

Comment on "The Brain of LB1, *Homo floresiensis*"

R. D. Martin,^{1*} A. M. MacLarnon,² J. L. Phillips,^{1,3} L. Dussubieux,¹
P. R. Williams,¹ W. B. Dobyns⁴

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 hominids 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 Geor-

gia) 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 slope, 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) analyzed virtual endocasts, including LB1 and a modern human microcephalic, and concluded that LB1 is closest to *H. erectus* and not a microcephalic. A subsequent study of 19 microcephalics identified one endocast as similar to LB1 (6), although this was questioned (7). In the Falk *et al.* study (3), the "European microcephalic" used (AMNH 2792a) is a plaster-based cast, not an original skull. The calotte is markedly paler and fits poorly with the rest of the cast, which was ap-

parently varnished. Inductively coupled plasma-mass spectrometry confirmed that the calotte was from a different batch of plaster. The cranial capacity of the AMNH cast is exceedingly small (260 cc) compared with a mean of 400 cc for microcephalics (6). The disproportionately large size of the cerebellum suggests severe brain malformation. The cast is inscribed "Plattenhardt" and "Tausch mit Stuttgart 1907," and the original skull was traced to the Staatliches Museum für Naturkunde, Stuttgart (5297/25523). The teeth (eight in the upper jaw, nine in the mandible) are highly unusual, as they are small, widely separated, and peg-like, with heavily worn, mushroomlike crowns. The skull was included in an early anthropological survey of microcephaly (8) and is that of Jakob Moegele from the village of Plattenhardt, who died aged 10 years. His recorded cranial capacity (272 cc) was the smallest in the survey and is substantially smaller than that of LB1. Three of his 10 siblings were also microcephalics.

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 *MCPHI*) have evolved rapidly in primates, seemingly contributing to hominid 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

¹The Field Museum, Chicago, IL 60605-2496, USA. ²School of Human and Life Sciences, Roehampton University, London SW15 4JD, UK. ³Department of Anthropology, University of Illinois at Chicago, IL 60607, USA. ⁴Department of Human Genetics, University of Chicago, Chicago, IL 60637, USA.

*To whom correspondence should be addressed. E-mail: rdmartin@fieldmuseum.org

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, $b_{\text{combined sexes}} = 0.17$, $b_{\text{males}} = 0.10$, $b_{\text{females}} = 0.03$ (22, 5).

Possible ancestral forms	Body weight estimates (kg) for dwarf hominid with cranial capacity 400 cc, based on various dwarfing models				
	Species/specimens (23–25)	Body weight estimate (kg)	Cranial capacity (cc)	Model A Dwarfing of <i>Elephas antiquus</i> to <i>Elephas falconeri</i>	Model B Typical mammalian intraspecific scaling
<i>Homo erectus</i> broadly defined	60	991	3.5–4.5	1.6	0.3, 0.007, <0.001
Ngandong <i>Homo erectus</i>	60	1149	2.2–2.9	0.9	0.1, 0.002, <0.001
Dmanisi hominids	50	664	10.3–11.8	6.6	2.5, 0.3, <0.001

and microcephaly exist (10). Several of these are associated with survival into adulthood, including the best studied, microcephalic osteodysplastic primordial dwarfism (MOPD) type

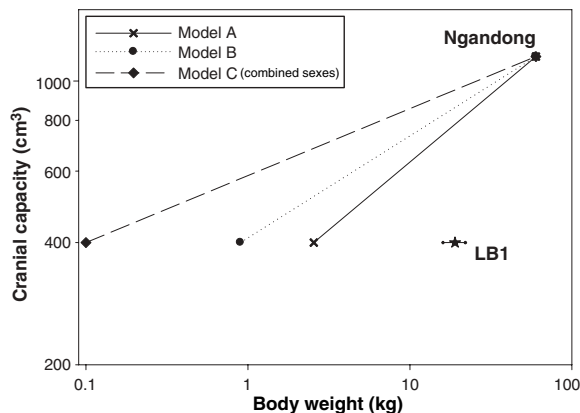


Fig. 1. Example of the dwarfing models presented in Table 1 showing the derivation of dwarf forms with the cranial capacity of LB1 from Ngandong *H. erectus* following the dwarfing models A to C. Body weight predictions for LB1 from all three models are substantially lower than the estimated values from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

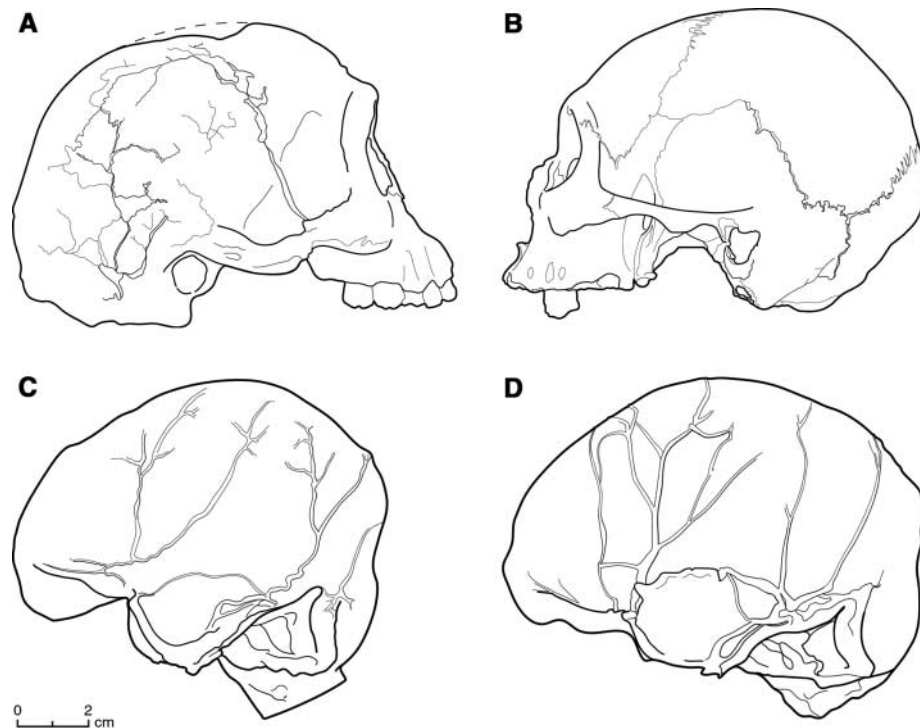


Fig. 2. Comparison of LB1 and microcephalic skulls. (A) LB1 (1). (B) Left half-skull of a dentally adult male human microcephalic from India (15, 16) held in the collections of the Hunterian Museum, London (RCSHM/Osteo 95.1). The two skulls are drawn to the same scale and are similar in overall size 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 (17). (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.

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 (13). We conclude that LB1 was not an insular dwarf and may have been a microcephalic modern human.

References and Notes

1. P. Brown *et al.*, *Nature* **431**, 1055 (2004).
2. M. J. Morwood *et al.*, *Nature* **437**, 1012 (2005).
3. D. Falk *et al.*, *Science* **308**, 242 (2005).
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.
5. R. D. Martin, P. H. Harvey, in *Size and Scaling in Primate Biology*, W. L. Jungers, Ed. (Plenum, New York, 1985), pp. 147–173.
6. J. Weber, A. Czarnetzki, C. Pusch, *Science* **310**, 2366 (2005).
7. D. Falk *et al.*, *Science* **310**, 236c (2005).
8. C. Vogt, *Arch. Anthropol.* **2**, 129 (1867).
9. C. G. Woods, J. Bond, W. Enard, *Am. J. Hum. Genet.* **76**, 717 (2005).
10. Online Mendelian Inheritance in Man, OMIM (TM). McKusick-Nathans Institute for Genetic Medicine, Johns Hopkins University (Baltimore, MD) and National Center for Biotechnology Information, National Library of Medicine (Bethesda, MD), 2000; www.ncbi.nlm.nih.gov/omim.
11. S. L. Gilbert, W. B. Dobyns, B. T. Lahn, *Nat. Rev. Genet.* **6**, 581 (2005).
12. M. J. Morwood *et al.*, *Nature* **431**, 1087 (2004).
13. M. Miles, D. Beer, *Hist. Psychiatry* **7**, 571 (1996).
14. M. Köhler, S. Moyà-Solà, *Brain Behav. Evol.* **63**, 125 (2004).
15. J. Shortt, *J. Anthropol. Inst. Brit. Irel.* **3**, 265 (1874).
16. G. Humphry, *J. Anat. Physiol.* **29**, 304 (1895).
17. E. G. Dru-Drury, *Trans. R. Soc. S. Afr.* **8**, 149 (1919/1920).
18. V. L. Roth, *Oxf. Surv. Evol. Biol.* **8**, 259 (1992).
19. A. M. Lister, *Symp. Zool. Soc. Lond.* **69**, 277 (1996).
20. F. S. Accardi, M. R. Palombo, *Atti Accad. Naz. Lincei Rendiconti* **51**, 111 (1971).
21. D. C. T. Kruska, *Brain Behav. Evol.* **65**, 73 (2005).
22. R. L. Holloway, *Am. J. Phys. Anthropol.* **53**, 109 (1980).
23. R. Stanyon, S. Consigliere, M. A. Morescalchi, *Hum. Evol.* **8**, 205 (1993).
24. J. Kappelman, *J. Hum. Evol.* **30**, 243 (1996).
25. G. P. Rightmire, D. Lordkipanidze, A. Vekua, *J. Hum. Evol.* **50**, 115 (2006).
26. We thank R. Akram, M. Cooke, E. Davion, J. Hall, E. Heizmann, J. Higham, J. Hughes, K. Mowbray, W. Pestle, G. Sawyer, J. Schwartz, J. Seagard, and I. Tattersall.

11 October 2005; accepted 18 April 2006
10.1126/science.1121144