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Brain size of *Homo floresiensis* and its evolutionary implications

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The extremely small endocranial volume (ECV) of LB1, the type specimen of *Homo floresiensis*, poses a challenge in our understanding of human brain evolution. Some researchers hypothesize dramatic dwarfing of relative brain size from *Homo erectus* presumably without significant decrease in intellectual function, whereas others expect a lesser degree of brain diminution from a more primitive, small-brained form of hominin currently undocumented in eastern Asia. However, inconsistency in the published ECVs for LB1 (380–430 cc), unclear human intraspecific brain–body size scaling and other uncertainties have hampered elaborative modelling of its brain size reduction. In this study, we accurately determine the ECV of LB1 using high-resolution micro-CT scan. The ECV of LB1 thus measured, 426 cc, is larger than the commonly cited figure in previous studies (400 cc). Coupled with brain–body size correlation in *Homo sapiens* calculated based on a sample from 20 worldwide modern human populations, we construct new models of the brain size reduction in the evolution of *H. floresiensis*. The results show a more significant contribution of scaling effect than previously claimed.

1. Introduction

Homo floresiensis is a diminutive, extinct hominin species from the Late Pleistocene of the Flores Island, eastern Indonesia. Since its initial publication [1,2], the extremely small endocranial volume (ECV) for the type specimen, LB1 (approx. 400 cc), which is comparable to *Australopithecus*, has been a point of intensive debate [1–14]. Two major explanatory hypotheses discussed are (i) *H. floresiensis* experienced dramatic brain size reduction from the condition of *Homo erectus* (approx. 1000 cc) on an isolated insular setting, and (ii) the species was derived directly from a more primitive and smaller-brained form such as *Homo habilis* (approx. 600 cc) or even *Australopithecus* (approx. 400 cc). Either possibility has major implication. The former implies that insular brain dwarfing to an unparalleled degree has been a significant factor in the hominin evolution on Flores, whereas the latter demands a revision of the current Out of Africa 1 hypothesis, which supposes *H. erectus* as the first hominin dispersed deep into Eurasia. Some researchers suspect that the LB1 cranium is from a microcephalic modern human, but so far such claims have failed to show a case of modern human patient with overall skeletal characteristics similar to LB1 (reviewed in [15], but see [16]). Although the possibility that LB1 was an archaic hominin individual with microcephaly may not be entirely rejected at the present stage of the research, the robust limb bones, phalanges with osteophytes and signs of healed trauma on the cranial vault and tibia point to an active life rather than a disabled condition in this individual [17].

In order to investigate the actual amount of brain size reduction in *H. floresiensis* and its evolutionary causes, we first need to know the ECV and body size in *H. floresiensis* as well as those of its ancestor candidates. Then, we will be able to evaluate proportions of the brain size decrease explained by intraspecific allometric scaling with body size and other factors such as insular dwarfism of the relative brain size. However, presently, there remain several issues to be resolved to discuss this question: (i) inconsistency in the published ECVs for LB1 (380–430 cc: [1,3,6,18]); (ii) uncertain intraspecific brain–body scaling in the

extant *Homo* species, *Homo sapiens* [19]; (iii) difficulty in estimating brain and body size in fossil hominins, and (iv) lack of our knowledge about possible degree of brain size reduction in insular primate and hominin species. The purposes of this study are to improve the situations of (i) and (ii) for more accurate modelling of possible brain reduction in the evolution of *H. floresiensis*. Although not only brain size but also neural arrangement and connectivity are important in understanding brain evolution of this species, we here focus on the former as a palaeontologically measureable element.

2. Background and research design

(a) CT-based endocranial volume measurement

Using traditional seed displacement methods, the ECV of LB1 was initially measured as 380 cc [1], whereas Jacob *et al.* [6] obtained 430 cc after removing some 'breccia' from the endocranial surface. Another report is 417 cc which is based on a virtual endocast from CT data taken by a medical CT scanner, with interpolation of missing areas and adjustment of slight taphonomic distortion [3]. Holloway *et al.* [18] independently examined the medical CT scan. They also found some distortion in the endocranial form, and suggested that the original undistorted endocast was somewhat smaller than 417 cc.

Advances in X-ray CT and computer imaging technology now allow us more accurate measurement of ECV from a fossil skull than has been possible. Still, a CT-based ECV measurement is affected by various types of error. Some are related to the nature of the cranial specimen (missing parts, damages, distortions, sedimentary matrix or adhesive left in the endocranial cavity, etc.), and others owing to calibration of the CT-scan system, scan resolution, artefacts such as beam hardening and methods of segmentation of the endocranium [20–22]. In this study, we attempt to minimize these errors.

We use a new, high-resolution/quality micro-CT scan of the LB1 cranium [23] to measure its ECV. Fortunately, the LB1 cranium is nearly complete with no substantial post-mortem deformation [1,23]. However, there are numerous cracking and small damages to be filled; small patches of sediments are still attached on the endocranial surfaces and these must be removed. The accuracy of ECV measurement in LB1 rests primarily on the accuracy of locating such damages and sediments, as well as that of reconstructing these damages. In order to facilitate such works, we prepared physical replicas (three-dimensional prints) of the virtually sectioned cranium, which enabled us three-dimensional 'direct' observation of the endocranial surface topography (figure 1).

(b) Intraspecific brain–body size scaling for

Homo sapiens

Martin *et al.* [7,8] cited values of 0.03–0.17 as intraspecific scaling exponents for *H. sapiens* when they claimed that the brain of LB1 is far too small to be attributed to intraspecific dwarfism in *H. erectus*. These figures are from a study on a modern Danish sample [24], and may not be appropriate for this polymorphic and geographically widely distributed species. Brain–body size correlation is normally weak within each regional group of *H. sapiens*, but becomes higher among the groups [19]. Because we are here dealing with evolution to a new species, we investigate not within- but between-regional group, species-wide trend of *H. sapiens* by analysing data from various regional samples.

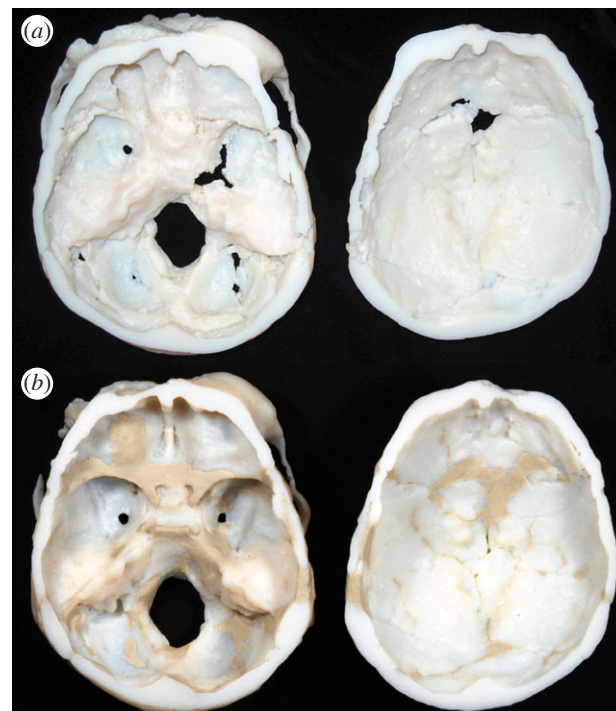


Figure 1. Physical replicas (three-dimensional prints) of horizontally sectioned cranium of LB1 (a) before and (b) after cleaning and clay-based reconstruction. (Online version in colour.)

(c) Evolutionary hypotheses

Researchers are debating whether *H. floresiensis* originated from *H. erectus* or more primitive forms of African *Homo* or even *Australopithecus* (reviewed in [15]). Some studies support the latter view [25,26], although currently we have no evidence for the presence of such primitive hominins in eastern Asia (see additional discussion about this issue in [23]). Recent craniological studies strongly suggest that *H. floresiensis* evolved from early Indonesian *H. erectus* from the Early Pleistocene of Java (ECV: approx. 800–1000 cc) [23,27], not from a generalized condition of *H. erectus sensu lato* represented by the mean of its global sample (ECV: approx. 991 cc) [7–11]. Importantly, this view is compatible with a recent finding that archaic hominins reached Flores by 1.0 Ma [28]. The early Indonesian *H. erectus* fossil assemblage can be further divided into stratigraphically upper and lower groups, which show significant morphological differences from each other [29,30]. Because the former likely postdate 1.0 Ma [31], the latter, which currently represents the oldest *H. erectus* assemblage from Java, is a likely ancestor candidate for *H. floresiensis*.

In this study, we construct models of brain size decrease from *H. habilis* and early Indonesian *H. erectus*. We pay particular attention to the latter not only because we believe it plausible, but also because this, the one supposing a dramatic relative brain size reduction, is the most challenging hypothesis in terms of human brain evolution.

3. Material and methods

(a) Endocranial volume calculation

(i) CT scan and three-dimensional prints

ECV measurement was performed based on the serial CT data reconstructed as a $512 \times 512 \times 593$ matrix of isotropic voxels of 0.260 mm size, which was obtained in 2009 by a microfocal

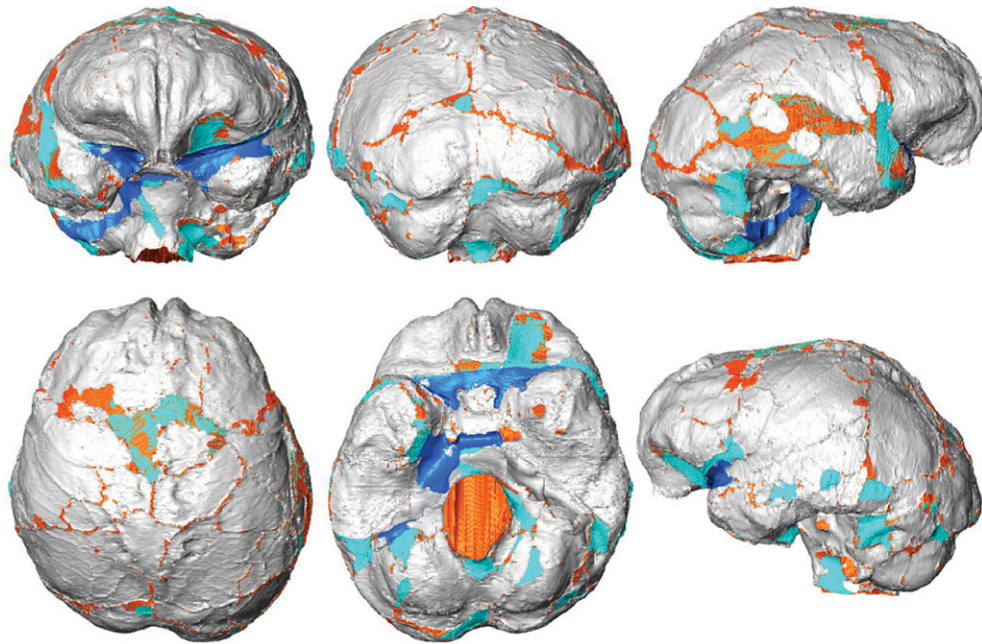


Figure 2. Virtual endocast of LB1 showing reconstructed areas. Anterior, posterior, right lateral, left lateral, basal and superior views (clockwise). Grey, intact original bone surface (untreated); light blue, clay reconstruction of relatively simple surfaces; blue, clay reconstruction of relatively complex structures (with minute digital correction when necessary); orange, anatomical foramina, and cracks and other damages treated digitally. See text for methodological details.

X-ray CT system TX225-ACTIS (Tesco Co.), at the University Museum, University of Tokyo [23]. Prior to the scan of the LB1 cranium, the system was calibrated with known size phantoms; linear measurement error in a horizontal plane was less than 0.1 per cent [20], and the error along the vertical axis, which mostly depends on machine accuracy of the specimen stage, was less than 10 μm .

In order to directly observe the endocranial surfaces, we created three-dimensional prints of horizontally sectioned neurocranium (figure 1*a*), based on the micro-CT scan and using a three-dimensional printer system (EDEN 260, Objet Geometries, MA, USA). Half maximum height (HMH) thresholding between the CT values of air and bone was used for segmentation. Polygon surface models were extracted from the volume data, using the marching cube routine in ANALYZE v. 8.1 (Mayo Clinic, MN, USA) to generate the three-dimensional prints.

(ii) Preparation, preservation and pathological alteration

The states of endocranial preservation and morphology were inspected based on the CT imagery, original specimen (from the anatomical foramina and holes caused by damages) and the horizontally sectioned three-dimensional prints (see the electronic supplementary material, figure S1 and text S1). On the endocranial surfaces of LB1, relatively large pieces of the bone are missing at the endobregma, left orbital surface, much of the sphenoid lesser wings including the anterior clinoid processes, right sphenosquamous suture, dorsum sellae, the anterior tip of right petrous and right sigmoid sinus. Otherwise, the endocranial surfaces of LB1 are well preserved, with some regions still covered by minute lumps or thin patches of sediments. The reconstructed alignment of the bones is also good [1,23]. Some parts of the bones are slightly dislocated inward owing to minor cracking inside the bone, but their effects on the ECV appear to be negligible. One small but noticeable distortion lies in the right petrous bone, but we left this distortion uncorrected because it would not significantly affect the ECV (see the electronic supplementary material, figure S1*d*).

Pathological alteration of endocranial bones, if present, may affect the ECV as a measure of the brain volume. Vannucci *et al.* [16] suggested that the LB1 brain was pathological showing

(i) 'very prominent gyri recti of the frontal lobes, suggestive of microgyria', (ii) 'asymmetry of the temporal lobes, the left appearing abnormally small on the lateral surface' and (iii) 'a keel-like dorsal expansion of the lower brain-stem'. Falk *et al.* [3,5] view the character (i) as a non-pathological, derived feature in *H. floresiensis*. The character (ii) may be ascribed to deformational plagiocephaly [17,32], and (iii) are not evident in our virtual endocast. In either case, these reflect aspects of the brain substance that should be included in ECV measurement.

Along the sagittal suture and around the vertex of the LB1 cranium, a relatively large area of the inner parietal bone surface (40 mm anteroposteriorly and 25 mm transversely) is depressed approximately 3 mm superiorly (evident in figure 2). No signs of bone fracture are evident, and the three-layer structure of the cranial bone (inner and outer tables, and diploe) appears to remain undisturbed in the CT sections, indicating that the depression was present when this individual was alive. Because depressions similar to this were also observed in a few modern human skulls, we decided to include the space for the endocranial depression (approx. 1.7 cc) in our ECV measurement.

(iii) Reconstruction of the endocast and its error estimation

We used ANALYZE v. 8.1 (Mayo Clinic), AMIRA v. 5.3 (Visage Imaging, Inc., CA, USA) and RAPIDFORM v. 2006 (INUS Technology, Inc., Seoul) to conduct the following works. By observing the original specimen and the CT sections, we first virtually removed sedimentary matrix attached to the endocranial surfaces (see the electronic supplementary material, figure S2), and we again made horizontally sectioned three-dimensional prints based on this 'virtually cleaned CT imagery'. Upon these replicas, we reconstructed the missing/damaged endocranial bones by putting and moulding modelling clay with reference to endocranial morphology of modern humans (figure 1*b*). Fortunately, sufficient endocranial bones remain intact for LB1, and clay reconstructions can be reasonably executed by extending preserved bone surfaces and/or mirror imaging the intact other side (see the electronic supplementary material, text S1). After these clay reconstructions, the upper and lower braincase replicas were physically joined together for another CT scan to create the 'replica CT imagery with clay reconstructions'.

Then, we digitally superimposed this 'replica CT imagery with clay reconstructions' on the 'virtually cleaned CT imagery', so that the replica parts of the former are replaced by the original CT scan of the cranial bones in the latter. Small gaps untreated by clay and parts of the clay reconstructions, when found to be inappropriate, were then further corrected in this integrated imagery to ensure smooth continuity of the endocranial surfaces (see the electronic supplementary material, figure S3). Based on this final imagery (virtually cleaned endocranial surface + clay reconstructions of the damaged parts with additional digital corrections), we segmented the endocranial region using the bone–air or clay–air HMM threshold values. Small anatomical foramina and minute cracking untreated by clay were then virtually sealed at the level of the endocranial opening. The foramen magnum was sealed by bridging between its anterior and posterior margins (horizontally most protruding points) in each sagittal section (figure 2). Finally, we calculated the total volume of voxels assigned to the endocranial region.

We also estimated the magnitudes of the following three types of error involved in our ECV measurement. First, in order to examine error related to delimitation of the endocranial cavity, we experimentally changed bone–air threshold value and observe variation in the resultant ECVs. Second, we estimated possible errors stemming from our clay reconstructions of the damaged bones. Reconstruction errors at smoothly curved endocranial surfaces should be negligible, but those parts with complex morphology (figure 2) may significantly affect our ECV measurement. We calculate a total surface area of such complex parts to approximate the effects of their inflation or deflation. Third, we evaluated error in size calibration of our CT scanning. In addition, in order to evaluate the effect from differences in plugging method of the foramen magnum, we tried another method to see associated volume change.

(b) Brain–body size scaling in *Homo sapiens*

We compared ECV with femoral head diameter (FHD), the most commonly used proxies for brain and body mass, respectively [33–35]. Various equations have been developed to estimate body mass from the FHD, but here, we do not attempt such conversion to avoid complicated effects of the choice of these equations [36]. Vertical head diameter (Martin's no. 18) was preferred as the FHD but transverse (Martin's no. 19) or maximum diameters, both of which are nearly equal to the former, were used when the former was not available.

We collected ECV and FHD data for 20 chrono-regional groups of Holocene *H. sapiens* worldwide from literature and our own data (table 1). The data and their sources are available from the electronic supplementary material, table S1. These include small- and large-bodied (group means of FHD: 37.7–48.6 mm for males, 35.5–42.5 mm for females) and small- and large-brained (group means of ECV: 1244–1543 cc for males, 1100–1368 cc for females) populations. We excluded ECV estimates based on linear cranial measurements. The samples consist of adult and a small number of adult-equivalent individuals. Although adult brain size is attained by juvenile in modern humans [37], for the sake of safety, we excluded juvenile individuals except for the Egypt sample that may include a small number of juveniles. In some cases, the measurements were taken by different authors based on different samples from the same population, and this is a potential source of (presumably minor) error.

Males and females were analysed separately due to the sexual differences in human body and brain sizes. Intraspecific scaling exponents were estimated based on natural logarithms of the sex-specific group mean data and the following four line fitting methods: two types of ordinary least-square regressions (OLSs), ECV on FHD ('inverse calibration', OLS-IC) and FHD on ECV ('classical calibration', OLS-CC), major axis (MA) and reduced major axis (RMA) [38]. Because we are aiming to predict

Table 1. Samples of modern humans.

| | |
|---------------|--|
| Asia | Andamanese, Philippine Negrito, Neolithic Japan (Jomon), Bronze Age Japan (Tanegashima Islanders), modern Japanese, Southern Chinese |
| Australia | Australian Aborigines (Murray Valley) |
| Polynesia | Easter Island |
| North America | Aleut, Alaska Eskimo, Old Zuni (Hawikuh), Pecos Pueblo |
| Europe | Sami (Lapp), Neolithic Denmark, England (Spitalfields) |
| Africa | Predynastic Egypt, Zulu, Western Pygmies, Eastern Pygmies, Khoisan |

the condition in a dwarfed hominin, we need to obtain a general slope to extrapolate conditions outside (particularly downside) the range of the reference sample (*H. sapiens*) distribution. Some researchers suggest that OLS-CC works better for extrapolation [38], but it remains uncertain if this is always the case [39]. In this paper, we mainly focus on MA and RMA as methods best describing the bivariate scatter of X and Y, and produce intermediate (thus 'conservative') results between the two OLS regressions [39]. The slopes and their 95% CIs were calculated using R software [40] and its package lmodel2 [41].

The ECV and FHD data were also collected from the following premodern fossil hominin samples (genera *Australopithecus* and *Homo*). These data are tabulated in the electronic supplementary material, table S2.

(i) *Australopithecus afarensis*

The 'small individual' is represented by A.L. 288-1 [42,43], whereas the 'large individual' is composite data from A.L. 444-2 and KSD-VP-1/1 [43,44]. The group mean is the average of these two datasets.

(ii) *Australopithecus africanus*

Means were calculated from five cranial (MLD 37/38; Sts 5; Stw 60, 71, 505) and six femoral (Sts 14; Stw 25, 99, 311, 392; 443) specimens [22,33].

(iii) *Homo habilis sensu lato*

Means calculated from three cranial (KNM-ER 1470, 1805, 1813) and two femoral (KNM-ER 1472, 1481a) specimens [34,43]. Although some researchers suggest that the sample includes multiple species [45], they are lumped together mainly because of uncertain association between the cranial and postcranial specimens.

(iv) *Dmanisi Homo*

A femur (D4167) from a large adult individual is inferred to be associated with a large mandible (D2600) [46]. Here, the femur is tentatively associated with a relatively robust adult cranium, D2280 which is probably male [47].

(v) *H. ergaster* (African *H. erectus*)

Owing to the lack of adult femoral heads, the species is represented here by an estimated adult condition of the large juvenile skeleton, KNM-WT 15000 [34,48].

(vi) Early Indonesian *H. erectus* (1.2–0.8 Ma)

Two chronological subsamples from the Early Pleistocene of Sangiran, Central Java are included. The 'Sangiran Upper' (Bapang-

Table 2. Slopes for the best-fit lines for *H. sapiens* (left columns) and expected ECV values after simulated body size reduction from the two hypothetical ancestors to the *H. floresiensis* conditions (right columns).

| model used | regression parameters | | | <i>H. habilis</i> (614 cc) | | earliest Indonesian <i>H. erectus</i> (860 cc) | |
|---------------|-----------------------|----------------------|-----------|----------------------------|------------------------|--|------------------------|
| | slope | 95% CI for the slope | intercept | expected ECV (cc) | decrease to 426 cc (%) | expected ECV (cc) | decrease to 426 cc (%) |
| OLS-IC male | 0.76 | 0.41–1.10 | 4.39 | 488 | 67 | 599–649 | 49–60 |
| OLS-IC female | 0.90 | 0.50–1.29 | 3.84 | 468 | 78 | 561–616 | 56–69 |
| MA male | 1.05 | 0.65–1.71 | 3.29 | 447 | 89 | 522–582 | 64–78 |
| MA female | 1.27 | 0.82–2.06 | 2.47 | 417 | 105 | 469–536 | 75–90 |
| RMA male | 1.03 | 0.74–1.44 | 3.34 | 449 | 88 | 525–585 | 63–77 |
| RMA female | 1.20 | 0.87–1.65 | 2.74 | 427 | 100 | 485–551 | 71–86 |
| OLS-CC male | 1.41 | 0.97–2.63 | 1.90 | 400 | 114 | 438–508 | 81–97 |
| OLS-CC female | 1.60 | 1.11–2.85 | 1.26 | 378 | 126 | 400–474 | 89–106 |

AG) subsample is chronologically younger, and represented by probable male (Sangiran 17) and female (Sangiran IX) crania [49]. The 'Sangiran Lower' (Grenzbank/Sangiran) subsample is older and currently represents the earliest Indonesian *H. erectus*. Relatively gracile (Sangiran 2) and robust (Sangiran 4) crania are available for its ECV [30,31]. The FHD of the earliest Indonesian *H. erectus* remains unknown. That for Trinil 3 is 45 mm (Y. Kaifu 2007, personal observation), but taxonomic assignment of this specimen to Indonesian *H. erectus* is questioned [50]. Because their cranial size and shape as well as dento-mandibular morphology are broadly comparable to or slightly more primitive than African *H. ergaster* [29,30], their mean FHD is expected to have been larger than *H. habilis* (40–44 mm) or Dmanisi *Homo* (40 mm), and lesser than the large *H. ergaster* individual, KNM-WT 15000, whose adult FHD is predicted as 51 mm (95% error range: 46.8–55.2 mm; [34]). In addition, FHDs estimated from pelvic acetabular sizes of African *Homo* specimens are 46.8 mm for KNM-ER 3228 (approx. 1.9 Ma) and 47.8 mm for OH 28 (0.7 Ma), respectively [34]. In consideration of these, 45–50 mm may be reasonable estimates for the earliest Indonesian *H. erectus*.

(vii) *Homo floresiensis*

The FHD for LB1 used here is the mean of vertical and transverse diameters (31 mm; [51]), and is slightly smaller than the FHD reported in ([1]; 31.5 mm).

4. Results

(a) Endocranial volume of LB1

The total amount of the matrix we virtually removed endocranially was approximately 1.5 cc, of which 0.8–1.0 cc was inside the original endocranial cavity (i.e. inside the boundary defined by our reconstruction described earlier). The rest of the removed matrix (0.5–0.7 cc) was distributed outside the original endocranial cavity (mostly within the areas of the damaged bones), and thus irrelevant to the ECV calculation.

For each of the cranial bone (inner table) and air, we measured CT values at arbitrarily selected 132 different voxels taken from three different CT slices to calculate their means. The median of these means was used to differentiate the bone and air. With this HMH thresholding, the volume of the endocranial cavity was 425.7 cc.

If we change the bone/air threshold value ± 5 per cent or ± 10 per cent of the difference between the average CT values for the bone and air, this ECV shifts by ± 0.5 cc or ± 1.3 cc, respectively. The total area of the endocranial surface prepared above was approximately 352 cm², 17 per cent of which (approx. 60 cm²) had been reconstructed either by clay or digital plugging. If we make an unrealistic assumption that all of these parts were erroneously delimited by one pixel (0.26 mm) either inward or outward, then the resultant volume change would be up to ± 1.5 cc. Clay-based reconstruction of complex morphology such as the central sphenoid, the medial part of the right petrous bone and the lower part of the right sigmoid sulcus may include some more substantial error (blue portions in figure 2). The total surface area of these parts was 14 cm², which would result in error of up to ± 1.4 cc assuming inflation or deflation of all of these parts by 1 mm either inward or outward. Finally, error owing to size calibration of the CT scanning is no more than ± 1 cc [20]. Taken together, given that many of the above error estimates are supposed maxima, we conclude that the original ECV of the LB1 cranium was 426 cc with only a limited degree of error, probably within ± 3 cc.

In our definition, the foramen magnum is sealed not by a flat plane but by a folded surface constituted by lines connecting the anterior and posterior margins of the foramen magnum defined separately in each mid/parasagittal CT section. If we change this definition and plug the foramen with a flat, horizontal plane passing through the line connecting endobasion and opisthion, then the ECV decreases by 0.5 cc.

(b) Endocranial volume reduction explained by intraspecific scaling

The log-transformed ECV and FHD are moderately correlated in the male and female *H. sapiens* samples ($r = 0.73$ or 0.75 , $p < 0.001$). As seen in table 2, the scaling exponents for male and female *H. sapiens* calculated by MA (1.05, 1.27) and RMA (1.03, 1.20) are almost identical, whereas those by OLS-IC (0.76, 0.90) and OLS-CC (1.38, 1.60) are lesser and higher, respectively. The slopes are slightly steeper in the female than in the male analyses. Log-transformed ECV and FHD values are plotted in figure 3, together with RMA lines for *H. sapiens*.

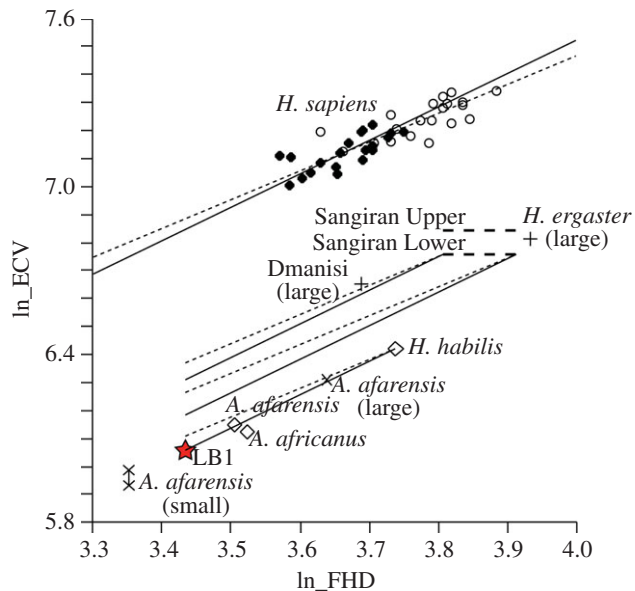


Figure 3. Relationship between the ECV and FHD. Open circle, *H. sapiens* (male); filled circle, *H. sapiens* (female); rhombus, mean data for the fossil hominin samples; x, individual data for *Australopithecus*; +, individual data for premodern *Homo*. Possible range of the ECV is indicated for the small *A. afarensis* individual (A.L. 288-1). Estimated ranges of the FHD for the two early Indonesian *H. erectus* samples (Sangiran Upper and Lower) are indicated by thick broken lines (3.81–3.91 in logarithmic form; see text for more details). The diagonal lines indicate expected brain size reductions from the *H. habilis* and Sangiran Lower (earliest Indonesian *H. erectus*) conditions following the scaling relationship for male (dotted lines) and female (solid lines) *H. sapiens* based on the RMA regressions. (Online version in colour.)

Table 2 also shows expected ECV reductions associated with body size (FHD) changes following different scaling models.

If the body size of LB1 reduced from the average *H. habilis* condition (ECV = 614 cc, FHD = 42 mm) following the MA or RMA scaling models based on the male data, then the resultant ECV would be 447–449 cc, 11–12% larger than the measured ECV for LB1 (426 cc). If LB1 is female as suggested previously [1,51], such brain size reduction is achieved by the body size scaling alone.

If the earliest Indonesian *H. erectus*, here represented by the Sangiran Lower sample, experienced body size reduction to the state of LB1, then the MA or RMA male models suggest that their ECV would reduce from 860 to 522–585 cc (63–78% reduction) depending on the ancestral FHD values (45–50 mm). When the female models are used, such expected reduction increases to 71–90%. In other words, 10–29% of the ECV reduction is to be explained by factors other than body size if LB1 was female. More of the ECV reduction is ascribed to body size scaling if we use the OLS-CC models, whereas such proportion becomes less in the OLS-IC models.

5. Discussion and conclusions

Previous studies are in agreement that the brain of *H. floresiensis* is too small to have been dwarfed from *H. erectus* following human intraspecific body size scaling [1–14]. Although this view is probably correct, the earlier-mentioned re-examination shows that the proportion of the

brain reduction unexplained by body size scaling is smaller (and thus less difficult) than previously claimed. This is because of the following reasons. First, the newly determined ECV of LB1, approximately 426 cc, which is based on high-quality micro-CT scan and elaborate cleaning, reconstruction and error estimations, is slightly larger than the previous estimate (approx. 400 cc). Second, scaling exponents for *H. sapiens* used previously [7,8] were based on a single regional population and thus considerably underestimated the actual species-wide trend. Although the exponent values cannot be compared directly owing to different scales taken (body weight [7,8] versus FHD (this study)), between-group analyses presented earlier and elsewhere [19] clearly indicate a relatively high level of correlation between body and brain sizes in our species. Several population samples used in this study are small ($n = 3–5$: electronic supplementary material, table S1), but broadly similar slopes derived from the male and female analyses (table 2) suggest that these reflect actual scaling exponent for *H. sapiens*. Finally, there are reasons to suppose early Indonesian *H. erectus* (mean ECV: approx. 860 cc), rather than generalized *H. erectus* (mean ECV: 991 cc), as an ancestor candidate for *H. floresiensis*.

In the model of Martin *et al.* [8], decreased body size from 60 (estimated average for generalized *H. erectus*) to 16 kg (smallest estimate for LB1 [1]) results in only moderate reduction of ECV from 991 to 794 cc. In our model of ancestor (early Indonesian *H. erectus*) and descendant (LB1) relationships, and RMA or MA scaling, the estimated body size decrease (changes in the FHD from 45–50 to 31 mm) would reduce the ECV from 860 to 469–585 cc (63–90% reduction) by body size scaling alone (table 2). Even if we use the OLS-IC models that are probably inappropriate for extrapolation [38], 49–69% of the brain size reduction could be explained by body size. The OLS-CC models, recommended by some researchers for extrapolation [38], predict even greater proportion, 81–100%. We cannot exactly determine which of these figures are more correct owing to unresolvable limitations such as small fossil samples, extrapolation and ultimately unknown scaling exponent for extinct *Homo*. Still, the earlier-mentioned results, based on the best available data and various regression methods, suggest that at least 50 per cent, probably much more, of the brain size reduction in *H. floresiensis* could occur as scaling effect if this little hominin derived from early Indonesian *H. erectus*. This means that 0–50% of its brain size decrease needs to be explained by other factors.

There are a few reports about relative brain size reduction in island mammals. Weston & Lister [10] suggested that approximately 30 per cent of brain size decrease occurred in an extinct dwarf species of Malagasy hippopotamus (*Hippopotamus lemerlei*), in addition to normal intraspecific scaling effect associated with body size decrease. Köhler & Moyà-Solà [52] examined ECV of *Myotragus*, an extinct, dwarfed caprine genus endemic to the Mediterranean island Majorca [53]. Although its Miocene continental ancestor is presently unknown, these authors found that (i) their continental bovid sample composed of a variety of extant and fossil taxa, including seven caprine species from three tribes (Rupicapriini, Capriini and Ovini) show a fairly consistent brain–body allometric scaling relationship, and (ii) the relative brain size of *Myotragus* was distinctly (approx. 50%) smaller than expected from this general trend for the mainland bovines.

Therefore, it is ‘mechanistically’ possible [10] that *H. floresiensis* evolved from early *H. erectus*, and 0–50% of

the total brain size reduction occurred independently from the scaling effect. However, such marked relative brain size reduction in insular mammals is generally considered to have occurred to reduce energetic demand. Because metabolic cost of the brain tissue is expensive, in an insular environment with limited food resources and increased intraspecific competition under the absence of predators, it is advantageous to reduce brain size at the cost of some neural functions such as sensory, motor, social and/or intellectual activities [50]. If one applies a similar energetic explanation for the brain size evolution in *H. floresiensis*, then we need to answer what aspects of central nervous system were sacrificed in this little hominin [13,14] who show no sign of retrogression at least in stone tool technology compared with earlier hominins on Flores or elsewhere in island Southeast Asia [54,55]. The absence of mammalian carnivores in the Pleistocene of Flores [28,56,57] may explain the situation, despite the presence of a giant lizard (*Varanus komodoensis*) and a giant marabou stork (*Leptoptilos robustus*); the close relative brain sizes between *H. habilis* and *H. floresiensis* documented above may imply that intellectual capacity comparable to the former was enough for the latter. Otherwise, *H. floresiensis* may have experienced 'neurological reorganization' where brain

functions are largely maintained in spite of its overall size change [5], but such proposal is unacceptable for other researchers [9].

We conclude that evolution from early Javanese *H. erectus* to *H. floresiensis* was possible in terms of brain size. Still, in this scenario, some amount of the brain size reduction remains to be explained by factors other than body size scaling, posing a challenge to our current knowledge about human brain size evolution. If *H. floresiensis* descended from *H. habilis*-like ancestor, the need for such relative brain size reduction is less significant, but we stress currently we have no convincing fossil evidence to support this hypothesis except for the brain size issue discussed here. Then which hypothesis is more correct? The question will be answered most effectively by future discoveries of skeletal evidence for the first hominins to colonize Flores [58].

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