

## LETTERS

## Further evidence for small-bodied hominins from the Late Pleistocene of Flores, Indonesia

M. J. Morwood<sup>1\*</sup>, P. Brown<sup>1\*</sup>, Jatmiko<sup>2</sup>, T. Sutikna<sup>2</sup>, E. Wahyu Saptomo<sup>2</sup>, K. E. Westaway<sup>3</sup>, Rokus Awe Due<sup>2</sup>, R. G. Roberts<sup>3</sup>, T. Maeda<sup>1</sup>, S. Wasisto<sup>2</sup> & T. Djubiantono<sup>2</sup>

*Homo floresiensis* was recovered from Late Pleistocene deposits on the island of Flores in eastern Indonesia, but has the stature, limb proportions and endocranial volume of African Pliocene *Australopithecus*<sup>1</sup>. The holotype of the species (LB1), excavated in 2003 from Liang Bua, consisted of a partial skeleton minus the arms. Here we describe additional *H. floresiensis* remains excavated from the cave in 2004. These include arm bones belonging to the holotype skeleton, a second adult mandible, and postcranial material from other individuals. We can now reconstruct the body proportions of *H. floresiensis* with some certainty. The finds further demonstrate that LB1 is not just an aberrant or pathological individual, but is representative of a long-term population that was present during the interval 95–74 to 12 thousand years ago. The excavation also yielded more evidence for the depositional history of the cave and for the behavioural capabilities of *H. floresiensis*, including the butchery of *Stegodon* and use of fire.

In 2003, archaeological excavations at Liang Bua, in western Flores, yielded a partial hominin skeleton (LB1) that proved to be about 18 thousand years (kyr) in age<sup>1,2</sup>. The skeleton is the holotype for a new species, *Homo floresiensis*, which we argued was the result of endemic dwarfing of an earlier *H. erectus* population<sup>1</sup>.

In 2004, we continued the excavation in Sector VII (from which the holotype skeleton was recovered) to a depth of 11 m without encountering bedrock. The adjoining Sector XI, located immediately to the south, was also excavated to recover further hominin remains, including additional elements of LB1, and to obtain more evidence for their stratigraphic and archaeological contexts (see Supplementary Information). Both sectors were excavated by stratigraphic layers as well as by 10-cm-deep spits.

The stratigraphic section of the combined Sector VII/XI trench indicates a consistent pattern of sediment deposition in this part of the cave during the Late Pleistocene (Fig. 1). At the northern, lower-lying end of the trench, layers of clayey silt (suspension deposits) accumulated in pools of standing water, with intrusions of gravel reflecting times of strong water flow from higher ground to the south. Elements of the LB1 skeleton, with some parts still articulated<sup>1</sup>, were recovered in both Sectors VII and XI, from a clayey silt (Layer R) accumulated on the lee side of a conglomerate deposit (Layer S). This suggests that natural processes were responsible for the rapid burial of the body by fine-grained sediments in a standing body of water. This pattern of sediment deposition changed about 12–11 kyr ago, when the lower sections of the cave floor were filled with thick, 'white' tuffaceous silts, another phase of suspension deposition, as evident in Sectors IV, VII and XI (see Supplementary Information). The overlying Holocene deposits were generally laid down horizontally by moving water.

A tiny hominin radius from Spit 42 in Sector XI was found immediately below the 'white' tuffaceous silts, and 40 cm above a calibrated radiocarbon age of 13.1 kyr from Sector VII (ANUA-27115; ref. 2). The inferred age of 12 kyr for the radius provides the youngest evidence for *H. floresiensis* and *Stegodon* at Liang Bua. In Sector VII, thermoluminescence dating of quartz grains from depths of 935 and 862 cm yielded maximum ages for sediment deposition of  $55 \pm 8$  kyr (sample LBS7-45a) (mean  $\pm$  total uncertainty at the 68% confidence interval) and  $41 \pm 10$  kyr (sample LBS7-46a) respectively, using the light-sensitive red thermoluminescence signal (see Supplementary Information). Although at a greater depth, the artefact- and bone-bearing deposits in this part of the site are not as old as those in the basal levels of Sector IV, where the earliest evidence for *H. floresiensis*, *Stegodon* and stone artefacts occurs at 95–74 kyr (ref. 2).

The uppermost 3.7 m of deposit in Sector XI yielded a complete Holocene sequence in which all hominin remains are of modern humans (*H. sapiens*). In contrast, none of the hominin remains recovered from the Pleistocene deposits are of modern humans. Instead, all diagnostic hominin elements are consistent with *H. floresiensis* size and morphology (Table 1). In total, there are now at least nine such individuals represented in the excavated finds from Sectors IV, VII and XI. This paper is concerned mainly with another mandible (LB6/1) and tibia (LB8), as well as the right humerus and ulna of LB1—all excavated from Sector XI in 2004.

During the Late Pleistocene, the southern, topographically higher area in the Sector VII/XI trench comprised dry, relatively level ground adjacent to a pool against the east wall of the cave. High densities of stone cores, flaking debris, retouched tools, anvils and faunal remains were found there, indicating that the area was a focus for a range of hominin activities and that *H. floresiensis* was capable of complex behaviour and cognition (see Supplementary Information). However, no pigments or symbolic items were found, in contrast with Holocene occupation levels.

Faunal remains included those of *Stegodon* (with cut marks evident on some bones), Komodo dragon, rat and bat, as well as the hominin mandible, scapula, radius and ulna from Spit 51 that were found on a well-defined occupation floor. Use of fire by hominins is indicated by charred bone and clusters of reddened and fire-cracked rocks. These include a cluster of three burnt, water-rolled, volcanic pebbles from Spit 84 ( $840 \pm 5$  cm depth) in Sector VII, and a circular arrangement of five similarly burnt pebbles from Spit 43 ( $435 \pm 5$  cm depth) in Sector XI.

With regards to the hominin remains, the adult mandible (LB6/1) from Spit 51 is undistorted, but has post-mortem damage to the left coronoid process and condyle. Most of the right ramus and the central and left lateral incisors were also lost post-mortem (Fig. 2).

<sup>1</sup>Archaeology and Palaeoanthropology, School of Human and Environmental Studies, University of New England, Armidale, New South Wales 2351, Australia. <sup>2</sup>Indonesian Centre for Archaeology, Jl. Raya Condok Pejaten No. 4, Jakarta 12001, Indonesia. <sup>3</sup>GeoQuEST Research Centre, School of Earth and Environmental Sciences, University of Wollongong, Wollongong, New South Wales 2522, Australia.

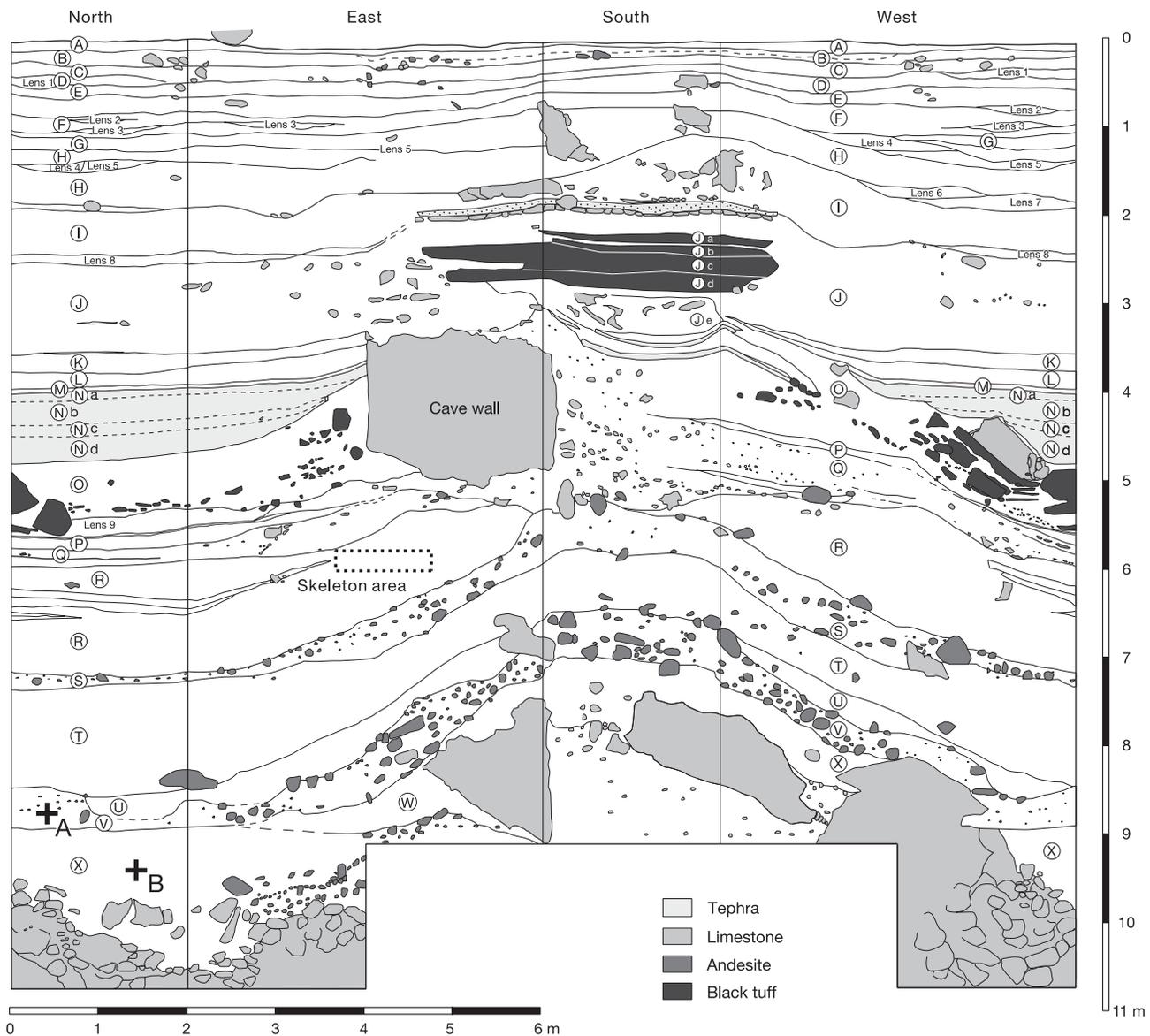
\*These authors contributed equally to this work.

The mandibular dental arch is narrow anteriorly and long relative to its breadth. The axis of P<sub>3</sub>–M<sub>3</sub> is straight, forming a more V-shaped tooth row than in the holotype, and in lateral view the inferior border of the mandible is not as arched as LB1. All permanent teeth had erupted and show evidence of occlusal wear, but less so than in LB1, and the Curve of Spee is not as well developed. The ramus root inserts on the corpus above the lateral prominence, and in lateral aspect obscures the distal M<sub>3</sub>. The ramus is broadest inferiorly, slopes slightly posteriorly and is thickened medio-laterally, and the extramolar sulcus is broader than in LB1, with a moderate lateral prominence. Bilaterally, there are multiple mental foramina in LB6/1, which is a common feature in Asian *H. erectus*<sup>3,4</sup>.

The anterior portion of the corpus is without a chin (no mental protuberance, mental tubercles or incurvatio mandibularis), but is not as rounded and bulbous as LB1. In the posterior symphyseal region, the alveolar planum inclines postero-inferiorly; there is a

moderate superior torus; the diagastric fossa is deep and broad; the inferior transverse torus is low and rounded, rather than shelf-like; and there is a strong posterior angulation of the symphyseal axis. D211 *H. erectus* from Dmanisi, Georgia, has similar symphyseal thickening and internal transverse tori, but differs in having a small mental protuberance<sup>5</sup>.

With the exception of P<sub>3</sub>, the size and morphology of the LB6/1 mandibular teeth follow the pattern in *H. erectus* and *H. sapiens*, and are consistent with the previously described attributes of *H. floresiensis*<sup>1</sup>: the molar size sequence is M1 ≥ M2 > M3. As with LB1 and LB2 (ref. 1), the P<sub>3</sub>s are mesio-distally elongated, and had a prominent protoconid and broad talonid when unworn. Both P<sub>3</sub>s also have bifurcated roots and the P<sub>4</sub>s have a mesiodistally compressed, broad Tomes' root. Mandibular P<sub>3</sub>s and P<sub>4</sub>s with similar crown and root morphology have been recorded for *Australopithecus* and early *Homo*<sup>6,7</sup>. Some Indonesian *H. erectus* mandibular premolars also have bifurcated or Tomes' roots<sup>4</sup>, as does Dmanisi D2600



**Figure 1 | Stratigraphy in the Sector VII/XI trench, Liang Bua.** Layers A–M are brownish clayey silts and sandy silts. N(a–d) comprise ‘white’ tuffaceous silts dated 12–11 kyr old. Evidence for *H. floresiensis* and *Stegodon* occurs up to the base of these. Layers O–R, T, U, W and X are brownish clayey silts and silts varying in texture, colour and proportions of rock. The holotype of

*H. floresiensis* occurred in Layer R, a clayey silt. Layers S and V are conglomerates with clayey silt matrix, from stronger water flow. Crosses labelled A and B indicate the locations of thermoluminescence samples LBS7-46a and LBS7-45a, respectively.

**Table 1 | Hominin remains excavated from the Late Pleistocene levels of Sector XI, Liang Bua, in 2004**

Spit no.	Bone	Description
42	Radius: child, left (LB4/1)	Proximal epiphyses unfused, articular surfaces not recovered, and distal quarter of shaft incomplete. Maximum length of fragment 101 mm.
43	Tibia: child, right (LB4/2)	Distal and proximal epiphyses unfused and articular surfaces not recovered. Maximum length 117 mm. Distal end recovered from Spit 44.
46	Cervical vertebra C1 (LB5/1) Metacarpal: adult (LB5/2)	Incomplete, represented by two fragments. Proximal end broken, length 58 mm.
51	Mandible: adult (LB6/1)	With incomplete left ramus and right coronoid process and condyle. Originally with a fracture through the corpus between right P <sub>3</sub> and P <sub>4</sub> and left M <sub>1</sub> and M <sub>2</sub> . Subsequently broken at the symphysis when removed from the Centre for Archaeology in Jakarta. This has altered the original arch dimensions, occlusion and the morphology of the symphysis. At the same time, cut marks, fill and glue altered the morphology of the lateral corpus and ramus.
	Radius: adult, right (LB6/2)	Complete. It has an angulated, healed fracture in the distal third with compensatory remodelling and extensive callus development. The forearm would have been bowed and distorted and movement of the hand restricted. Maximum length 157 mm.
	Ulna: adult, left (LB6/3)	Proximal shaft. Maximum length 137 mm.
	Scapula: adult, right (LB6/4)	With incomplete superior border, medial spine, inferior angle and coracoid process. Maximum breadth of glenoid cavity 25.1 mm, length of the auxiliary border 82 mm.
	Metatarsal (LB6/5)	Articular surfaces not preserved.
	Phalanx: 1st of foot (LB6/6)	Articular surfaces not preserved.
	Phalanx: 3rd of hand (LB6/7)	Complete. Maximum length 10 mm.
52	Phalanx: 1st of hand (LB6/8)	Complete. Maximum length 30.5 mm.
	Phalanx: 2nd of hand (LB6/9)	Complete. Maximum length 16 mm.
	Phalanx: 2nd of hand (LB6/10)	Distal end not preserved.
	Phalanx: 1st of hand (LB6/11)	Complete. Maximum length 10.5 mm.
	Phalanx: 3rd of hand (LB6/12)	Complete. Maximum length 12.5 mm.
	Phalanx: 1st of foot (LB6/13)	Complete. Maximum length 16 mm.
53	Incisor: mandibular I <sub>1</sub> (LB6/14)	
56B	Phalanx: 1st of hand (LB7)	Proximal end not preserved.
58A*	Humerus: adult, right (LB1)	Lateral epicondyle and capitulum are incomplete, and the greater and lesser tubercles are not preserved. Maximum length 243 mm.
	Ulna: adult, right (LB1)	Distal end of shaft and head not preserved. Estimated maximum length 205 mm.
	Fibula: adult, left (LB1)	Complete but with fracture through distal end of shaft. Maximum length 226 mm. This pairs with the right fibula of LB1 recovered from Sector VII in 2003 and is the same length.
	Tibia: adult, right (LB8)	Medial condyle incomplete and medial malleolus not preserved. Estimated maximum length 216 mm. This tibia duplicates that found with the skeleton and is smaller. It is therefore from another individual. Reassembled when removed from the Centre for Archaeology in Jakarta. Now has altered morphology and adhering glue.
	Ulna: adult, left (LB1)	Both epiphyses missing. 167 × 16.5 mm. (Note: from baulk collapse.)
65B	Femur (LB9)	Fragment. Shaft split longitudinally. 91 × 17 mm.

\*The northern part of Spit 58 in Sector XI (designated 58A) was part of Layer R, a clayey silt deposited in a body of standing water. In Sector VII, Layer R contained the partial skeleton (LB1).



**Figure 2 | Occlusal and lateral views of LB1 and LB6/1 *H. floresiensis* mandibles.** LB1 mandible (left) from Spit 59, Sector VII, and LB6/1 mandible (right) from Spit 51, Sector XI. Scale bar, 1 cm.



**Figure 3 | LB8 right tibia morphology.** Posterior and anterior views of the LB8 right tibia, from Spit 58A, and anterior view of an African female Pygmy tibia scaled to the same length. Scale bar, 1 cm.

(ref. 8). Dmanisi D2735 has  $P_3$ s with a similar crown shape to LB6/1, but the associated root morphology has not been described.

The LB6/1 mandible has smaller tooth and corpus dimensions than that of LB1, and is probably from a slightly smaller adult<sup>1,9</sup> (see Supplementary Information). It also has a more V-shaped tooth row and is thicker in the posterior corpus (see Supplementary Information). Apart from such evidence of individual variation, LB6/1 has numerous detailed similarities with LB1 in overall size, morphology and symphysis, but is about 15 kyr in age—that is, 3 kyr younger than LB1. The second mandible therefore provides another line of evidence that LB1 was not aberrant, but is instead representative of a long-term, morphologically unique, small-bodied population with a configuration of features never recorded in normal or pathological



**Figure 4 | LB1 right humerus morphology.** Posterior (b) and anterior (d) views of the right humerus of LB1 *H. floresiensis*, with a small-bodied modern human (African Pygmy) humerus scaled to the same length (a, c). Scale bar, 1 cm.

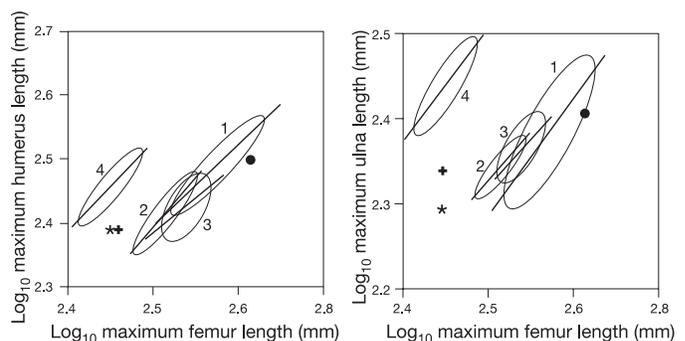


**Figure 5 | LB1 right ulna morphology.** Lateral (a), posterior (b) and anterior (c) views of the right ulna of LB1 *H. floresiensis*, and anterior view (d) of a small-bodied modern human (African Pygmy) ulna scaled to the same length. Scale bar, 1 cm.

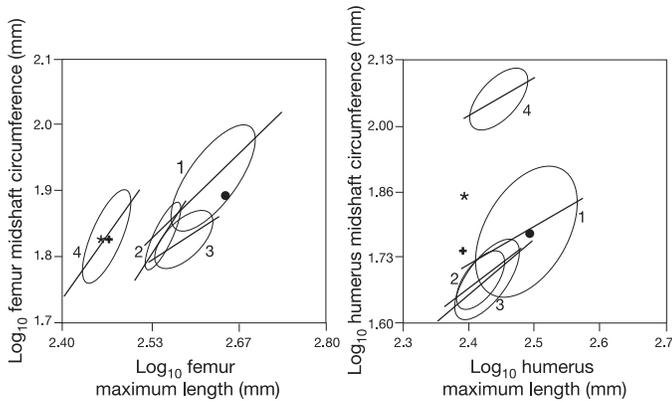
*H. sapiens*<sup>10–12</sup>. In fact, morphologically and metrically, the LB1 and LB6/1 mandibles are more similar to those of early *H. erectus* in east Africa or Georgia than those in Java or China, whereas the symphyses most resemble those of Plio-Pleistocene hominins, such as LH4 *A. afarensis*<sup>13</sup>, and to a lesser extent KNM WT-15000 (ref. 14) and D211 (ref. 5) *H. erectus* (see Supplementary Information).

An extremely small adult right tibia (LB8), with fused distal and proximal epiphyses, was recovered from Spit 58A, in the same layer as LB1 (Fig. 3 and Supplementary Information). There is damage to the medial condyle and the medial malleolus is not preserved. In common with the holotype of *H. floresiensis*, the shaft is laterally concave and oval in cross-section (mid-shaft 194 mm<sup>2</sup>)—similar to *Pan*—without a sharp anterior border, and relatively thickened medio-laterally in the distal half compared with *H. sapiens*. Estimated maximum length of this tibia is 216 mm (see Supplementary Information), compared with 235 mm for LB1 (ref. 1). The relationship between midshaft circumference (56 mm) and the length of the tibia is in the *Pongo* and *Pan* range of variation, and distinct from *Homo*<sup>15</sup>.

Stature estimates for small-bodied hominins, with relative limb proportions and bone lengths similar to AL 281-1, are most appropriately estimated with coefficients derived from small-bodied modern humans, particularly African Pygmies<sup>16,17</sup>. On the basis of Pygmy male coefficients<sup>16</sup>, the LB8 tibia indicates a stature of 109 cm



**Figure 6 | Limb proportions in *H. floresiensis*.** Relationship of humerus and ulna length in LB1 (star) to femur length, compared with those in KNM WT-15000 *H. erectus* (filled circle)<sup>4</sup>, AL 288-1 *A. afarensis* (cross)<sup>20,24</sup>, modern humans (numbers 1–3) and *Pan paniscus* (number 4). The modern human comparative series is from the robust global sample used previously<sup>1</sup>, with the addition of African Pygmies (2) and Andaman Islanders (3). Least squares regression lines and 95% confidence ellipses are shown.



**Figure 7 | Femur and humerus shaft robusticity in *H. floresiensis*.**

Relationship between mid-shaft circumference and maximum length for the LB1 *H. floresiensis* femur and humerus (star) compared with those for KNM WT-15000 *H. erectus* (filled circle)<sup>4</sup>, AL 288-1 *A. afarensis* (cross)<sup>20</sup>, modern humans (numbers 1–3) and *Pan paniscus* (number 4). The modern human comparative series is from the robust global sample used previously<sup>1</sup>, with the addition of African Pygmies (2) and Andaman Islanders (3). Least squares regression lines and 95% confidence ellipses are shown.

for LB8. However, the tibia is considerably smaller in all dimensions than the holotype and, given the population-specific correlations between limb segment length and stature<sup>16</sup>, LB8 was probably a shorter individual than LB1, who had an estimated stature of 106 cm on the basis of femur length<sup>1</sup>, a more reliable proxy for stature.

The right humerus, right ulna and left fibula from Spite 58A occurred at the same level as, and immediately adjacent to, the LB1 remains found in Sector VII, and in the same layer of clayey silt. The humerus articulates with the ulna, and the fibula pairs with the right fibula of LB1 excavated in 2003—both left and right fibulas are 226 mm in length. On the basis of size, representation and disposition, all these elements are part of LB1.

The LB1 right humerus is complete, apart from post-mortem damage to the anterior surface of the head and greater tubercle, and has a maximum length of 243 mm. Although the mid-shaft was broken post-mortem, there is no distortion. When compared with a modern human humerus scaled to the same length, the most obvious differences are the greater thickness of the LB1 shaft and the limited degree of humeral torsion (that is, rotation of the humerus head medially relative to the mediolateral axis of the distal end; Fig. 4). In LB1, humeral torsion is approximately 110°, which is the norm for *Hyllobates* and quadrupedal primates such as *Macaca*, but is significantly less than in large-bodied apes, modern humans (141–178°) and other known hominins, including *Australopithecus*<sup>18–20</sup>.

The LB1 right ulna is not as completely preserved as the humerus, and the distal end is not present (Fig. 5). There are relatively few well-preserved Pleistocene or Pliocene hominin ulnae, but comparing the LB1 ulna with those of modern humans, KNM WT-15000 *H. erectus*<sup>14</sup> or AL 288-1 *A. afarensis*<sup>20</sup>, the most obvious differences are the greater robusticity of the shaft of LB1 and the broader subtrochlear region, with considerably greater areas of attachment for the flexor, pronator and brachialis muscles. The length of the preserved shaft is 190 mm, and comparison with modern human ulnae suggests that, when complete, the ulna would have had a maximum length of 205 mm (see Supplementary Information). The arms of LB1 share the distinctive elongated distal segment common to tropical modern humans<sup>21,22</sup>, including populations of small average stature, and have an estimated brachial index ((radius length × 100)/humerus length) of 78, which is close to the African human male average<sup>23</sup> (see Supplementary Information).

In association with the previously described femur, tibia and pelvis<sup>1</sup>, the humerus and ulna permit an estimate of relative limb and body proportions for the *H. floresiensis* holotype. The only

reported *H. erectus* skeleton, KNM WT-15000, has limb proportions and a body shape similar to *H. sapiens*<sup>14</sup>, which differ from the relatively short legs, more teardrop-shaped thoracic cavity and laterally flaring pelvis in AL 288-1 *A. afarensis*<sup>20,24</sup>. Both the humerus and ulna of LB1 are long relative to femur length (Fig. 6). For example, the humerofemoral index ((humerus length × 100)/femur length) of 85.4 is outside the range of variation for *H. sapiens*, but is the same as AL 288-1 *A. afarensis*, and midway between the indices for apes and humans. The more complete left ilium<sup>1</sup> also indicates that the pelvis is flared antero-laterally, consistent with an australopithecine-shaped thoracic region. Body proportions of LB1 are the same as AL 288-1 *A. afarensis*, but differ from all other hominins for which there are reliable data, including *H. erectus*. Abnormal growth seems an unlikely explanation, as growth-hormone-related dwarfism and microcephaly in modern humans result in normal limb and pelvic proportions<sup>25</sup>.

All the major limb bones of LB1 have shaft and articular surface dimensions that are robust relative to length. For the femur and humerus, midshaft circumference differs from predictions for *H. sapiens* of similar body size, with femur robusticity at the centre of the *Pan paniscus* range of variation, and humerus robusticity midway between the *P. paniscus* and *H. sapiens* ranges (Fig. 7). Thus, estimations of musculature and body mass in *H. floresiensis* would be more accurate if based on chimpanzee rather than human models<sup>1</sup>. Although the endocast of LB1 has a gross morphology most similar to *H. erectus*, and distinct from *H. sapiens*, *Australopithecus* and *Pan*<sup>26</sup>, the encephalization quotient and body-weight-to-brain-weight relationships are similar to *A. afarensis* and *Pan*, not *H. erectus*<sup>1,27</sup>.

This new evidence has implications for the taxonomy, evolutionary history and physiology of *H. floresiensis*. The cranial morphology, skeletal proportions and endocast of LB1, together with the combination of primitive and derived features evident in both excavated mandibles, confirm that this population of hominins cannot be referred to either *H. sapiens* or *H. erectus*. However, although tooth size and facial morphology dictate inclusion of the species in the genus *Homo*, the genealogy of *H. floresiensis* remains uncertain. Similarities in stature and body proportions with *Australopithecus*, for example, may reflect phylogeny or secondary evolutionary convergence. Either way, *H. floresiensis* is not just an allometrically scaled-down version of *H. erectus*. Other *H. floresiensis* morphological traits, for example in the humeral torsion and ulna, are not shared with any other known hominin species and could have evolved *in situ* as a response to island-specific conditions and associated behavioural changes (see refs 28, 29).

Received 13 January; accepted 12 July 2005.

1. Brown, P. *et al.* A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature* **431**, 1055–1061 (2004).
2. Morwood, M. J. *et al.* Archaeology and age of a new hominin from Flores in eastern Indonesia. *Nature* **431**, 1087–1091 (2004).
3. Weidenreich, F. The mandible of *Sinanthropus pekinensis*. A comparative study. *Palaontologica Sinica* **D7**, 1–132 (1936).
4. Kaifu, Y. *et al.* Taxonomic affinities and evolutionary history of the early Pleistocene hominids of Java: Dentognathic evidence. *Am. J. Phys. Anthropol.* published online 10 March 2005 (doi:10.1002/ajpa.10425).
5. Vekua, A. K. *et al.* A new skull of early *Homo* from Dmanisi, Georgia. *Science* **297**, 85–89 (2002).
6. Wood, B. A. & Uytterschaut, H. Analysis of the dental morphology of the Plio-Pleistocene hominids. III. Mandibular premolar crowns. *J. Anat.* **154**, 121–156 (1987).
7. Wood, B. A., Abbott, S. A. & Uytterschaut, H. Analysis of the dental morphology of Plio-Pleistocene hominids. IV. Mandibular postcanine root morphology. *J. Anat.* **156**, 107–139 (1988).
8. Gabounia, L., de Lumley, M.-A., Vekua, A., Lordkipanidze, D. & de Lumley, H. Découverte d'un nouvel hominidé à Dmanissi (Transcaucasie, Géorgie). *C.R. Palevol* **1**, 243–253 (2002).
9. Wolpoff, M. H. in *Size and Scaling in Primate Biology* (ed. Jungers, W. L.) 273–318 (Plenum, New York, 1985).
10. Schwartz, J. & Tattersall, I. The human chin revisited: what is it and who has it? *J. Hum. Evol.* **38**, 367–409 (2000).

11. Lavelle, C. L. Investigation of mandibular and neurocranial form. *Acta Anat.* **125**, 238–244 (1986).
12. Lavelle, C. L. A preliminary craniofacial profile evaluation of normo-, micro- and macro-cephalics. *Br. J. Orthod.* **13**, 13–21 (1986).
13. White, T. D. & Johanson, D. C. Pliocene hominid mandibles from the Hadar formation, Ethiopia: 1974–1977 collections. *Am. J. Phys. Anthropol.* **57**, 501–544 (1982).
14. Walker, A. C. & Leakey, R. (eds) *The Nariokotome Homo erectus Skeleton* (Harvard Univ. Press, Cambridge, 1993).
15. Haeusler, M. & McHenry, H. M. Body proportions of *Homo habilis* reviewed. *J. Hum. Evol.* **46**, 433–465 (2004).
16. Oliver, G. The stature of *Australopithecus*. *J. Hum. Evol.* **5**, 529–534 (1976).
17. Hens, S. M., Konigsberg, L. W. & Jungers, W. L. Estimating stature in fossil hominids: which regression model and reference sample to use. *J. Hum. Evol.* **38**, 767–784 (2000).
18. Evans, F. G. & Krahl, V. E. The torsion of the humerus: a phylogenetic study from fish to man. *Am. J. Anat.* **76**, 303–337 (1945).
19. Larson, S. G. Subscapularis function in gibbons and chimpanzees: implications for interpretation of humeral head torsion in hominoids. *Am. J. Phys. Anthropol.* **76**, 449–462 (1988).
20. Johanson, D. C. *et al.* Morphology of the Pliocene partial hominid skeleton (A.L. 288–1) from the Hadar Formation, Ethiopia. *Am. J. Phys. Anthropol.* **57**, 403–451 (1982).
21. Roberts, D. F. in *Addison-Wesley Module in Anthropology* 1–38 (Addison-Wesley, Reading, 1973).
22. Ruff, C. B. Morphological adaptation to climate in modern and fossil hominids. *Yb. Phys. Anthropol.* **37**, 65–107 (1994).
23. Aiello, A. & Dean, C. *An Introduction to Human Evolutionary Anatomy* (Academic, London, 1990).
24. Schmid, P. Eine rekonstruktion des skelettes von A.L. 288–1 (Hadar) und deren konsequenzen. *Folia Primatol. (Basel)* **40**, 283–306 (1983).
25. Hiralal, G. M., Silverman, B. L., Dupuis, J. & Baumann, G. Phenotype and genetic analysis of a syndrome caused by an inactivating mutation in the growth hormone-releasing hormone receptor: Dwarfism of Sindh. *J. Clin. Endocrinol. Metab.* **83**, 4065–4074 (1998).
26. Falk, D. *et al.* The brain of LB1, *Homo floresiensis*. *Science* **308**, 242–245 (2005).
27. Martin, R. D. Relative brain size and basal metabolic rate in terrestrial vertebrates. *Nature* **293**, 57–60 (1981).
28. Köhler, M. & Moyà-Solà, S. Reduction of brain and sense organs in the fossil insular bovid *Myotragus*. *Brain Behav. Evol.* **63**, 125–140 (2004).

29. van der Geer, A. A. E. On the astragalus of the Miocene endemic deer *Hoplitomeryx* from the Gargano (Italy). *Deinsea* **7**, 325–336 (1999).

**Supplementary Information** is linked to the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

**Acknowledgements** The 2004 excavations at Liang Bua were funded by a Discovery Project grant from the Australian Research Council (ARC) to M.J.M. The ARC also supported R.G.R. through a Senior Research Fellowship. K.E.W. was in receipt of postgraduate scholarships from the University of Wollongong, and P.B. and T.M. received a grant from the University of New England. Excavations were undertaken under Asisten Deputi Urusan Arkeologi Nasional, Surat Rekomendasi No: 565/Kesbang.IV/VII/2004β. R. P. Soejono was the Indonesian Institutional Counterpart. Other participants included C. Lentfer, G. van den Bergh, C. Turney, D. Hobbs, K. Grant, D. Y. Yuniawati, A. Brumm, Rikus, Deus, Leo, Ansel, Agus, Seus, Camellus, Gaba, Rius, Beni and Piet. P. Jordan, D. Falk, S. G. Larson and K. Morwood commented on an earlier version of the paper, and D. Hobbs redrafted Fig. 1. P.B. and T.M. thank R. Kruszynski (Natural History Museum, London), R. Orban (Institut Royal des Sciences Naturelles de Belgique, Bruxelles) and W. Wendelen (Royal Museum of Central Africa, Tervuren) for providing access to skeletal collections in their care.

**Author Contributions** M.J.M. was Chief Investigator and the Australian Institutional Counterpart in this ARC project. P.B. was responsible for analysis and interpretation of the hominin remains. T.S., J., E.W.S., R.A.D. and S.W. directed aspects of the excavations, recording and analyses. Thermoluminescence ages were provided by R.G.R. and K.E.W., who also described the stratigraphy. T.M. and P.B. collected comparative data on small-bodied modern humans and non-human primates. As Director of the Indonesian Centre for Archaeology, T.D. authorized the excavations, provided support and assisted with stratigraphic interpretation.

**Author Information** Reprints and permissions information is available at [npg.nature.com/reprintsandpermissions](http://npg.nature.com/reprintsandpermissions). The authors declare no competing financial interests. Correspondence and requests for materials should be addressed to M.J.M. ([mmorwood@pobox.une.edu.au](mailto:mmorwood@pobox.une.edu.au)) and P.B. ([pbrown3@pobox.une.edu.au](mailto:pbrown3@pobox.une.edu.au)).