

# A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia

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Currently, it is widely accepted that only one hominin genus, *Homo*, was present in Pleistocene Asia, represented by two species, *Homo erectus* and *Homo sapiens*. Both species are characterized by greater brain size, increased body height and smaller teeth relative to Pliocene *Australopithecus* in Africa. Here we report the discovery, from the Late Pleistocene of Flores, Indonesia, of an adult hominin with stature and endocranial volume approximating 1 m and 380 cm<sup>3</sup>, respectively—equal to the smallest-known australopithecines. The combination of primitive and derived features assigns this hominin to a new species, *Homo floresiensis*. The most likely explanation for its existence on Flores is long-term isolation, with subsequent endemic dwarfing, of an ancestral *H. erectus* population. Importantly, *H. floresiensis* shows that the genus *Homo* is morphologically more varied and flexible in its adaptive responses than previously thought.

The LB1 skeleton was recovered in September 2003 during archaeological excavation at Liang Bua, Flores<sup>1</sup>. Most of the skeletal elements for LB1 were found in a small area, approximately 500 cm<sup>2</sup>, with parts of the skeleton still articulated and the tibiae flexed under the femora. Orientation of the skeleton in relation to site stratigraphy suggests that the body had moved slightly down slope before being covered with sediment. The skeleton is extremely fragile and not fossilized or covered with calcium carbonate. Recovered elements include a fairly complete cranium and mandible, right leg and left innominate. Bones of the left leg, hands and feet are less complete, while the vertebral column, sacrum, scapulae, clavicles and ribs are only represented by fragments. The position of the skeleton suggests that the arms are still in the wall of the excavation, and may be recovered in the future. Tooth eruption, epiphyseal union and tooth wear indicate an adult, and pelvic anatomy strongly supports the skeleton being that of a female. On the basis of its unique combination of primitive and derived features we assign this skeleton to a new species, *Homo floresiensis*.

## Description of *Homo floresiensis*

Order Primates Linnaeus, 1758  
Suborder Anthropoidea Mivart, 1864  
Superfamily Hominoidea Gray, 1825  
Family Hominidae Gray, 1825  
Tribe Hominini Gray, 1825  
Genus *Homo* Linnaeus, 1758  
*Homo floresiensis* sp. nov.

**Etymology.** Recognizing that this species has only been identified on the island of Flores, and a prolonged period of isolation may have resulted in the evolution of an island endemic form.

**Holotype.** LB1 partial adult skeleton excavated in September 2003. Recovered skeletal elements include the cranium and mandible, femora, tibiae, fibulae and patellae, partial pelvis, incomplete hands and feet, and fragments of vertebrae, sacrum, ribs, scapulae and clavicles. The repository is the Centre for Archaeology, Jakarta, Indonesia.

**Referred material.** LB2 isolated left mandibular P<sub>3</sub>. The repository is the Centre for Archaeology, Jakarta, Indonesia.

**Localities.** Liang Bua is a limestone cave on Flores, in eastern Indonesia. The cave is located 14 km north of Ruteng, the provincial capital of Manggarai Province, at an altitude of 500 m above sea level and 25 km from the north coast. It occurs at the base of a limestone

hill, on the southern edge of the Wae Racang river valley. The type locality is at 08° 31' 50.4" south latitude 120° 26' 36.9" east longitude.

**Horizon.** The type specimen LB1 was found at a depth of 5.9 m in Sector VII of the excavation at Liang Bua. It is associated with calibrated accelerator mass spectrometry (AMS) dates of approximately 18 kyr and bracketed by luminescence dates of 35 ± 4 kyr and 14 ± 2 kyr. The referred isolated left P<sub>3</sub> (LB2) was recovered just below a disconformity at 4.7 m in Sector IV, and bracketed by a U-series date of 37.7 ± 0.2 kyr on flowstone, and 20 cm above an electron-spin resonance (ESR)/U-series date of 74<sup>+14</sup><sub>-12</sub> kyr on a *Stegodon* molar.

**Diagnosis.** Small-bodied bipedal hominin with endocranial volume and stature (body height) similar to, or smaller than, *Australopithecus afarensis*. Lacks masticatory adaptations present in *Australopithecus* and *Paranthropus*, with substantially reduced facial height and prognathism, smaller postcanine teeth, and posteriorly orientated infraorbital region. Cranial base flexed. Prominent maxillary canine juga form prominent pillars, laterally separated from nasal aperture. Petrous pyramid smooth, tubular and with low relief, styloid process absent, and without vaginal crest. Superior cranial vault bone thicker than *Australopithecus* and similar to *H. erectus* and *H. sapiens*. Supraorbital torus arches over each orbit and does not form a flat bar as in Javan *H. erectus*. Mandibular P<sub>3</sub> with relatively large occlusal surface area, with prominent protoconid and broad talonid, and either bifurcated roots or a mesiodistally compressed Tomes root. Mandibular P<sub>4</sub> also with Tomes root. First and second molar teeth of similar size. Mandibular coronoid process higher than condyle, and the ramus has a posterior orientation. Mandibular symphysis without chin and with a posterior inclination of the symphyseal axis. Posteriorly inclined alveolar planum with superior and inferior transverse tori. Ilium with marked lateral flare. Femur neck long relative to head diameter, the shaft circular and without pilaster, and there is a high bicondylar angle. Long axis of tibia curved and the midshaft has an oval cross-section.

## Description and comparison of the cranial and postcranial elements

Apart from the right zygomatic arch, the cranium is free of substantial distortion (Figs 1 and 2). Unfortunately, the bregmatic region, right frontal, supraorbital, nasal and subnasal regions were damaged when the skeleton was discovered. To repair post-mortem

pressure cracks, and stabilize the vault, the calvarium was dismantled and cleaned endocranially before reconstruction. With the exception of the squamous suture, most of the cranial vault sutures are difficult to locate and this problem persists in computed tomography (CT) scans. As a result it is not possible to locate most of the standard craniometric landmarks with great precision.

The LB1 cranial vault is long and low. In comparison with adult *H. erectus* (including specimens referred to as *Homo ergaster* and *Homo georgicus*) and *H. sapiens* the calvarium of LB1 is extremely small. Indices of cranial shape closely follow the pattern in *H. erectus* (Supplementary Table 1). For instance, maximum cranial breadth is in the inflated supramastoid region, and the vault is broad relative

to its height. In posterior view the parietal contour is similar to *H. erectus* but with reduced cranial height<sup>2,3</sup>. Internal examination of the neurocranium, directly and with CT scan data, indicates that the brain of LB1 had a flattened platycephalic shape, with greatest breadth across the temporal lobes and reduced parietal lobe development compared with *H. sapiens*. The cranial base angle (basion–sella–foramen caecum) of 130° is relatively flexed in comparison with both *H. sapiens* (mean 137°–138° (refs 4, 5)) and Indonesian *H. erectus* (Sambungmacan 4 141° (ref. 6)). Other small-brained hominins, for instance STS 5 *Australopithecus africanus*, have the primitive less-flexed condition.

The endocranial volume, measured with mustard seed, is



**Figure 1** The LB1 cranium and mandible in lateral and three-quarter views, and cranium in frontal, posterior, superior and inferior views. Scale bar, 1 cm.

380 cm<sup>3</sup>, well below the previously accepted range for the genus *Homo*<sup>7</sup> and equal to the minimum estimates for *Australopithecus*<sup>8</sup>. The endocranial volume, relative to an indicator of body height (maximum femur length 280 mm), is outside the recorded hominin normal range (Fig. 3). Medially, laterally and basally, the cranial vault bone is thick and lies within the range of *H. erectus* and *H. sapiens*<sup>9,10</sup> (Supplementary Table 1 and Fig. 2). Reconstruction of the cranial vault, and CT scans, indicated that for most of the cranial vault the relative thickness of the tabular bone and diploë are similar to the normal range in *H. erectus* and *H. sapiens*. In common with *H. erectus* the vault in LB1 is relatively thickened posteriorly and in areas of pneumatization in the lateral cranial base. Thickened vault bone in LB1, relative to that in *Australopithecus* and early *Homo*<sup>2</sup>, results in a substantially reduced endocranial volume in comparison to Pliocene hominins with similar external vault dimensions.

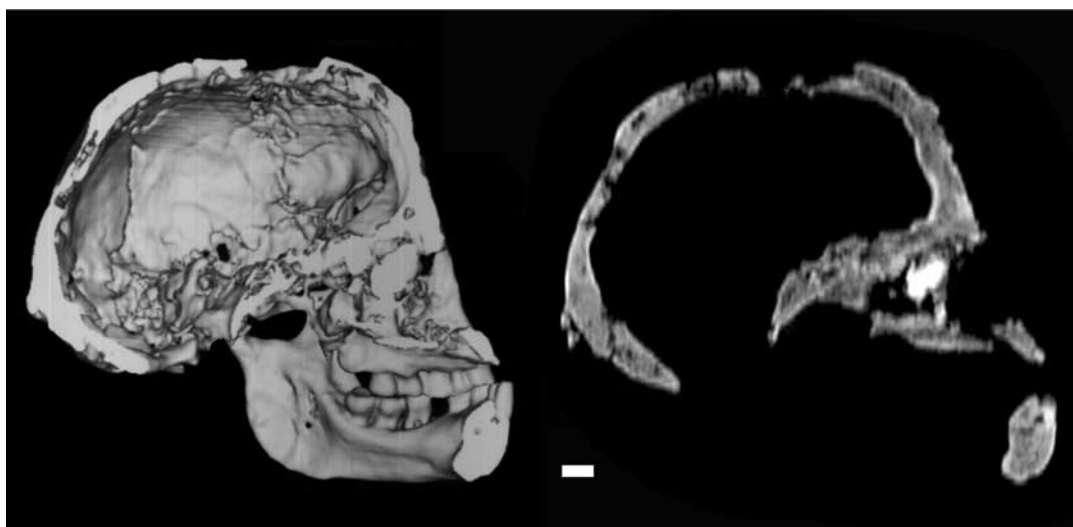
The occipital of LB1 is strongly flexed, with an occipital curvature angle of 101° (Supplementary Information), and the length of the nuchal plane dominates over the occipital segment. The occipital torus forms a low extended mound, the occipital protuberance is not particularly prominent compared with Indonesian *H. erectus* and there is a shallow supratoral sulcus. The endinion is positioned 12 mm inferior to the inion, which is within the range of *H. erectus* and *Australopithecus*<sup>10</sup>. Compared with *Australopithecus* and early *Homo*<sup>2</sup> the foramen magnum is narrow (21 mm) relative to its length (28 mm), and mastoid processes are thickened medio-laterally and are relatively deep (20.5 mm). In common with Asian, and some African, *H. erectus* a deep fissure separates the mastoid process from the petrous crest of the tympanic<sup>10,11</sup>. Bilaterally there is a recess between the tympanic plate and the entoglenoid pyramid. These two traits are not seen in modern humans, and show varied levels of development in Asian and African *H. erectus* and Pliocene hominins<sup>10</sup>. The depth and breadth of the glenoid fossae and angulation of the articular eminence are within the range of variation in *H. sapiens*. The inferior surface of the petrous pyramid has numerous similarities with Zhoukoudian *H. erectus*<sup>12</sup>, with a smooth tubular external surface as in chimpanzees, and a constricted foramen lacerum. Styloid processes and vaginal crests are not present.

The temporal lines approach to within 33 mm of the coronal suture and have a marked posterior extension. There are no raised angular tori as is common in *H. erectus*<sup>10</sup> and some terminal Pleistocene Australians, and no evidence of parietal keeling. Posteriorly there is some asymmetrical obelionic flattening and CT scans

indicate that the parietals reduce in thickness in this slightly depressed area (Fig. 2). A principal component analysis (PCA) of five cranial vault measurements separates LB1, STS5 (*A. africanus*) and KNM-ER 1813 (early *Homo*) from other hominin calvaria in size and shape. Shape, particularly height and breadth relationships, placed LB1 closest to ER-3883, ER-3733 and Sangiran 2 *H. erectus* (Supplementary Fig. 1).

The face of LB1 lacks most of the masticatory adaptations evident in *Australopithecus* and its overall morphology is similar to members of the genus *Homo*<sup>2,3</sup>. In comparison with *Australopithecus*, tooth dimensions and the alveolar segment of the maxillae are greatly reduced, as are facial height and prognathism. The facial skeleton is dominated by pronounced canine juga, which form prominent pillars lateral to the nasal aperture. However, these are distinct from the anterior pillars adjacent to the nasal aperture in *A. africanus*<sup>2,3</sup>. The infraorbital fossae are deep with large infra-orbital foramina, the orbits have a particularly arched superior border and a volume of 15.5 cm<sup>3</sup> (ref. 13). On the better preserved right-hand side, the supraorbital torus arches over the orbit and does not form a straight bar, with bulbous laterally projecting trigones, as in Indonesian *H. erectus*<sup>11</sup>. The preserved section of the right torus only extends medially slightly past mid-orbit, and the morphology of the glabella region and medial torus is unknown. In facial view the zygo-maxillary region is medially deep relative to facial height, and the inferior border of the malars are angled at 55° relative to the coronal plane. In lateral view the infraorbital region is orientated posteriorly as in other members of the genus *Homo*, rather than the more vertical orientation in *A. africanus*<sup>2,3</sup>. The root of the maxillary zygomatic process is centred above the first molar, and the incisive canal is relatively large and has an anterior location, contrasting with African and Javan *H. erectus*. In lateral view, curvature of the frontal squama is more similar to African early *Homo* and Dmanisi *H. ergaster*<sup>3,14</sup> than it is to the Javan hominins. The frontal squama is separated from the supraorbital torus by a supraorbital sulcus. In the middle third of the frontal there is a slight sagittal keel, extending into the remains of a low, broad prebregmatic eminence. On the midfrontal squama there is a circular healed lesion, probably the remains of a depressed fracture, which is about 15 mm across.

The mandible is complete, apart from some damage to the right condyle (Fig. 4) and combines features present in a variety of Pliocene and Pleistocene hominins. Post-mortem breaks through the corpus at the right P<sub>3</sub> and M<sub>2</sub>, and the left canine have resulted in some lateral distortion of the right ramus. There is a strong Curve of



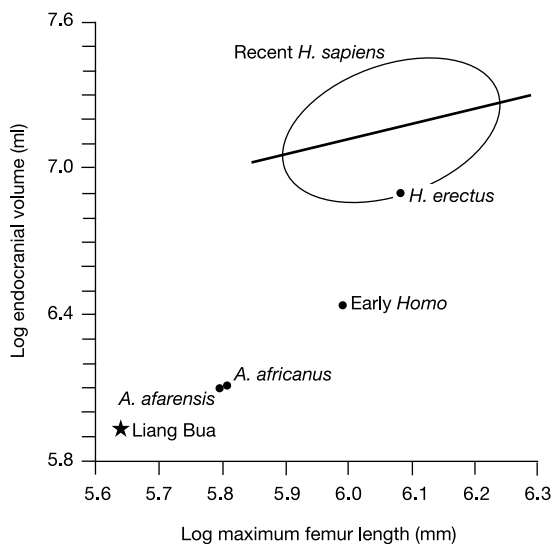
**Figure 2** Rendered three-dimensional and individual midsagittal CT section views of the LB1 cranium and mandible. Scale bar, 1 cm.

Spee. 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 coronoid process is higher than the condyle. The right condyle has a maximum breadth of 18 mm. There is a narrow and shallow extramolar sulcus and moderate lateral prominence. The anterior portion of the corpus is rounded and bulbous and without a chin. In the posterior symphyseal region the alveolar planum inclines postero-inferiorly, there is a moderate superior torus, deep and broad diagastric fossa, and the inferior transverse torus is low and rounded rather than shelf-like (Fig. 4). There is a strong posterior angulation of the symphyseal axis, and the overall morphology of the symphysis is very similar to LH4 *A. afarensis* and unlike Zhoukoudian and Sangiran *H. erectus*. There are bilaterally double mental foramina, with the posterior foramina smaller and located more inferiorly. Double mental foramina are common in Indonesian *H. erectus*<sup>15</sup>. While 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 laterally convex rather than straight (Fig. 4).

The right P<sub>4</sub> is absent and the alveolus completely fused, the left P<sub>4</sub> was lost after death, and CT scans indicate that the maxillary right M<sup>3</sup> was congenitally absent. The relatively small and conical alveolus for the missing left M<sup>3</sup> suggests that it had a much smaller crown than M<sup>1</sup> and M<sup>2</sup>. Size, spacing and angulation of the maxillary incisor alveoli, and absence of a mesial facet on the canines suggest that incisor I<sup>2</sup> was much smaller than I<sup>1</sup>, and there may have been a diastema. Occlusal wear has removed details of cusp and fissure morphology from most of the maxillary and mandibular teeth. The canines have worn down to a relatively flat surface and there would have been an edge-to-edge bite anteriorly. Interproximal wear is pronounced and in combination with the loss of crown height means that mesio-distal crown dimensions convey little phylogenetic information. With the exception of P<sub>3</sub> the size and morphology of the mandibular teeth follow the pattern in *H. erectus* and *H. sapiens* (Fig. 5, Supplementary Table 2). There is not a great deal of difference between the size of the molar teeth in each quadrant, and the size sequence for both mandibular and maxillary teeth is M<sub>1</sub> ≥ M<sub>2</sub> > M<sub>3</sub>. Using the megadontal quotient as a measure of relative tooth size<sup>16</sup>, and substituting P<sub>3</sub> crown area for the missing

P<sub>4</sub>s, LB1 is megadont (1.8) relative to *H. sapiens* (0.9) and *H. ergaster* (0.9), but not *H. habilis* (1.9) (ref. 8) (Supplementary Information). The P<sub>3</sub>s have a relatively great occlusal surface area (molariform) and when unworn had a prominent protoconid and broad talonid. Both P<sub>3</sub>s have bifurcated roots and the alveolus for the left P<sub>4</sub> indicates a mesiodistally compressed, broad Tomes' root. A larger, less worn, isolated left P<sub>3</sub> from the deposit (LB2) has a more triangular occlusal outline, and a Tomes' root (Supplementary Fig. 2). 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>17,18</sup>, and some Indonesian *H. erectus* mandibular premolars also have bifurcated or Tomes' roots<sup>15</sup>. Unusually, both maxillary P<sub>4</sub>s are rotated parallel to the tooth row, a trait that seems to be unrecorded in any other hominin. Maxillary canines and P<sub>3</sub>s have long roots and very prominent juga. The P<sub>3</sub> juga are emphasized by the rotation of the adjacent P<sub>4</sub> roots.

The pelvic girdle is represented by a right innominate, with damage to the iliac crest and pubic region, and fragments of the sacrum and left innominate. The right innominate, which is undistorted, has a broad greater sciatic notch suggesting that LB1 is a female (Fig. 6). In common with all bipedal hominins, the iliac blade is relatively short and wide<sup>19</sup>; however, the ischial spine is not particularly pronounced. Compared with modern humans the LB1 ilium has marked lateral flare, and the blade would have projected



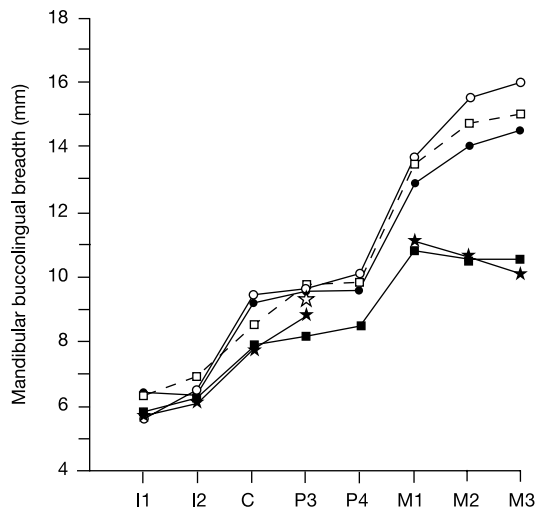
**Figure 3** Relationship between endocranial volume and femur length in LB1, *A. afarensis*, *A. africanus*, early *Homo* sp., *H. erectus* and modern *H. sapiens*. Modern human data, with least squares regression line and 95% confidence ellipse, from a global sample of 155 individuals collected by P.B. Details of the hominin samples are in the Supplementary Information.



**Figure 4** Right lateral and occlusal views of the LB1 mandible, sagittal profile of the symphysis, occlusal view of the mandibular dentition and occlusal views of the mandibular premolars. Scale bars, 1 cm.

more laterally from the body, relative to the plane of the acetabulum. The left acetabulum is of circular shape, and has a maximum width of 36 mm.

Apart from damage to the lateral condyle and distal shaft, the right femur is complete and undistorted (Fig. 7). The overall anatomy of the femur is most consistent with the broad range of variation in *H. sapiens*, with some departures that may be the result of the allometric effects of very small body size. The femur shaft is

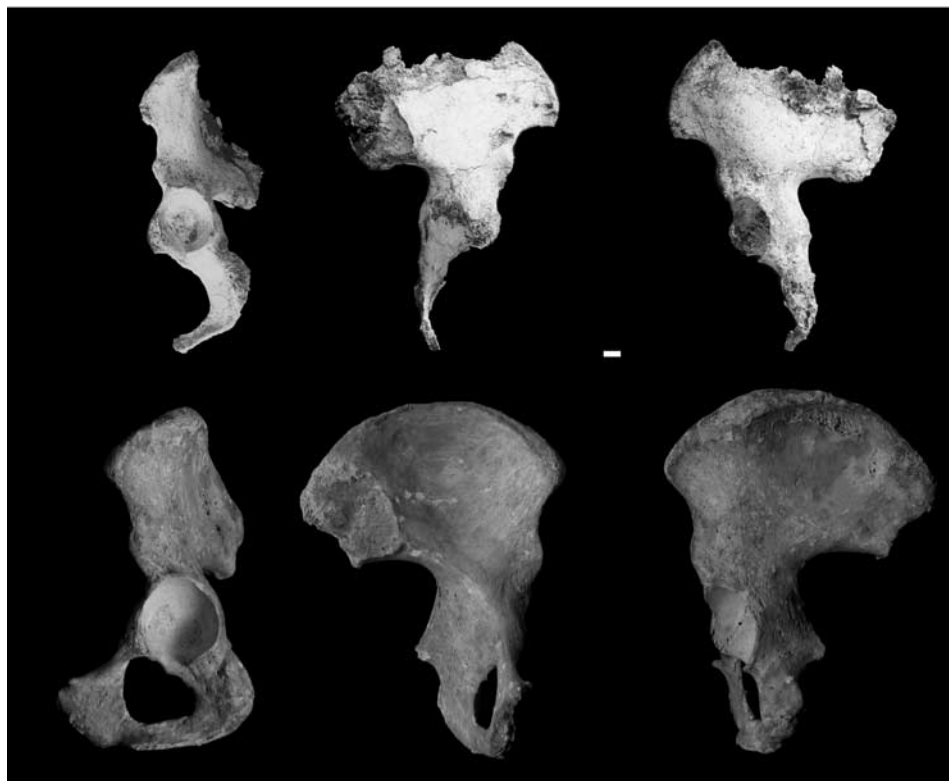


**Figure 5** Mean buccolingual tooth crown breadths for mandibular teeth in *A. afarensis* (filled circles), *A. africanus* (open circles), early *Homo* sp. (open squares), modern *H. sapiens* (filled squares), LB1 (filled stars) and LB2 (open stars). There are no mandibular P<sub>4</sub>s preserved for LB1. Data for *Australopithecus* and early *Homo* are from ref. 49. Modern human data from a global sample of 1,199 individuals collected by P.B.

relatively straight, and areas of muscle attachment, including the linea aspera, are not well developed. In contrast with some examples of Asian and African *H. erectus*, the femora do not have reduced medullary canals<sup>20</sup>. On the proximal end, the lesser trochanter is extremely prominent and the strong development of the intertrochanteric crest is similar to *H. sapiens* rather than the flattened intertrochanteric area in *Australopithecus* and *H. erectus* (KNM-ER 1481A, KNM-WT 15000). The biomechanical neck length is 55.5 mm and the neck is long relative to the femoral head diameter (31.5 mm), as is common to both *Australopithecus* and early *Homo*<sup>19</sup>. The neck-head junction is 31.5 mm long, with a shaft-neck angle of 130°, and the femur neck is compressed antero-posteriorly (Fig. 7). Several indices of femoral size and shape, for example the relationship between femoral head size and midshaft circumference (66 mm), and femur length and sub-trochanteric shaft size<sup>21</sup>, fall within the chimpanzee and australopithecine range of variation. The femur shaft does not have a pilaster, is circular in cross-section, and has cross-sectional areas of 370 mm<sup>2</sup> at the midshaft and 359 mm<sup>2</sup> at the midneck. It is therefore slightly more robust than the best-preserved small-bodied hominin femur of similar length (AL288-1; ref. 21). Distally there is a relatively high bicondylar angle of 14°, which overlaps with that found in *Australopithecus*<sup>22</sup>.

The right tibia is complete apart from the tip of the medial malleolus (Fig. 7). Its most distinctive feature, apart from its small size (estimated maximum length 235 mm, bicondylar breadth 51.5 mm) and the slight curvature in the long axis, is a shaft that is oval in cross-section (midshaft 347 mm<sup>2</sup>), without a sharp anterior border, and relatively thickened medio-laterally in the distal half. The relationship between the midshaft circumference and the length of the tibia is in the chimpanzee range of variation and distinct from *Homo*<sup>21</sup>.

Additional evidence of a small-bodied adult hominin is provided by an unassociated left radius shaft, without the articular ends, from



**Figure 6** Comparison of the left innominate from LB1 with a modern adult female *H. sapiens*. Lateral (external), and medial and lateral views of maximum iliac breadth. The pubic region of LB1 is not preserved and the iliac crest is incomplete. Scale bar, 1 cm.

an older section of the deposit (74–95 kyr). The estimated maximum length of this radius when complete is approximately 210 mm. Although the arms of LB1 have not been recovered, the dimensions of this radius are compatible with a hominin of LB1 proportions.

Although there is considerable interspecific variation, stature has been shown to have phylogenetic and adaptive significance among hominins<sup>23</sup>. Broadly speaking, *Australopithecus* and the earliest members of the genus *Homo* are shorter than *H. erectus* and more recent hominins<sup>8</sup>. The maximum femur length of LB1 (280 mm) is just below the smallest recorded for *A. afarensis* (AL-288-1, 281 mm<sup>24</sup>) and equal to the smallest estimate for the OH 62 *H. habilis* femur (280–404 mm)<sup>21</sup>. Applying stature estimation formulae developed from human pygmies<sup>25</sup> gives a stature estimate of 106 cm for LB1 (Supplementary Information). This is likely to be an overestimation owing to LB1's relatively small cranial height.

A stature estimate for LB1 of 106 cm gives a body mass of 16 to 28.7 kg, and a femur cross-sectional area of 525 mm<sup>2</sup> gives a mass of 36 kg (Supplementary Information). The brain mass for LB1, calculated from its volume<sup>26</sup>, is 433.2 g; this gives an encephalization quotient (EQ)<sup>27</sup> range of 2.5–4.6, which compares with 5.8–8.1 for *H. sapiens*, 3.3–4.4 for *H. erectus/ergaster* and 3.6–4.3 for *H. habilis*, and overlaps with the australopithecine range of variation<sup>28,29</sup>. If LB1 shared the lean and relatively narrow body shape typical of Old World tropical modern humans then the smallest body weight estimate, based on Jamaican school children data<sup>19</sup>, is probably most appropriate. This would support the higher EQ estimate and place LB1 within the *Homo* range of variation. Although neurological organization is at least as important as EQ in determining behavioural complexity, these data are consistent with *H. floresiensis* being the Pleistocene toolmaker at Liang Bua.

### Origins and evolution

The LB1 skeleton was recovered from Flores, an island of 14,000 km<sup>2</sup> east of the Wallace Line, in Indonesia. It combines extremely small stature and an endocranial volume in the early australopithecine range, with a unique mosaic of primitive and derived traits in the cranium, mandible and postcranial skeleton. Both its geographic location and comparatively recent date suggest models that differ to

those for more expected geological contexts, such as Pliocene eastern Africa. Among modern humans, populations of extremely small average stature were historically found in predominantly rainforest habitat in the equatorial zone of Africa, Asia and Melanesia<sup>30,31</sup>. Explanations for the small body size of these people generally focus on the thermoregulatory advantages for life in a hot and humid forest, either through evaporative cooling<sup>32</sup> or reduced rates of internal heat production<sup>30</sup>. For African pygmies, smaller body size is the result of reduced levels of insulin-like growth factor 1 (IGF-1) throughout the growth period<sup>33</sup>, or reduced receptivity to IGF-1 (ref. 34). Although adult stature is reduced, cranio-facial proportions remain within the range of adjacent larger-bodied populations, as does brain size<sup>35,36</sup>. The combination of small stature and brain size in LB1 is not consistent with IGF-related postnatal growth retardation. Similarly, neither pituitary dwarfism, nor primordial microcephalic dwarfism (PMD) in modern humans replicates the skeletal features present in LB1 (refs 37–40).

Other mechanisms must have been responsible for the small body size of these hominins, with insular dwarfing being the strongest candidate. Although small body size was an attribute of Pliocene australopithecines, the facial and dental characteristics of LB1 link it with larger-bodied Pleistocene *Homo*. In this instance, body size is not a direct expression of phylogeny. The location of these small hominins on Flores makes it far more likely that they are the end product of a long period of evolution on a comparatively small island, where environmental conditions placed small body size at a selective advantage. Insular dwarfing, in response to the specific ecological conditions that are found on some small islands, is well documented for animals larger than a rabbit<sup>41,42</sup>. Explanations of the island rule have primarily focused on resource availability, reduced levels of interspecific competition within relatively impoverished faunal communities and absence of predators. It has been argued that, in the absence of agriculture, tropical rainforests offer a very limited supply of calories for hominins<sup>43</sup>. Under these conditions selection should favour the reduced energy requirements of smaller individuals. Although the details of the Pleistocene palaeoenvironment on Flores are still being documented, it is clear that until the arrival of Mesolithic humans the faunal suit was relatively impoverished, and the only large predators were the Komodo dragon and another larger varanid. Dwarfing in LB1 may have been the end product of selection for small body size in a low calorific environment, either after isolation on Flores, or another insular environment in southeastern Asia.

Anatomical and physiological changes associated with insular dwarfing can be extensive, with dramatic modification of sensory systems and brain size<sup>44</sup>, and certainly exceed what might be predicted by the allometric effects of body size reduction alone. Evidence of insular dwarfing in extinct lineages, or the evolution of island endemic forms, is most often provided by the fossil record. Whereas there is archaeological evidence of hominins being on Flores by approximately 840 kyr<sup>45</sup>, there is no associated hominin skeletal material, and the currently limited evidence from Liang Bua is restricted to the Late Pleistocene. The first hominin immigrants may have had a similar body size to *H. erectus* and early *Homo*<sup>21,46</sup>, with subsequent dwarfing; or, an unknown small-bodied and small-brained hominin may have arrived on Flores from the Sunda Shelf.

### Discussion

When considered as a whole, the cranial and postcranial skeleton of LB1 combines a mosaic of primitive, unique and derived features not recorded for any other hominin. Although LB1 has the small endocranial volume and stature evident in early australopithecines, it does not have the great postcanine tooth size, deep and prognathic facial skeleton, and masticatory adaptations common to members of this genus<sup>2,47</sup>. Instead, the facial and dental proportions, postcranial anatomy consistent with human-like obligate bipedalism<sup>48</sup>,



**Figure 7** Anterior and posterior views of the LB1 right femur and tibia, with cross-sections of the femur neck and midshaft, and tibia midshaft. The anterior surfaces of the medial and lateral condyles of the femur are not preserved. With the exception of the medial malleolus, the tibia is complete and undistorted. Scale bar, 1 cm.

and a masticatory apparatus most similar in relative size and function to modern humans<sup>48</sup> all support assignment to the genus *Homo*—as does the inferred phylogenetic history, which includes endemic dwarfing of *H. erectus*. For these reasons, we argue that LB1 is best placed in this genus and have named it accordingly.

On a related point, the survival of *H. floresiensis* into the Late Pleistocene shows that the genus *Homo* is morphologically more varied and flexible in its adaptive responses than is generally recognized. It is possible that the evolutionary history of *H. floresiensis* is unique, but we consider it more likely that, following the dispersal of *Homo* out of Africa, there arose much greater variation in the morphological attributes of this genus than has hitherto been documented. We anticipate further discoveries of highly endemic, hominin species in locations similarly affected by long-term genetic isolation, including other Wallacean islands. □

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