally across the temporal lobe inferior to the Sylvian fissure. Similar orbital contributions are common in apes and have been reported for certain *Homo erectus* endocasts by some workers (21) but not others who used a scoring system for modern humans (22). Traces of meningeal vessels are also reproduced in the right parietal region, and several arachnoid granulations appear near vertex on the right. LB1 reproduces somewhat (artificially) distorted transverse and sigmoid sinuses. A cast of the parietal emissary foramen appears near the medial end of the left lambdoid suture.

The right side of LB1's endocast reproduces part of the Sylvian fissure, and numerous small sulci on the lateral temporal and dorsolateral frontal lobes (Fig. 3). The right orbital surface reveals three small sulci that do not extend onto the dorsal surface (the left orbital surface is damaged). In the left occipital region, LB1 reproduces an inferior occipital sulcus, and a small crescent-shaped lunatic sulcus medial to it and caudal to the lambdoid suture. The position of the lunatic sulcus is derived and suggests cortical reorganization in the posterior parietal association cortex compared with apes (2, 23).

LB1's orbital caps are not delimited rostrally by apelike orbitofrontal sulci that incise the borders and course toward the temporal poles on the orbital surfaces (23, 24). Instead, LB1's gyrification, orientation, and relationship of the lateral prefrontal cortex relative to the temporal poles appear derived. Following Connolly (23), we decline to identify rami that border the human *pars triangularis* (part of Broca's area) on the left, although the general morphology in this region would be consistent with their existence. On the left (and to lesser extent right), a distinct Sylvian notch separates the temporal from frontal lobe, and continues caudally as a depression. This region corresponds to a Sylvian crest within the skull of LB1 that, in humans, sometimes occurs in particularly thick skulls and is correlated with Sylvian depressions on endocasts although the brains are, if anything, more opercularized in the corresponding area (23).

The depression for the superior sagittal sinus on LB1's frontal lobes is bordered laterally by large convolutions [which probably contained additional furrows not reproduced on the endocast (23)] that curve around the rostral tip of the endocast onto the orbital surface and meet at the foramen caecum. Dimples separate these convolutions laterally from swellings that square off the frontal lobes and give their outline a ruffled appearance in dorsal view (Fig. 1A). Although hints of such contours may be seen in chimpanzee and hominin endocasts such as in the No. 2 specimen from Sterkfontein (9), the extent of these expansions in the frontal polar region of LB1 is unusual. This part of the prefrontal cortex in humans and apes consists of Brodmann's area 10, which in humans may be involved in higher cognitive processes such as the undertaking of initiatives and the planning of future activities (25). Human frontal lobes are not larger than expected for apes of similar brain volume (26), but area 10 is both absolutely and relatively enlarged in *Homo sapiens* compared with apes (25). LB1's polar convolutions appear derived compared with *Homo erectus* and other early hominins. Unlike the frontal lobes, human temporal lobes appear to be somewhat larger than expected for an ape brain of human size (26–28); thus, LB1's extremely wide temporal lobes (brachycephaly; fig. S3) may represent another derived feature.

Our data show that LB1's well-convoluted brain could not have been a miniaturized version of the brain of either *Homo sapiens* or *Homo erectus*. Nevertheless, its similarities with *Homo erectus* strongly suggest a phylogenetic connection, although its australopithecine-like brain-size/body-size ratio and morphology of the femur and pelvis (29) are not expected in a miniaturized descendant of a larger-bodied *Homo erectus* (which, instead, would be expected to scale allometrically along the ontogenetic curve predicted for *Homo erectus*) (fig. S1). Although it is possible that *Homo floresiensis* represented an endemic island dwarf that, over time, became subjected to unusual allometric constraints, an alternative hypothesis is that *Homo erectus* and *Homo floresiensis* may have shared a common ancestor that was an unknown small-bodied and small-brained hominin (1).

## References and Notes

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## Supporting Online Material

[www.science.mag.org/cgi/content/full/1109727/DC1](http://www.science.mag.org/cgi/content/full/1109727/DC1)

Materials and Methods

SOM Text

Figs. S1 to S5

Tables S1 to S3

References

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**Fig. 1.** Comparisons of virtual endocasts of LB1 (center). (A) Dorsal views; (B) right lateral views: *Hs*, *Homo sapiens*; *Pt*,

*Pan troglodytes*; *mcHs*, a human microcephalic; *He*, *Homo erectus*.

**Fig. 2.** Plots of principal components and key for basal view measurements. **(A)** Plots of the first three principal components resulting from the analysis of the endocast indices listed in Table 1 [excluding B-FB/H, which was highly correlated with B-FB/L ( $r = 0.98$ )]. First, second, and third principal components are aligned along the  $x$ ,  $y$ , and  $z$  axes. **(B)** Plots of the first three principal components resulting from the analysis of basal-view endocast indices listed in table S2. **(C)** Key for basal view data analyzed in (B) (9). Measurements obtained from basal views were projected onto the horizontal (basal) plane from endocasts. Landmarks: bat, most anterior point on temporal lobe from basal view; mat, most lateral point on endocast at the level of bat in basal plane; mbat, middle of the line connecting the two bats; rof, the most rostral point on the orbital surfaces of the frontal lobes; cob, caudal boundary of olfactory bulbs (cribriform plate) in midline; rob, rostral boundary of olfactory bulbs in midline; bcp, most posterior point on cerebellum in basal view.

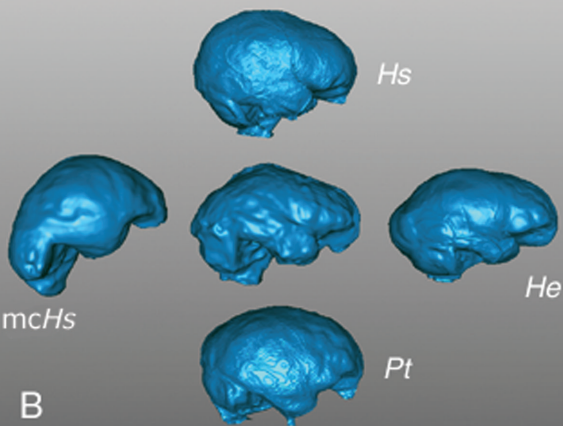
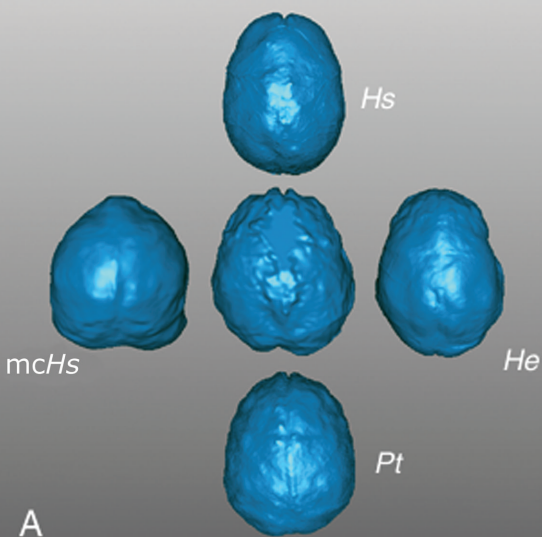
**Fig. 3.** Virtual endocast of LB1 (above); Views: **(A)** left lateral; **(B)**, posterior; **(C)**, right lateral; **(D)**, frontal. Identifications of features on corresponding sketches below (damaged areas blackened): ag, arachnoid granulations; c, frontal lobe convolutions; lb, lambdoid suture; L, lunate sulcus; mv, meningeal vessels; mmv, middle meningeal vessels; oci, inferior occipital sulcus; omv, orbital meningeal vessels; pf, foramen for parietal emissary vein; s, frontal lobe swelling; si, sigmoid sinus; Snd, Sylvian notch and depression; Syl, Sylvian fissure; t, transverse sinus.

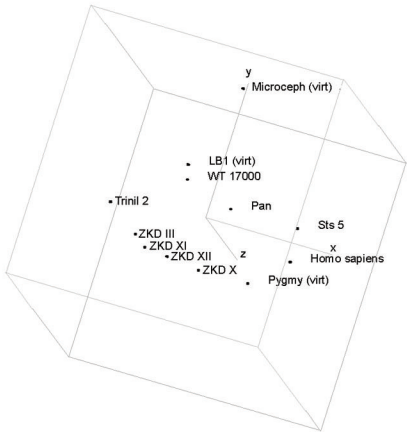
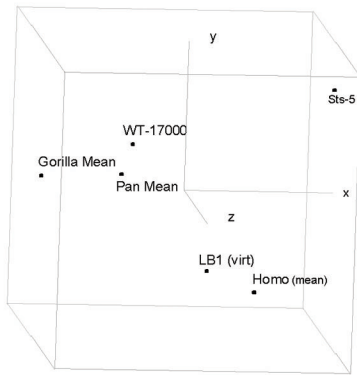
**Table 1.** Endocast measurements (mm) of length, breadth, height, frontal breadth, and resulting indices.

	Length [1]	Breadth [2]	Height [3]	Frontal breadth [4]	Breadth/ length	Height/ length	Frontal breadth/ Length	Breadth - frontal breadth/ length	Breadth - frontal breadth/ height	Height/ breadth
<i>Pan troglodytes</i> (n = 7)	108.8	88	75.3	72.8	0.81	0.69	0.67	0.14	0.20	0.86
<i>Homo sapiens</i> (n = 7)	168.0	128.0	122.0	114.0	0.76	0.73	0.68	0.08	0.11	0.95
KNM-WT 17000*	113.4	92.9	72.5	78.1	0.82	0.64	0.69	0.13	0.20	0.78
Sts 5†	119.1	93.5	86.3	85.6	0.79	0.72	0.72	0.07	0.09	0.92
ZKD III (skull E1)‡	158.6	124.5	99.7	91.4	0.78	0.63	0.58	0.21	0.33	0.80
ZKD X (skull LI)‡	174.6	130.4	114.9	106.7	0.75	0.66	0.61	0.14	0.21	0.88
ZKD XI (skull LI)‡	165.9	127.2	103.7	97.1	0.77	0.63	0.59	0.18	0.29	0.82
ZKD XII (skull LIII)‡	167.4	128	108.5	97.8	0.76	0.65	0.58	0.18	0.28	0.85
Trinil 2§	156.7	126.9	95	92.5	0.81	0.61	0.59	0.22	0.36	0.75
Microcephalic	89.1	84.4	66.3	63.7	0.95	0.74	0.71	0.23	0.31	0.79
Pygmy	165.7	123.9	116.9	102.6	0.75	0.71	0.62	0.13	0.18	0.94
LB1	119.6	102.8	81.4	77.7	0.86	0.68	0.65	0.21	0.31	0.79

\**Paranthropus aethiopicus*. †*Australopithecus africanus*. ‡*Homo erectus* (formerly *Sinanthropus*, China).

§*Homo erectus* (formerly *Pithecanthropus*, Java). ||Computer model, virtual endocast.



**A****B****C**