Comment on “The Brain of LB1, Homo floresiensis”

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Endocast analysis of the brain Homo floresiensis by Falk et al. (Reports, 8 April 2005, p. 242) implies that the hominid is an insular dwarf derived from H. erectus, but its tiny cranial capacity cannot result from normal dwarfing. Consideration of more appropriate microcephalic syndromes and specimens supports the hypothesis of modern human microcephaly.

The proposed new hominid species Homo floresiensis is based primarily on a diminutive 18,000-year-old adult skull and partial skeleton (LB1) (1). Additional, much less complete specimens have been attributed to eight other individuals (2). Initially interpreted as an insular dwarf derived from Homo erectus (1), alternatively LB1 may be a microcephalic modern human, although some have dismissed this hypothesis (1, 3). Its cranial capacity (~400 cc (1, 3)) is within the normal range for great apes and is smaller than other undoubted hominid except for two Australopithecus afarensis individuals dating back 3 to 3.5 million years (343 cc, AL 333-105; 375 cc, AL 162-28).

The tiny cranial capacity of LB1 cannot be attributed to intraspecific dwarfism in H. erectus. Body size reduction in mammals is usually associated with only moderate brain size reduction. Starting from three potential ancestral forms (H. erectus broadly defined; the chronologically and geographically closest H. erectus specimens from Ngandong, Java; and the substantially earlier Dmanisi hominids from Georgia) and following a range of possible dwarfing models, the predicted body size of a dwarf hominid with the cranial capacity of LB1 ranges from less than 1 g to 11.8 kg (Table 1 and Fig. 1) (4). Most of the figures calculated are at least an order of magnitude smaller than the estimates for LB1 (16 to 29 kg) (1). The largest are based on the insular dwarfing of elephants on Mediterranean islands (Model A) from 10,000 to 15,000 kg down to 100 kg. Despite the extreme dwarfing involved, and the relatively steep brain-body size scaling, the predicted body size for the dwarf hominid is still unrealistically small. Typical mammalian intraspecific scaling (Model B) indicates a maximum body weight less than half that estimated for LB1. Intraspecific brain-body size scaling in primates, including humans, is notably flat, particularly for males and females separately (5). This model (Model C) predicts tiny body weights for LB1.

Falk et al. (3) assumed only one type of “primary microcephaly,” whereas the term merely means unusually small brain size at birth (9), and skulls are quite variable (6). Low, sloping foreheads and pointed vertices are not universal (9). The more than 400 associated genetic syndromes (10) typically have autosomal recessive inheritance and hence recur in small, inbred populations. They comprise high-functioning and low-functioning types (11). LB1 was an adult, so consideration should focus on high-functioning forms that may survive to adulthood. Jakob Moegele’s early death alone renders comparison inappropriate. Four human genes in which mutations may result in high-functioning microcephaly have been cloned (11). Two of these (ASPM and MCPH1) have evolved rapidly in primates, seemingly contributing to hominin brain size increase (11). LB1 could represent a microcephalic individual from a small-bodied hominid population with a mutation in such a gene.

Alternatively, LB1 could derive from a normal-sized human population. More than a dozen syndromes with severe growth retardation

Table 1. Estimates of the body weight of a dwarf hominid with the cranial capacity of LB1 (400 cc), derived from various possible ancestral forms and following various dwarfing models (4). Scaling exponents (b) for dwarfing models: Model A, b = 0.32 to 0.35 (18–20); Model B, b = 0.25 (5, 21); Model C, bcombined sexes = 0.17, bmales = 0.10, b females = 0.03 (22, 5).

<table>
<thead>
<tr>
<th>Species/specimens (23–25)</th>
<th>Body weight estimate (kg)</th>
<th>Cranial capacity (cc)</th>
<th>Model A: Dwarfing of Elephas antiquus to Elephas falconeri</th>
<th>Model B: Typical mammalian intraspecific scaling</th>
<th>Model C: Intraspecific scaling for Homo sapiens: combined sexes, males, females</th>
</tr>
</thead>
<tbody>
<tr>
<td>Homo erectus broadly defined</td>
<td>60</td>
<td>991</td>
<td>3.5–4.5</td>
<td>1.6</td>
<td>0.3, 0.007, &lt;0.001</td>
</tr>
<tr>
<td>Ngandong Homo erectus</td>
<td>60</td>
<td>1149</td>
<td>2.2–2.9</td>
<td>0.9</td>
<td>0.1, 0.002, &lt;0.001</td>
</tr>
<tr>
<td>Dmanisi hominids</td>
<td>50</td>
<td>664</td>
<td>10.3–11.8</td>
<td>6.6</td>
<td>2.5, 0.3, &lt;0.001</td>
</tr>
</tbody>
</table>

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and microcephaly exist (10). Several of these are associated with survival into adulthood, including the best studied, microcephalic osteodysplastic primordial dwarfism (MOPD) type 2, although none can be matched exactly with LB1 from the limited evidence available. However, the group of syndromes shares several features of interest with LB1, including very small stature and brain size, a small receding jaw, dental dysplasias and missing teeth, and postcranial anomalies.

Microcephalic skulls and endocasts similar to LB1 include the specimens shown in Fig. 2. Doubling of the volume for half-skull B yields a cranial capacity of 432 cc, close to that of LB1. Specimen C has a volume of 340 cc. Both lack obvious pathologies. For example, the cerebellum is tucked under the cerebrum (3). The stone tools reported at the LB1 site (12) clearly include types that are consistently associated with Homo sapiens and have not previously been linked with H. erectus or other early hominids. In addition to genetic factors increasing the likelihood of microcephalics occurring together, it is conceivable that cultural factors might have enhanced this, as at a recent religious site to which microcephalics were brought (15). We conclude that LB1 was not an insular dwarf and may have been a microcephalic modern human.

References and Notes
4. The well-known insular dwarf bovid Myotragus from Majorca (14) is not included as a model for the dwarfing of LB1 because the mainland ancestor is unknown, the genus diverged from other bovids more than 5 million years ago and, unlike LB1, the orbits and presumably associated neurological structures are very small.

Fig. 1. Example of the dwarfing models presented in Table 1 showing the derivation of dwarf forms with the cranial capacity of LB1 from Ngandong H. erectus following the dwarfing models A to C. Body weight predictions for LB1 from all three models are substantially lower than the estimated values from the skeleton itself.

Fig. 2. Comparison of LB1 and microcephalic skulls. (A) LB1 (1). (B) Left half-skull of a dentally adult male human microcephalic from India (15, 16) held in the collections of the Hunterian Museum, London (RCSHM/Osteo 95.1). The two skulls are drawn to the same scale and are similar in overall size and proportions and in features such as the receding forehead. (C) The left side of a human microcephalic endocast from the collections of the Field Museum, Chicago (accession no. A219680) derived from the skull of a 32-year-old woman from Lesotho who had the body size of a 12-year-old child (27). (D) An endocast from the Hunterian microcephalic specimen. Both (C) and (D) have relatively normal external appearance despite their very small size. Drawings by Jill Seagard.